

# Middle and Upper Ordovician Symmetrical Univalved Mollusks (Monoplacophora and Bellerophontina) of the Cincinnati Arch Region

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U.S. GEOLOGICAL SURVEY PROFESSIONAL PAPER 1066-O

*Prepared in cooperation with the  
Commonwealth of Kentucky, University of  
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# Middle and Upper Ordovician Symmetrical Univalved Mollusks (Monoplacophora and Bellerophontina) of the Cincinnati Arch Region

By G.P. WAHLMAN

CONTRIBUTIONS TO THE ORDOVICIAN PALEONTOLOGY OF KENTUCKY  
AND NEARBY STATES

*Edited by* JOHN POJETA, JR.

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Commonwealth of Kentucky, University of  
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*Stratigraphic distribution, ecology, functional  
morphology, phylogeny, and systematic  
paleontology of 86 species of Ordovician  
symmetrical univalved mollusks from the  
midcontinent*



**U.S. DEPARTMENT OF THE INTERIOR**

**MANUEL LUJAN, Jr., *Secretary***

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# CONTENTS

	Page		Page
Abstract.....	01	Paleoecology of Symmetrical Univalved Mollusks—Continued	
Introduction.....	2	Autecology of Bellerophontaceans.....	030
Acknowledgments.....	3	Previous Ordovician Paleoeological Studies.....	32
Stratigraphy and Geologic Setting.....	3	Ordovician Clastic Environments.....	32
Biostratigraphic Classification.....	3	Ordovician Carbonate Environments.....	34
Structural-Paleogeographic History.....	4	Post-Ordovician Paleoeological Studies of Note.....	34
Ordovician Lithostratigraphy of Central Tennessee.....	6	Paleoecology of Symmetrical Univalved Mollusks of the	
Stones River Group.....	6	Tyrone Limestone and the Lexington Limestone of	
Nashville Group.....	8	Central Kentucky.....	34
“Eden Group”.....	12	Tyrone Limestone.....	36
“Maysville Group”.....	12	Lexington Limestone.....	37
“Richmond Group”.....	12	Comments on the Paleoeology of the Stones River Group	
Middle Ordovician Lithostratigraphy of Kentucky.....	13	of Central Tennessee.....	39
High Bridge Group.....	13	Comments on the Paleoeology of the Nashville Group of	
Lexington Limestone.....	14	Central Tennessee.....	39
Upper Ordovician Lithostratigraphy of Kentucky,		Hermitage Formation.....	39
Southwestern Ohio, and Southeastern Indiana.....	17	Bigby-Cannon Limestone.....	39
Upper Ordovician Lithostratigraphy of South-Central		Comments on the Paleoeology of Upper Ordovician	
Kentucky.....	19	Faunas.....	40
Clays Ferry Formation.....	19	Shell Sculpturing and Encrustation as Defenses Against	
Garrard Siltstone.....	20	Predation.....	41
Calloway Creek Limestone.....	20	Functional Morphology.....	42
Ashlock Formation.....	20	Introduction.....	42
Drakes Formation.....	21	Monoplacophora.....	42
Upper Ordovician Lithostratigraphy of North-Central		Tryblidiida.....	42
Kentucky and Southwestern Ohio.....	22	Cyrtionellida.....	43
Kope Formation.....	22	Bellerophontacea.....	44
Fairview Formation.....	22	Shell Coiling.....	44
Bellevue Limestone.....	23	Functional Aspects of Selected Bellerophontacean	
Miamitown Shale.....	23	Shell Forms.....	47
Grant Lake Limestone.....	23	Explanate Shells.....	47
Bull Fork Formation.....	23	Trilobed Shells.....	48
Drakes Formation.....	24	Pallial System and Labral Emargination.....	49
Upper Ordovician Lithostratigraphy of Southeastern		Parietal Deposits.....	50
Indiana.....	24	Muscle Scars and their Functional Significance.....	51
Kope Formation (Indiana).....	24	Phylogeny and Classification.....	53
Dillsboro Formation.....	24	The Bellerophont Conundrum.....	53
Saluda Formation.....	25	Classification and Phylogeny of the Monoplacophora.....	58
Whitewater Formation.....	25	Suprageneric Classification and Phylogeny of the	
Material and Preservation.....	25	Bellerophontacean Gastropoda.....	61
Measurements.....	26	Systematic Paleontology.....	64
Stratigraphic Distribution of Ordovician Monoplacophora and		References Cited.....	186
Bellerophontacean Gastropoda in the Cincinnati Arch		Appendix: Locality Register.....	196
Region.....	27	U.S. Geological Survey Localities.....	196
Paleoecology of Symmetrical Univalved Mollusks.....	27	Non-USGS Collections.....	203
Introduction.....	27	Index.....	205
Autecology of Monoplacophorans.....	27		

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ILLUSTRATIONS

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[Plates follow index]

PLATE	1. <i>Micropileus</i> and <i>Vallatotheca</i> .
	2. <i>Helcionopsis</i> and <i>Archinacella</i> .
	3. <i>Archinacella?</i> and <i>Archinacella</i> .
	4. <i>Archinacella</i> , <i>Cyrtolites</i> ( <i>Cyrtolites</i> ), and <i>Carinaropsis</i> .
	5. <i>Cyrtolites</i> ( <i>Cyrtolites</i> ) and <i>Archinacella</i> .
	6. <i>Cyrtolites</i> ( <i>Cyrtolites</i> ).
	7, 8. <i>Cyrtolites</i> ( <i>Cyrtolites</i> ) and <i>C.</i> ( <i>Paracyrtolites</i> ).
	9–11. <i>Sinuities</i> .
	12–17. <i>Bucania</i> .
	18. <i>Bucania</i> and <i>Bellerophon</i> .
	19. <i>Bucania</i> .
	20. <i>Bucania</i> , <i>Kokenospira</i> , and <i>Tetranota</i> .
	21, 22. <i>Tetranota</i> .
	23. <i>Undulabucania</i> .
	24, 25. <i>Salpingostoma</i> .
	26. <i>Salpingostoma</i> and <i>Pterotheca</i> .
	27. <i>Bucanopsis</i> and <i>Bucania</i> .
	28. <i>Bellerophon</i> ( <i>Bellerophon</i> ) and <i>Sphenosphaera</i> .
	29–32. <i>Sphenosphaera</i> .
	33. <i>Sphenosphaera</i> and <i>Bellerophon</i> ( <i>Bellerophon</i> ).
	34–36. <i>Sphenosphaera</i> .
	37. <i>Carinaropsis</i> .
	38. <i>Carinaropsis</i> and <i>Tetranota</i> .
	39. <i>Pterotheca</i> .
	40. <i>Pterotheca</i> and <i>Carinaropsis</i> .
	41. <i>Sphenosphaera</i> and <i>Tropidodiscus</i> .
	42. <i>Tropidodiscus</i> , <i>Temnodiscus</i> , and <i>Phragmolites</i> .
	43, 44. <i>Phragmolites</i> .
	45. <i>Sinuities</i> and <i>Phragmolites</i> .

		Page
FIGURE	1. Map showing outcrop areas of Ordovician sedimentary deposits in Eastern North America and area of present study ..	02
	2. Chart showing late Middle and Upper Ordovician Series and Stages in Eastern North America.....	4
	3, 4. Maps showing:	
	3. Major structural features of the Cincinnati arch and location of the Appalachian basin and the associated orogenic belt during Ordovician continental convergence.....	4
	4. General paleogeographic settings in the Eastern United States during Middle and Late Ordovician time .....	5
	5–8. Charts showing:	
	5. Lithofacies relationships of Middle and Upper Ordovician stratigraphic units in the Cincinnati arch region of southeastern Indiana, southwestern Ohio, central Kentucky, and central Tennessee.....	6
	6. Champlainian and Edenian lithostratigraphic units in central Tennessee .....	7
	7. Facies relationships of the members of the Hermitage Formation in central Tennessee.....	8
	8. Facies relationships of the members of the Bigby-Cannon Limestone across the central Tennessee high .....	10
	9. Diagram showing idealized paleogeographic setting in central Tennessee during deposition of the Bigby-Cannon Limestone.....	10
	10. Map showing depositional facies of the Bigby-Cannon Limestone in central Tennessee .....	11
	11, 12. Charts showing:	
	11. Facies relationships between the major members of the Lexington Limestone and the Clays Ferry Formation in central Kentucky .....	14
	12. Cincinnati lithostratigraphic units in Ohio, Indiana, Kentucky, and central Tennessee .....	18
	13, 14. Drawings showing:	
	13. Common measurements made on fossil specimens .....	27
	14. Paths of water currents through the shells and mantle cavities of monoplacophorans .....	43
	15. Chart showing morphological and corresponding ecological trends in Middle Ordovician bellerophonaceans .....	46
	16. Drawings showing paths of water currents through the shells and mantle cavities of some Ordovician bellerophonacean gastropods.....	50

	Page
17. Chart showing four primary models suggesting possible phylogenetic relationships between monoplacophorans, bellerophontaceans, and pleurotomariaceans .....	O57
18. Drawing showing four general morphotypes of monoplacophorans representing four superfamilies .....	60
19. Diagram showing phylogenetic relationships of bellerophontacean slit-bearing subfamilies present in Eastern North America during the Late Cambrian-Middle Ordovician .....	64
20. Graph illustrating apparent growth rate of the holotype of <i>Helcionopsis striata</i> .....	67
21-23. Bivariate plots of measurements made on specimens of:	
21. <i>Vallatotheca unguiformis</i> .....	71
22. <i>Archinacella simulatrix</i> .....	77
23. <i>Archinacella indianensis</i> .....	85
24. Chart showing stratigraphic ranges of species of <i>Cyrtolites</i> ( <i>Cyrtolites</i> ) and <i>C.</i> ( <i>Paracyrtolites</i> ) in the Middle and Upper Ordovician of the Cincinnati arch region .....	89
25-33. Bivariate plots of measurements made on specimens of:	
25. <i>Cyrtolites</i> ( <i>Cyrtolites</i> ) <i>ornatus</i> .....	93
26. <i>Cyrtolites</i> ( <i>Cyrtolites</i> ) <i>retrorsus</i> from the Logana Member of the Lexington Limestone in central Kentucky...	97
27. <i>Cyrtolites</i> ( <i>Cyrtolites</i> ) <i>retrorsus</i> from the Grier Limestone Member of the Lexington Limestone in central Kentucky .....	98
28. <i>Cyrtolites</i> ( <i>Cyrtolites</i> ) <i>claysferryensis</i> new species from the Clays Ferry Formation in north-central Kentucky .....	101
29. <i>Cyrtolites</i> ( <i>Cyrtolites</i> ) <i>minor</i> .....	103
30. <i>Cyrtolites</i> ( <i>Cyrtolites</i> ) <i>hornyi</i> .....	105
31. <i>Salpingostoma kentuckyense</i> and <i>S. buelli</i> .....	153
32. <i>Salpingostoma richmondensis</i> and <i>Bucania simulatrix</i> .....	156
33. <i>Bucanopsis carinifera</i> and <i>B. diabloensis</i> new species .....	163

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## TABLES

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TABLE		Page
1.	Distribution of bellerophontaceans in the Stones River Group of central Tennessee .....	O27
2.	Distribution of monoplacophorans and bellerophontaceans in the Nashville Group of central Tennessee .....	27
3.	Distribution of species of monoplacophorans and bellerophontacean gastropods in the Tyrone Limestone of the High Bridge Group, the members of the Lexington Limestone, and the Clays Ferry Formation of central Kentucky ....	28
4.	Distribution of species of monoplacophorans and bellerophontacean gastropods in the Upper Ordovician stratigraphic units of the Cincinnati arch region .....	29
5-14.	Relative abundance of species in USGS silicified samples from the:	
5.	Tyrone Limestone .....	36
6.	Curdsville Limestone Member of the Lexington Limestone .....	37
7.	Logana Member of the Lexington Limestone .....	37
8.	Grier Limestone Member of the Lexington Limestone .....	37
9.	Perryville Limestone Member of the Lexington Limestone .....	37
10.	Devils Hollow Member of the Lexington Limestone .....	38
11.	Millersburg Member of the Lexington Limestone .....	38
12.	Tanglewood Limestone Member of the Lexington Limestone .....	38
13.	Clays Ferry Formation .....	38
14.	Dillsboro Formation in Indiana .....	40
15.	Examples of post-Cambrian bellerophontiform molluscan univalves for which muscle scars have been described .....	52
16.	Classification of the class Monoplacophora to family level .....	61
17.	Suprageneric classification of the Bellerophontacea, with diagnoses of family-level taxa .....	63
18.	<i>Helcionopsis striata</i> .....	66
19.	Distances between growth lines of the holotype of <i>Helcionopsis striata</i> (USNM 45827) .....	66
20.	<i>Vallatotheca unguiformis</i> .....	70
21.	<i>Micropileus variabilis</i> .....	73
22.	<i>Archinacella simulatrix</i> .....	77
23.	<i>Archinacella cingulata</i> .....	79
24.	<i>Archinacella indianensis</i> .....	83
25.	<i>Cyrtolites</i> ( <i>Cyrtolites</i> ) <i>ornatus</i> .....	92
26.	<i>Cyrtolites</i> ( <i>Cyrtolites</i> ) <i>retrorsus</i> .....	95
27.	<i>Cyrtolites</i> ( <i>Cyrtolites</i> ) <i>claysferryensis</i> .....	100
28.	<i>Cyrtolites</i> ( <i>Cyrtolites</i> ) <i>minor</i> .....	103
29.	<i>Cyrtolites</i> ( <i>Cyrtolites</i> ) <i>hornyi</i> .....	104

TABLES 18–88. Measurements of:	Page
30. <i>Cyrtolites (Cyrtolites) disjunctus</i> .....	106
31. <i>Cyrtolites (Paracyrtolites) subplanus</i> .....	107
32. <i>Cyrtolites (Paracyrtolites) carinatus</i> .....	108
33. <i>Sinuities cancellatus</i> .....	111
34. <i>Sinuities obesus</i> .....	113
35. <i>Sinuities granistriatus</i> .....	114
36. <i>Sinuities globularis</i> .....	115
37. <i>Tropidodiscus subacutus</i> .....	119
38. <i>Tropidodiscus cristatus</i> .....	119
39. <i>Tropidodiscus magnus</i> .....	120
40. <i>Phragmolites compressus</i> .....	121
41. <i>Phragmolites grandis</i> .....	122
42. <i>Phragmolites cellulosus</i> .....	122
43. <i>Phragmolites bellulus</i> .....	123
44. <i>Phragmolites elegans</i> .....	123
45. <i>Phragmolites dyeri</i> .....	124
46. <i>Temnodiscus nitidula</i> .....	126
47. <i>Bucania emmonsii</i> (lectotype) .....	129
48. <i>Bucania halli</i> .....	129
49. <i>Bucania subangulata</i> .....	130
50. <i>Bucania lindsleyi</i> .....	131
51. <i>Bucania nashvillensis</i> .....	132
52. <i>Bucania frankfortensis</i> (holotype) .....	134
53. <i>Bucania peracuta</i> (holotype) .....	134
54. <i>Bucania sublata</i> (lectotype) .....	135
55. <i>Bucania micronema</i> (holotype) .....	136
56. <i>Bucania rugatina</i> .....	137
57. <i>Bucania singularis</i> (lectotype) .....	137
58. <i>Bucania pojetai</i> .....	138
59. <i>Bucania simulatrix</i> (lectotype) .....	139
60. <i>Bucania crassa</i> .....	140
61. <i>Kokenospira costalis</i> .....	141
62. <i>Undulabucania gorbyi</i> (holotype) .....	142
63. <i>Undulabucania punctifrons</i> .....	143
64. <i>Tetranota bidorsata</i> .....	145
65. <i>Tetranota obsoleta</i> .....	147
66. <i>Tetranota sexcarinata</i> .....	147
67. <i>Tetranota wisconsinensis</i> .....	148
68. <i>Salpingostoma buelli</i> .....	151
69. <i>Salpingostoma kentuckyense</i> .....	152
70. <i>Salpingostoma richmondensis</i> .....	155
71. <i>Bellerophon (Bellerophon) subglobulus</i> .....	159
72. <i>Bellerophon (Bellerophon) bilineatus</i> .....	160
73. <i>Bellerophon (Bellerophon) nana</i> .....	160
74. <i>Bellerophon (Bellerophon) subpatula</i> .....	161
75. <i>Bucanopsis carinifera</i> .....	164
76. <i>Bucanopsis diabloensis</i> .....	165
77. <i>Sphenosphaera clausus</i> .....	168
78. <i>Sphenosphaera troosti</i> .....	170
79. <i>Sphenosphaera burginensis</i> .....	170
80. <i>Sphenosphaera recurvus</i> .....	171
81. <i>Sphenosphaera subangularis</i> .....	172
82. <i>Sphenosphaera capax</i> .....	172
83. <i>Sphenosphaera mohri</i> .....	173
84. <i>Carinaropsis acuta</i> .....	177
85. <i>Carinaropsis cunulae</i> .....	178
86. <i>Carinaropsis cymbula</i> .....	179
87. <i>Pterotheca saffordi</i> .....	183
88. <i>Pterotheca expansa</i> .....	184

## MIDDLE AND UPPER ORDOVICIAN SYMMETRICAL UNIVALVED MOLLUSKS (MONOPLACOPHORA AND BELLEROPHONTINA) OF THE CINCINNATI ARCH REGION

By G.P. WAHLMAN<sup>1</sup>

### ABSTRACT

The taxonomy, phylogenetic relationships, biostratigraphy, functional morphology, and paleoecology of Middle and Upper Ordovician (Blackriveran-Richmondian) symmetrical univalved mollusks of the Cincinnati arch region are discussed. Six genera and 30 species of tryblidiids and cyrtoneilliids, and 13 genera and 56 species of bellerophontaceans, are evaluated. The study centered on extensive collections of silicified fossils made by the U.S. Geological Survey during a geologic mapping program of the State of Kentucky. Museum collections, including the type specimens for most species discussed, were also examined.

Recent sedimentological and structural studies suggest that a proto-Cincinnati arch existed during Middle and Late Ordovician time as a discontinuous positive platform running northwest-southeast, paralleling the continental margin. This proto-Cincinnati arch may have resulted from the continental convergence of North America with Europe and possibly Africa, and it reflects upward movement along a hinge line between the miogeocline to the east and the craton to the west. During Middle Ordovician time, carbonate deposition was more dominant on this platform than in the adjacent lower lying areas, which were dominated by shale deposition. Shale deposition increased on the platform during Late Ordovician time as a result of erosion of tectonic lands to the east.

Ordovician symmetrical univalved mollusks are found throughout a spectrum of shallow marine shelf paleoenvironments. Bellerophontacean faunas of low diversity often dominated very shallow, restricted marine paleoenvironments. In normal marine shelf paleoenvironments, fewer individuals are found, but a greater diversity of taxa is seen. Ordovician symmetrical univalved mollusks probably led a variety of modes of life, and could inhabit both firm- and soft-bottom environments. Different taxa were probably algal mat grazers, algal foliage dwellers and feeders, deposit feeders, scavengers, and possibly even predators feeding on such sedentary benthos as sponges and bryozoans. Paleoeecological analyses of the faunas of the individual members of the Lexington Limestone in central Kentucky do not show any clear trends in the distribution of most taxa. Future synecological analyses may reveal trends.

In the Cincinnati arch, symmetrical molluscan univalved fauna, all limpet-form taxa, and all sinuate planispiral taxa are assigned to the

Monoplacophora. Assignment of some planispiral taxa to the Monoplacophora is based on known muscle scar patterns (multiple discrete pairs) and on the possible functional significance of diamond-shaped apertures and umbilical reentrants, both of which may have channeled water currents to a posterior mantle cavity. Assignment of the planispiral Bellerophontacea to the Gastropoda is based on known muscle scar patterns (single circumumbilical pair), the presence of a median labral slit (especially a deep slit), a trilobate aperture, massive parietal deposits, or an inner apertural parietal platform. It is concluded that in some cases the functional analysis of shell morphology is more reliable than muscle scar patterns in distinguishing planispiral monoplacophorans from planispiral bellerophontacean gastropods.

Four models for the phylogenetic relationships of monoplacophorans, bellerophontaceans, and pleurotomariacean archaeogastropods are considered. One model considers bellerophontaceans to be monoplacophorans and not ancestral to the pleurotomariaceans. The other three consider bellerophontaceans to be gastropods, and to be either an independent group, or ancestral to or descended from the pleurotomariaceans. However, before any of these models is accepted, a great deal more morphological and phylogenetic analysis is needed. Primarily because many of the taxa have a median labral slit, I believe that the bellerophontaceans and pleurotomariaceans are closely related phylogenetically.

Within the Bellerophontacea, there was a trend during the Late Cambrian and Ordovician toward tighter coiling of the shell and an increased rate of whorl expansion, both of which acted to make the shell more compact and more mobile. The increased mobility allowed bellerophontaceans to occupy higher energy environments and a greater variety of niches. This greater adaptability, along with the environmental heterogeneity resulting from tectonism during the Ordovician, the radiation of marine algal groups, and the general diversification of the marine biota, was responsible for the radiation of the Bellerophontacea during the Middle and Late Ordovician.

Proposed classifications for the Monoplacophora and Bellerophontacea are morphologically and phylogenetically based. Within the Monoplacophora, two orders are recognized—Tryblidiida and Cyrtoneilliida. The more primitive order, Tryblidiida, includes three superfamilies—the Kirengellaceae, Tryblidiaceae, and Archinacellaceae. The Cyrtoneilliida includes the superfamily Cyrtolitaceae. The slit-bearing families of the superfamily Bellerophontacea are, in order of increasing phylogenetic advancement, the Trepidodiscidae, Bucaniidae, Bellerophontidae, and Carinaropsidae. Tentatively recognized within the Bellerophontacea,

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<sup>1</sup>Amoco Production Company, Houston, Tex.

although none were present in the fauna under consideration, are the sinuate planispiral families Bucanellidae, Grandostomatidae, Tremantidae, and Euphemitidae.

New taxa of Monoplacophora named herein are *Micropileus variabilis*, *Archinacella alta*, *Archinacella? davisi*, *Archinacella arca*, *Cyrtolites (Cyrtolites) claysferryensis*, *Cyrtolites (Cyrtolites) hornyi*, and the subgenus *Cyrtolites (Paracyrtolites)*. New taxa of Bellerophontacea named herein are subfamily Undulabucaniinae, genus *Undulabucania*, subfamily Bucanopsisinae, *Bucanopsis diabloensis*, *Bucania pojetai*, and subfamily Pedasiolinae.

## INTRODUCTION

The purpose of this paper is to discuss the taxonomy, functional morphology, paleoecology, biostratigraphy, and phylogenetic relationships of the Middle and Upper Ordovician Monoplacophora and bellerophontacean Gastropoda of the Cincinnati arch region in central Kentucky, Tennessee, southwestern Ohio, and southeastern Indiana (fig. 1). The most recent comprehensive treatment of these faunas was a monograph by Ulrich and Scofield in 1897. Although fossil monoplacophorans and gastropods can be locally common elements of North

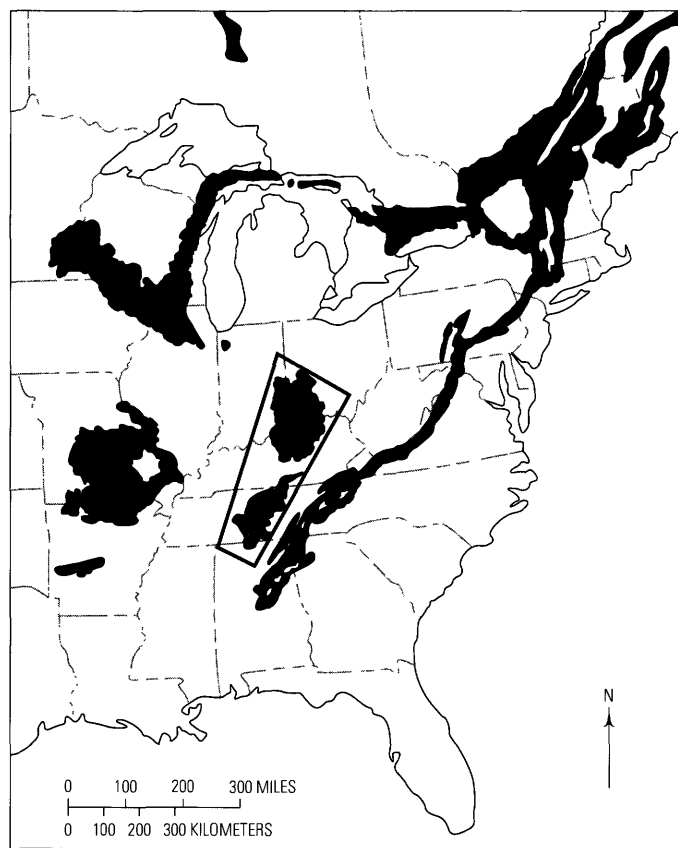


FIGURE 1.—Outcrop areas of Ordovician sedimentary deposits (shaded) in Eastern North America. Area of present study (enclosed by solid lines) includes outcrop areas around the Cincinnati arch in southeastern Indiana, southwestern Ohio, central Kentucky and central Tennessee.

American Ordovician faunas, they have received almost no modern study. The lack of attention to these faunas is due primarily to the scarcity of well-preserved specimens. The original aragonitic skeletons of these mollusks generally were dissolved in early diagenesis, and therefore most known specimens are preserved as internal molds. Fortunately, silicification of fossils is widespread in the Middle Ordovician limestones of central Kentucky and Tennessee. Many of the specimens described by Ulrich and Scofield (1897) were silicified specimens that had weathered out of these limestones. Silicified fossils are much less common in the Upper Ordovician strata of the Cincinnati arch region, so most mollusk taxa from these rocks are known mainly from internal molds and from scarce calcitic replicas.

The present work centered on abundant new silicified fossil collections made by the U.S. Geological Survey (USGS) during the geologic mapping program of the State of Kentucky conducted in cooperation with the Kentucky Geological Survey (Pojeta, 1979). Field samples were taken as bulk limestone blocks, which were later etched in acid baths in the laboratories of the USGS in Washington, D.C., to release a residue of abundant silicified fossils. These new collections provide numerous specimens of many heretofore poorly known species. Moreover, the field samples were precisely located both stratigraphically and geographically, unlike many earlier collections for which locality and formation data are vague and outdated. Thus, these collections provide a superior new data base for taxonomic, paleoecologic, and biostratigraphic studies. Because of the abundance of new material and the great diversity of the Cincinnati arch fauna, only the symmetrical molluscan univalves are covered herein. Previous reports on other invertebrate fossil groups from the new collections have dealt with trilobites (Ross, 1967, 1979), brachiopods (Neuman, 1967; Alberstadt, 1979; Howe, 1979; Pope, 1982; Walker, 1982), echinoderms (Bell, 1979; Branstrator, 1979; Parsley, 1981), corals (Elias, 1983), ostracodes (Warshauer and Berdan, 1982; Berdan, 1984), and bryozoans (Karklins, 1984).

The Cincinnati arch fauna includes 19 genera and 86 species of monoplacophorans and bellerophontacean gastropods from 89 localities. In addition to the new silicified collections, many museum collections were also examined, including the type specimens for most of the species discussed; altogether, about 3,000 specimens were examined. Photographs of many of the type specimens are presented here for the first time.

Middle and Upper Ordovician symmetrical molluscan univalves have important bearing on a current controversy in molluscan phylogenetic studies concerning the class-level assignment of the Bellerophontida and their evolutionary role, if any, in the origin of the class

Gastropoda. One group of paleontologists believes the Bellerophontida were evolutionary intermediates between the monoplacophorans and the archaeogastropods, while another group believes the Bellerophontida were monoplacophorans and were not ancestral to the archaeogastropods. Early and Middle Cambrian symmetrical molluscan univalved faunas, all of which are minute in size, have been found to be diverse and widespread, but their relation to later Paleozoic faunas is still a matter of active debate (Berg-Madsen and Peel, 1978; Yochelson, 1978, 1979; Runnegar, 1983). During the Late Cambrian and Early Ordovician, there appeared relatively larger molluscan univalves that are related to later Paleozoic taxa, but these faunas are uncommon and apparently of low diversity. Therefore, the diverse Middle and Late Ordovician symmetrical molluscan univalved faunas are particularly significant, because they represent the first radiation of bellerophonitiform taxa that persisted throughout the Paleozoic. These Ordovician faunas provide the first adequate sample of typical Paleozoic morphotypes on which to base a range of functional morphological interpretations and taxonomic conclusions.

From analyses of functional morphology, I conclude that the bellerophontaceans are archaeogastropods, but that some sinuate planispiral taxa can be interpreted to be monoplacophorans.

### ACKNOWLEDGMENTS

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For the generous loan of museum specimens, I thank the curatorial staffs of the Museum of Natural History, Smithsonian Institution, Washington, D.C.; the American Museum of Natural History, New York, N.Y.; the Field Museum of Natural History, Chicago, Ill.; the Geology Museum at the University of Cincinnati, Cincinnati, Ohio; and the Geology Museum at the University of

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## STRATIGRAPHY AND GEOLOGIC SETTING

### BIOSTRATIGRAPHIC CLASSIFICATION

The Middle and Upper Ordovician time-stratigraphic units adopted herein were defined by Sweet and Bergstrom (1971, p. 624, fig. 10; 1976, figs. 2, 3) and Sweet (1979, fig. 3) on the basis of conodont zonation. They recognized the traditional separation of Middle and Upper Ordovician rocks into the Champlainian and Cincinnati Series, respectively, but proposed a partly new stadial classification, which has been accepted by the U.S. Geological Survey (Pojeta, 1979, p. A14, A15).

Sweet and Bergstrom (1971, p. 624) accepted the long-standing tripartite subdivision of the Cincinnati Series into the (ascending) Edenian, Maysvillian, and Richmondian Stages. These three divisions had historically been used dually as lithostratigraphic (Groups) and time-stratigraphic (Stages) units (Orton, 1873; Foerste, 1903; Cumings, 1908). Their restriction to stadial usage was facilitated by a complete revision of the lithostratigraphic nomenclature of the Cincinnati strata of the type area, which is discussed in a later section.

The standard upper Champlainian section for North America is in the Black River and Mohawk Valleys of New York. Traditionally, these rocks have been divided into the Black River Group below and the Trenton Group above. Kay (1948, p. 1401) proposed the term "Trentonian" as a series name, and since then it has sometimes been used as a stadial term. Twenty years later, Kay (1968) reverted back to using the Trenton Group purely as a lithic term, and proposed an entirely new lithic subdivision to replace the traditional formations, which he had concluded were actually faunal-based units. Kay (1968) then proposed that the older geographically named, faunal-based subdivisions be converted to time-stratigraphic units. These were, in ascending order, the Rocklandian, Kirkfieldian, Shermanian, and Cobourgian Stages. Sweet and Bergstrom (1971, p. 624) accepted Kay's (1968) stadial classification for the most part. However, they concluded from conodont studies that the top of the Shermanian Stage in New York was at the

same stratigraphic level as the base of the Edenian Stage in the Cincinnati area. Because the name "Edenian" had priority over "Cobourgian," the latter term was rejected. Sweet and Bergstrom (1976, fig. 3) maintained the term "Blackriveran" for the stage below the Rocklandian.

The resulting classification for upper Middle (upper Champlainian) and Upper (Cincinnatian) Ordovician rocks of North America, which has been accepted by the USGS (Pojeta, 1979, p. A13–A15), is, in ascending order, the Blackriveran, Rocklandian, Kirkfieldian, Shermanian, Edenian, Maysvillian, and Richmondian Stages (fig. 2).

#### STRUCTURAL-PALEOGEOGRAPHIC HISTORY

The Middle and Late Ordovician was a period of continental convergence. The Iapetus (proto-Atlantic) Ocean was being closed by convergence of the North American Plate with the plates of Eurasia and Africa. As these three plates approached one another during the Middle Ordovician, a subduction zone and island-arc system formed along the orogenic belt running approximately parallel to the present eastern coast of North America (fig. 3) (Bird and Dewey, 1970; Hatcher, 1972).

Landward of this orogenic belt, the Appalachian geosyncline became a composite foreland basin during the

SERIES	STAGES
Cincinnatian	Richmondian
	Maysvillian
	Edenian
Champlainian	Shermanian
	Kirkfieldian
	Rocklandian
	Blackriveran

FIGURE 2.—Late Middle and Upper Ordovician Series and Stages in Eastern North America.

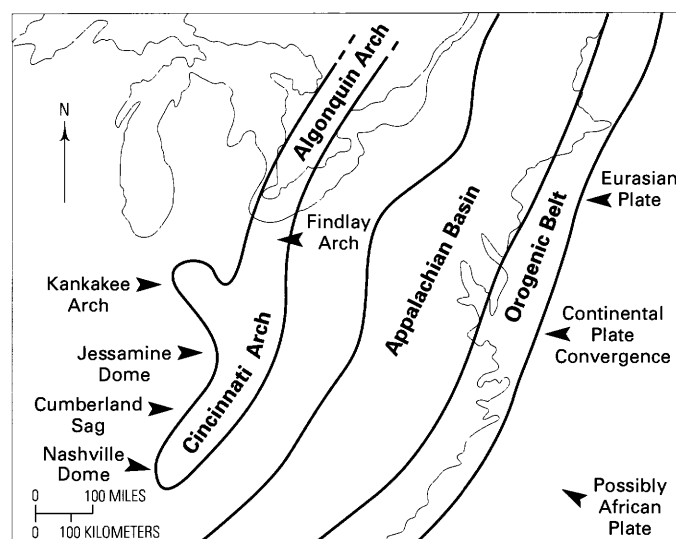


FIGURE 3.—Major structural features of the Cincinnati arch and location of the Appalachian basin and the associated orogenic belt during Ordovician continental convergence.

Middle Ordovician, with a miogeocline plunging seaward toward the subduction zone (fig. 4A) (Dickenson, 1981). During this time, deposition on the craton and upper miogeoclinal shelf was primarily carbonate, while deep marine shales were being deposited in the eugeosyncline, or foredeep basin, directly adjacent to the arc (Kay, 1951, p. 15; Reed, 1980; Shanmugam and Walker, 1980; Shanmugam and Lash, 1982).

As convergence continued, the orogenic belt apparently built into a continuous linear tectonic landmass. This tectonic landmass shed great amounts of sediment into the foreland basin, eventually nearly filling it. By Late Ordovician time, great deltas, most notably the Queenston delta, built out across the basin landward (fig. 4B).

This sequence of events is reflected in the Middle and Upper Ordovician sediments of the Cincinnati arch region. There is a marked increase in the clastic portion of the section in latest Middle Ordovician time. The Upper Ordovician strata of the area are characterized by interbedding, in varying proportions, of limestone and shale.

The Cincinnati arch runs roughly parallel to the Appalachian Basin, basically forming a geanticline (Kay, 1951, p. 17) between it and the cratonic interior (fig. 3). A matter of great controversy since the original description of the Cincinnati "geanticline" (Locke, 1838) has been the timing of the first expression of an arch. Schuchert (1943, p. 539–545) summarized the history of that controversy to the time of his writing. Borella and Osborne (1978) more recently addressed the problem, bringing to bear new stratigraphic evidence resulting from Wilson's



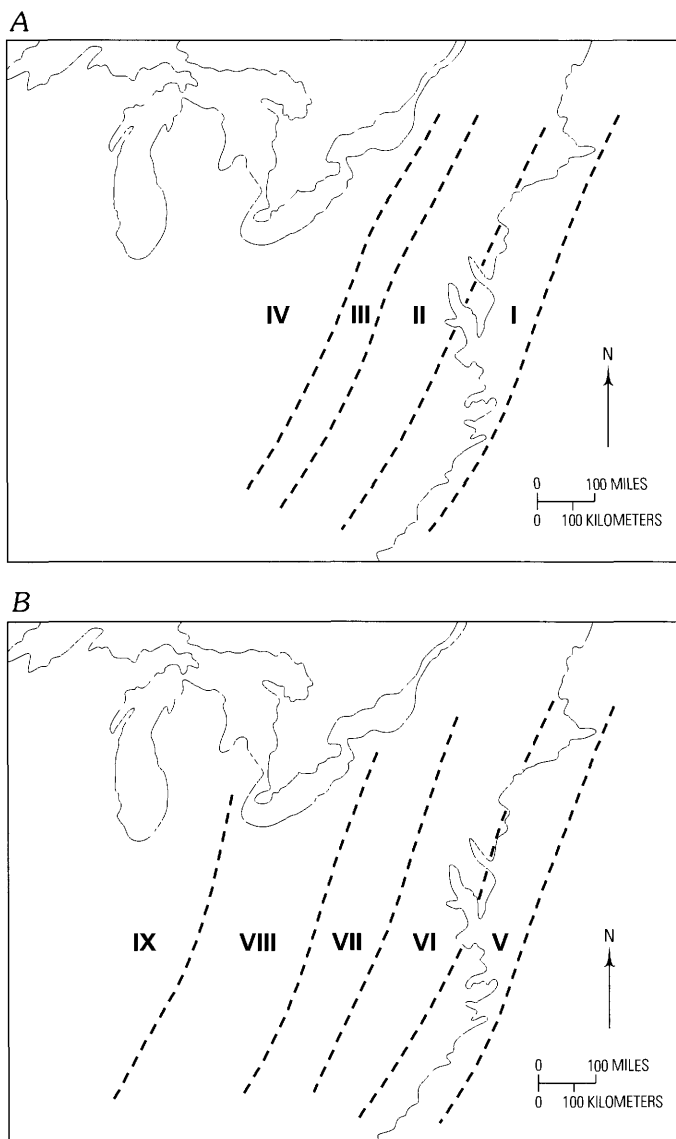


FIGURE 4.—General paleogeographic settings in the Eastern United States during Middle and Late Ordovician time. A, Early Middle to middle Middle Ordovician time: I, Tectonic land; II, Foreland basin (eugeosyncline); III, Shelf (miogeocline); and IV, Cratonic interior. B, Latest Middle and Late Ordovician time: V, Tectonic land (eroding and shedding sediment westward); VI, Fluvia-deltaic systems (transporting sediment westward); VII, Shallow to deep marine shelf (site of deposition of shales of Martinsburg formation); VIII, Carbonate platform (proto-Cincinnati arch); and IX, Cratonic interior basin (site of deposition of Maquoketa Group).

(1949, 1962) work around the Nashville dome of Tennessee and from work done by numerous geologists during the USGS mapping project around the Jessamine dome of Kentucky.

The Cincinnati arch is composed of five primary structural elements (fig. 3). These are, from north to south, the Kankakee arch of Indiana and the Findlay arch of Ohio, which merge near Cincinnati; the Jessamine dome

of central Kentucky; the Cumberland sag (or saddle) at the Kentucky-Tennessee border; and the Nashville dome of central Tennessee. Of primary concern herein are the Jessamine and Nashville domes, as they are primarily responsible for the fine exposures of Ordovician strata in the study area.

Wilson (1962, p. 494, fig. 16) suggested that the Nashville dome was initiated as a small bulging in Kirkfieldian time during deposition of the Hermitage Formation. He referred to this proto-Nashville dome as the central Tennessee bank or high. He further suggested that the same period of crustal movement produced the much more prominent Ozark dome to the west and the tectonic lands (Appalachia) to the east, both of which were high enough to be eroded and provide fine clastic sediments to the intervening low area. Ervin and McGinnis (1975, p. 1290) also considered the Ozark dome to have been initiated during the Ordovician, and they agreed that the origin of the Nashville dome was related.

Borella and Osborne (1978) summarized the continuing controversy over the origin of the Jessamine dome. Using facies distribution maps for the Kirkfieldian-Shermanian-age Lexington Limestone and sedimentologic-stratigraphic data from other authors, they concluded that the Jessamine and Nashville domes, or precursors of these domes, were present during late Middle and early Late Ordovician time. However, they claimed that there was no continuous Cincinnati arch at that time, it being created by renewed activation in the Late Devonian during the final closing of the proto-Atlantic Ocean. E.R. Cressman (written commun., Dec. 1988) disagreed with Borella and Osborne's (1978) interpretations, and cited erosional unconformities in the Ordovician section west of the Cincinnati arch as evidence that there was no structural arch during Ordovician time.

Elias (1982, text-fig. 4) and Meyer and others (1981, fig. 3) showed that during the Late Ordovician, carbonate sedimentation was concentrated along the Algonquin-Cincinnati line (Kay, 1951, p. 21), with fine clastics of the Maquoketa Group to the west and the Martinsburg Formation to the east. They referred to this area of carbonate deposition as a "carbonate platform," and did not really address the structural controversy. However, the insinuation is that it was paleotopographically high.

It is concluded here that the Cincinnati arch formed a hinge line between the Appalachian foreland basin and the cratonic interior. As such, its origin, degree of expression, areal extent, and orientation were directly related to continental margin tectonic activity. Stratigraphic evidence presented by some workers supports the contention that although the arch as now known did not exist until the middle Paleozoic, it was initiated

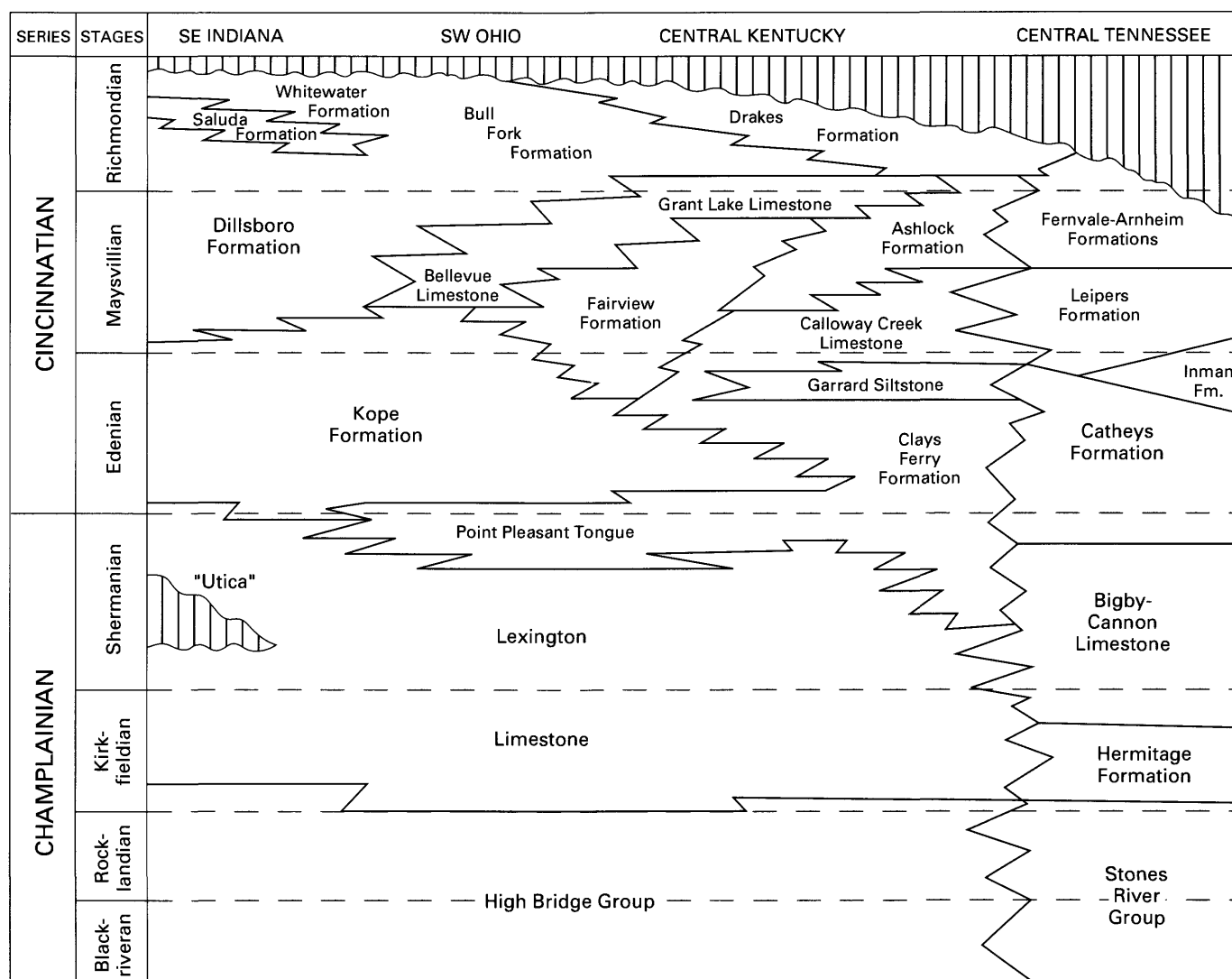


FIGURE 5.—Lithofacies relationships of Middle and Upper Ordovician stratigraphic units in the Cincinnati arch region of southeastern Indiana, southwestern Ohio, central Kentucky, and central Tennessee. (Modified from Sweet, 1979).

during the Middle Ordovician and must have been a low, broad, discontinuous, linear, paleotopographic high extending from southern Ontario (Algonquin arch) to central Tennessee (Nashville dome).

#### ORDOVICIAN LITHOSTRATIGRAPHY OF CENTRAL TENNESSEE

The following discussion concerns only the Middle and Upper Ordovician stratigraphy of the Central Basin of Tennessee; it does not cover the strata of eastern Tennessee. Nearly all of the information related here was drawn directly from the works of Charles W. Wilson, Jr. (1949, 1962). Stratigraphic correlations are based largely on Sweet (1979) and Pojeta and Repetski (1982). The Central Basin Ordovician section consists of, in ascend-

ing order, the Stones River, Nashville, "Eden," "Maysville," and "Richmond" Groups.

#### STONES RIVER GROUP

The Stones River Group is Blackriveran-Kirkfieldian in age and correlates with the High Bridge Group and lowest Lexington Limestone of central Kentucky (figs. 5, 6). The group consists of, in ascending order, the Murfreesboro Limestone, Pierce Limestone, Ridley Limestone, Lebanon Limestone, and Carters Limestone (fig. 6).

*Murfreesboro Limestone.*—The Murfreesboro is the oldest Ordovician formation exposed in the Central Basin of Tennessee. The base of the formation is not exposed, but the maximum known surface thickness is 70 ft (feet). It is overlain conformably by the Pierce Limestone.

CENTRAL TENNESSEE	
Nashville Group	Catheys Formation
	Bigby-Cannon Limestone
	Hermitage Formation
Stones River Group	Carters Limestone
	Lebanon Limestone
	Ridley Limestone
	Pierce Limestone
	Murfreesboro Limestone

FIGURE 6.—Champlainian and Edenian lithostratigraphic units in central Tennessee.

The Murfreesboro Limestone is mainly dark gray, very fine grained, and massively bedded. Locally, it has laminations, mud cracks, intraformational conglomerate, and selectively dolomitized burrows. Chert is common. The fauna is dominantly mollusks, particularly gastropods.

Evidence indicates that the Murfreesboro was deposited in a shallow, probably restricted marine environment, most likely inner shelf lagoons and associated tidal flats.

*Pierce Limestone.*—The Pierce is 23–28 ft of dense, very fine grained, gray, blue-gray, or dove-colored limestone. It is essentially a thin-bedded unit separating the more massively bedded overlying Ridley and underlying Murfreesboro Limestones. The thin beds (average 2 inches thick) are separated by partings of gray calcareous shale. The fauna is abundant and is concentrated on the bedding surfaces; it consists mainly of a diverse brachiopod and bryozoan assemblage. This unit represents fairly quiet subtidal, normal marine environments.

*Ridley Limestone.*—The Ridley consists of about 90 to 115 ft of massive-bedded (up to 4 ft thick), gray to bluish-gray to tan limestone. It is chiefly fine grained, but medium to coarse textures are common. Selectively dolomitized burrows and chert are common. A widespread thin-bedded, clay-rich member is present 25–30 ft

above the base of the formation. The Ridley fauna is dominated by a diverse assemblage of brachiopods and bryozoans.

This formation was deposited in a normal marine subtidal environment. The thin-bedded member seems to reflect a temporary return to conditions similar to those under which the Pierce Limestone was deposited.

*Lebanon Limestone.*—The Lebanon is 74–118 ft of gray, bluish-gray, or tan, dense, fine-grained limestone, with interbeds of coarser grained limestones. The 1- to 6-in-thick limestone beds are separated by thin calcareous shale partings. Very characteristic of this unit are dolomitic and clayey burrows that weather differentially, giving the limestone a “worm-eaten” appearance.

The Lebanon Limestone is conformable with the underlying Ridley, but it is overlain unconformably by the Carters Limestone. Similar to the Pierce Limestone, the Lebanon also has a thin-bedded unit separating two more massively bedded units. The Lebanon fauna is diverse and is concentrated on the platy bedding surfaces. It is dominated by a bryozoan-brachiopod assemblage. The environment of deposition was quiet subtidal and normal marine.

*Carters Limestone.*—The Carters is divided into two informal members—the lower and upper members.

*Lower member.*—This member ranges from 27 to 65 ft thick. Beds are 1 to 4 ft thick, though some beds are thinner. Limestone lithologies vary from fine grained and dense, through medium to coarse grained and even coquinooid.

Alberstadt, Walker, and Zurawski (1974) described patch reefs in southern Tennessee from the lower Carters Limestone built primarily by stromatoporoids, corals, and algae. Wilson (1949, p. 56) cited colonial corals such as *Columnaria* and *Tetradium* as the most characteristic fossils in the lower member.

*Upper member.*—This member reaches 28 ft in thickness and consists mainly of dense, fine-grained, laminated, argillaceous, gray to tan limestone. The most characteristic fossils are ribbonlike bryozoans and the colonial coral *Tetradium celluloseum*, but there is also a moderately diverse assemblage of gastropods, ostracodes, and brachiopods.

The Carters represents shallow marine shelf facies, mainly of normal salinity but of variable energy conditions. The lower member appears to represent generally higher energy carbonate bank conditions. The lower and upper members are conformable, but the upper member is overlain unconformably by the Hermitage Formation of the Nashville Group.

*Summary of Stones River Group facies.*—As is apparent from the preceding descriptions, two basic facies make up the Stones River Group. The first facies, Wilson's (1949, p. 67) Facies A, consists of pure, massive-

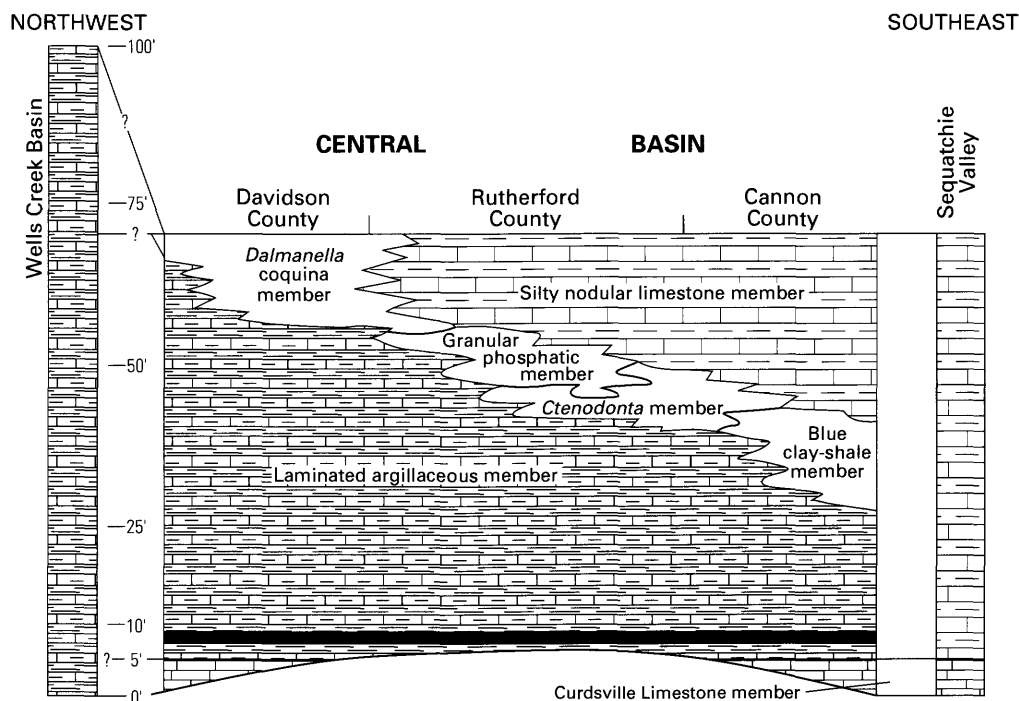


FIGURE 7.—Facies relationships of the members of the Hermitage Formation in central Tennessee (from Wilson, 1949).

bedded limestone that commonly contains dolomitized burrows, chert, and a fauna of corals, stromatoporoids, brachiopods, bryozoans, mollusks, and others. The second facies, Wilson's (1949) Facies B, consists of thin limestone beds separated by shale partings and containing a fauna characterized by fragile ramose and ribbon-like bryozoans, brachiopods, and some mollusks and ostracodes. The alternation of these two facies defines the succession of formations in the Stones River Group.

Wilson (1949) believed that silt and clay—their presence or absence—were the primary controls over facies and faunal distributions within the Stones River Group. He suggested that the alternation of the two facies in the group was the result of periodic uplifting and erosion of surrounding positive areas.

It should be noted that sedimentary features characteristic of tidal flat conditions (for example, lamination and fenestral fabric) are present locally throughout the Stones River Group but characterize only the basal formation, the Murfreesboro Limestone. The only widespread unconformities recognized in this group of rocks are at the base and the top of the Carters Limestone.

#### NASHVILLE GROUP

The Nashville Group is Kirkfieldian, Shermanian, and Edenian in age (figs. 5, 6). It correlates with the Lexington Limestone, Clays Ferry Formation, and Kope Formation of Kentucky. The included formations are, in

ascending order, the Hermitage Formation, Bigby-Cannon Limestone (as used by Wilson, 1949), and Catheys Formation (figs. 5, 6).

*Hermitage Formation.*—The Hermitage Formation thickens westward across the Central Basin from 70 to 180 ft maximum. Wilson (1949, p. 82, 83) subdivided the formation into numerous members, including the basal Curdsville Limestone Member, which onlaps the Carters Limestone on the flanks of the Nashville dome island; two tongues, the laminated argillaceous member, which thickens westward, and the silty nodular limestone member, which thickens eastward in complement; and four lentils, the *Dalmanella coquina* member, the granular phosphatic member, the "*Ctenodonta* member," and the blue clay-shale member (fig. 7). These lentils rise diagonally northwestward through the formation between the two tongues (Wilson, 1949, fig. 15).

*Curdsville Limestone Member.*—This thin- to medium-bedded, coarsely crystalline limestone onlapped the Nashville dome island, lying unconformably on the Carters Limestone. The member is only 7 ft thick on the western flank, but is 10 to 15 ft thick on the eastern flank. It is absent over the top of the island.

The limestone is blue to gray in color and is coarsely crystalline. Beds are 1 to 10 in thick, averaging 2 to 3 in, and are separated by thin gray shale partings. Fossils are abundant. Brachiopods and bryozoans predominate, but mollusks, trilobites, corals, crinoids, and ostracodes

also are present. The Curdsville is interpreted as a shallow subtidal, normal marine, transgressive unit.

**Laminated argillaceous member.**—This tongue thickens westward across the Central Basin from 20 to 70 ft, but it has been reported to be as thick as 180 ft in the subsurface. It is conformable with the underlying Curdsville and with the various overlying lentils of the Hermitage Formation.

The limestone is bluish gray and argillaceous, and commonly is evenly laminated. Fossils are sparse, but those species found are typical of the entire formation. Beds are 2 to 10 in thick and are separated by shale partings or thin shale beds. Penecontemporaneous bedding deformation is common, with contorted and rolled-up beds being interbedded with beds consisting of rounded cobbles and boulders of the same lithology. The even lamination and the sparse fauna suggest a relatively deep, stagnant depositional environment.

***Dalmanella coquina* member.**—This lentil is present in a north-south belt that attains a thickness of 30 ft. It is a massive-bedded, grayish-blue, silty limestone containing a great profusion of dalmanellid shells, which contribute to a coquinoïd character. The lentil grades westward into the laminated argillaceous member and eastward into the silty nodular limestone member. The Bigby-Cannon Limestone overlies the lentil across a local minor unconformity (fig. 7).

The abundant dalmanellid shells are generally unbroken, but they are shingled. Wilson (1962, p. 485, 486) suggested that the environment of deposition was relatively deep and quiet, with the currents strong enough to stack the rather thin delicate shells but not strong enough to break them.

**Granular phosphatic member.**—This member is probably a series of several lentils rather than one continuous lentil. It ranges from 5 to 30 ft thick in any single exposure. The limestone is coarse grained and crossbedded, and it contains varying amounts of phosphate. Bedding is massive to irregular. The lentils are surrounded by, and grade into, the laminated argillaceous member and the silty nodular limestone member.

The fauna is mostly worn and broken, and generally the only well-preserved fossils are sturdy equidimensional brachiopods and massive bryozoans. This member represents shoaling areas that were acted upon by intense waves and currents. Wilson (1962, p. 486) suggested that the lentils formed in a north-south shoal belt.

***Ctenodonta* member.**—This lentil is nearly circular in outcrop outline and reaches a maximum thickness of about 20 ft. The limestone is thin bedded, laminated, argillaceous, and fine to medium grained. Beds are separated by shale partings. The blue-gray limestone weathers to yellowish brown as a result of oxidation of disseminated iron. The fauna is dominated by the pelec-

ypod "*Ctenodonta hermitagensis* and other mollusks, which in many places cover the surfaces of slabs. The lentil grades westward into the laminated argillaceous member and eastward into the silty nodular limestone member.

**Blue clay-shale member.**—This lentil consists of calcareous blue clay-shale. It grades into the laminated argillaceous member to the west and reaches a thickness of 30 ft to the southeast. Fossils are sparse.

**Silty nodular limestone member.**—This tongue thickens eastward across the Central Basin to a thickness of about 30 ft, and grades westward into the *Dalmanella coquina*, granular phosphatic, *Ctenodonta*, and blue clay-shale members. It consists of nodular beds of limestone 3 to 8 in thick separated by irregular clay-shale partings. The fauna is moderately diverse and common, the most characteristic elements being bryozoans and corals, but also with other normal marine fossils. This unit contains less clastic silt than any other member of the Hermitage. Wilson (1949) suggested that this reflects a western to southwestern source for the clastics in the formation.

**Bigby-Cannon Limestone.**—The Bigby-Cannon Limestone is Kirkfieldian-Shermanian in age, and correlates with much of the Lexington Limestone of central Kentucky (fig. 5). The formation ranges from about 60 to 100 ft thick and consists of three major lithofacies, which are distributed in north-south-trending belts through the Central Basin. From west to east, these lithofacies are the Bigby facies, the dove-colored facies, and the Cannon facies (figs. 8–10).

The contact between the Bigby-Cannon Limestone and the underlying Hermitage Formation is locally unconformable. In apparent paleotopographic high areas, the Hermitage shows thinning resulting from erosion. However, in other areas, lithologies of the two formations clearly intertongue, demonstrating continuous deposition. Other than the papers of Wilson (1949, 1962) and Alberstadt (1973), very little has been written in the modern literature about this interesting and important unit.

**Bigby facies.**—This facies makes up the westernmost facies belt in the formation. It rarely exceeds 60 ft in composite thickness, and its facies belt has a maximum width of 40 miles.

The Bigby Limestone is coarse grained and crossbedded, and the constituent grains are mainly thoroughly broken and abraded skeletal fragments. The fauna was so damaged by the intense wave action under which it was deposited that it is generally poorly preserved. Fossils are better preserved eastward, and a diverse fauna is known, the most prominent being brachiopods, bryozoans, gastropods, pelecypods, and corals. Locally within the Bigby, there are lentils of massive, coarse-grained, gray limestone that have long been referred to

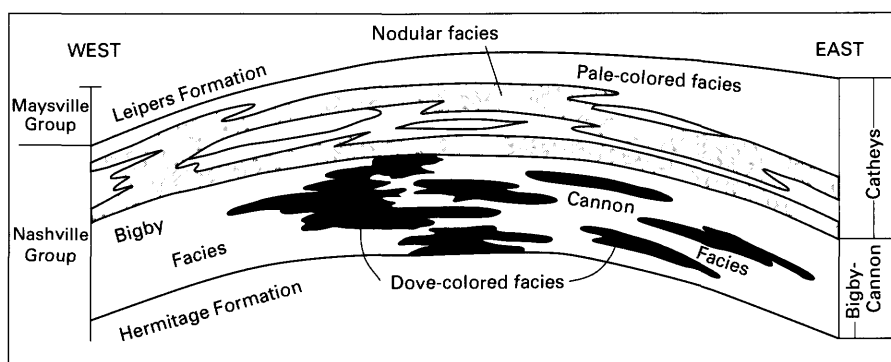


FIGURE 8.—Facies relationships of the members of the Bigby-Cannon Limestone across the central Tennessee high (from Wilson, 1949).

as the “*Cyrtodonta*” beds or member. The fauna in this latter unit consists almost entirely of the pelecypods *Cyrtodonta* and *Vanuxemia* and the gastropods *Lophospira*, *Bucania*, and *Bellerophon*.

The Bigby facies represents the limits of Wilson’s (1949) central Tennessee bank, which he interpreted as a topographically high, broad shoaling area where the water never exceeded 30 ft in depth (fig. 9). Westward off this bank, the water deepened rapidly and a laminated argillaceous limestone facies was deposited; this facies is now exposed only in the Western Highland Rim of the Central Basin. Eastward off the bank, the Bigby grades into the dove-colored facies, which represents shallow lagoonal and tidal flat conditions (fig. 8).

**Dove-colored facies.**—This facies consists of lentils present in a north-south belt between the Bigby and Cannon facies belts (fig. 8). Its maximum composite

thickness is 60 to 70 ft. The bases of these lentils in many places show evidence of scouring prior to deposition.

The facies is so named because of its light-gray color on fresh surfaces; however, it becomes chalky upon weathering. The limestone is very fine grained, dense, and brittle. Beds vary in thickness from 2 in to 3 ft and average about 1 ft. The beds are characteristically laminated, and fenestral fabric and mud cracks are common. Fossils are rare and are generally restricted to ostracodes and high-spined gastropods, with occasional small vertical burrows. Beds of corals, brachiopods, and other normal marine fauna are present in some places, but Wilson (1949, 1962) interpreted these as detritus washed off the Bigby bank during storms.

**Cannon facies.**—This easternmost facies of the Bigby-Cannon Limestone thickens eastward from its inter-tonguing with the dove-colored facies to a maximum

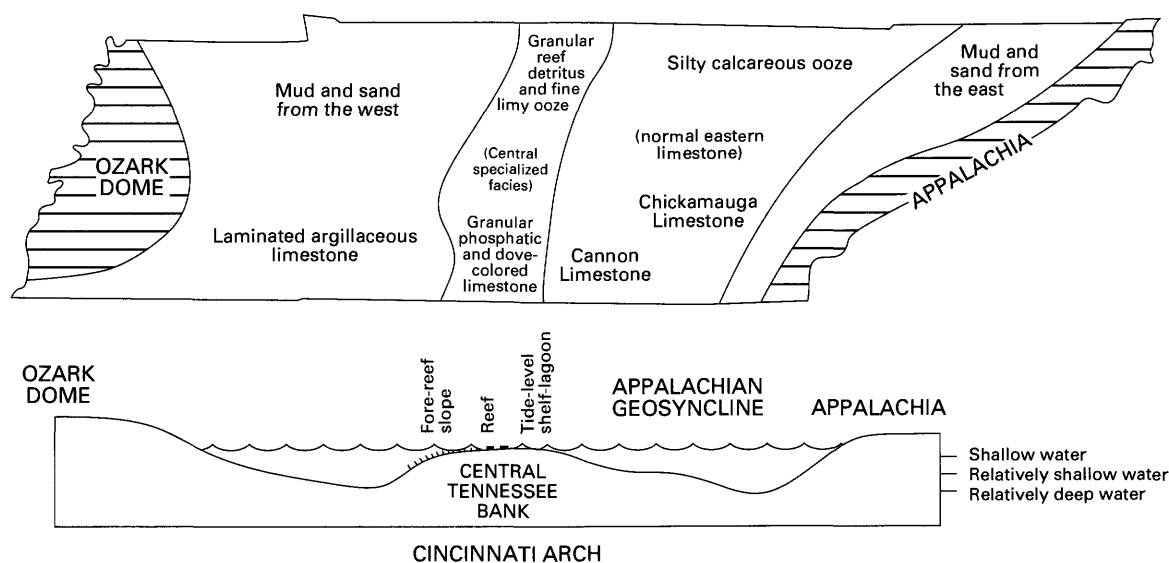


FIGURE 9.—Idealized paleogeographic setting in central Tennessee during deposition of the Bigby-Cannon Limestone (from Wilson, 1949).

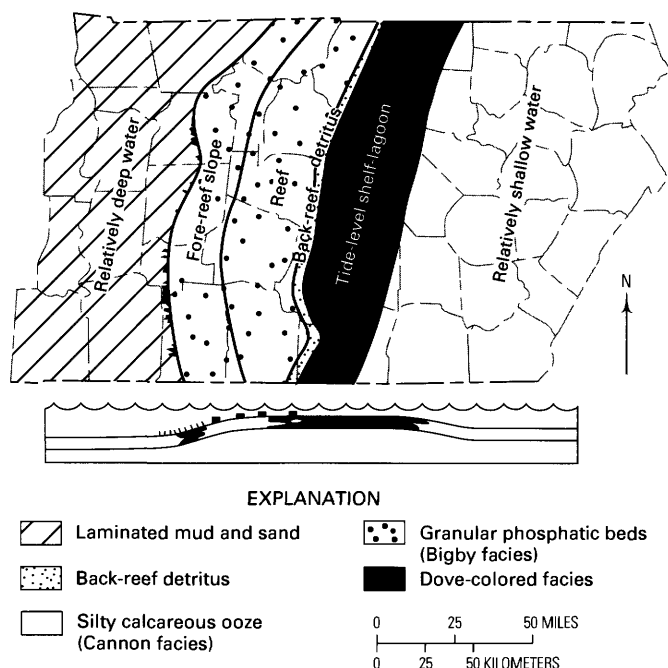


FIGURE 10.—Depositional facies of the Bigby-Cannon Limestone in central Tennessee (from Wilson, 1949).

thickness of 100 ft in the eastern Central Basin and the Sequatchie Valley of southeastern Tennessee (figs. 8–10).

The Cannon Limestone is dark gray, fine to medium grained, moderately fossiliferous, and evenly bedded. Beds average about 1 ft thick and in many places have silty partings, though silt is nearly absent in the limestone itself.

Fossils are moderately abundant and well preserved in the Cannon; they consist mainly of brachiopods, gastropods, corals, and other normal marine fauna (Wilson, 1949). Alberstadt (1973, p. 630) cited work demonstrating that most Cannon communities were dominated by bellerophontid and lophospired gastropods and leperditid ostracodes, which might indicate somewhat restricted conditions. Alberstadt further reported encrusting and boring blue-green algae, green algae, and the red alga *Solenopora* in the Cannon facies.

Because of the algal-gastropod-ostracode assemblage and the predominance of a carbonate mud matrix, Alberstadt (1973) concluded that the Cannon was deposited under relatively quiet lagoonal conditions. The salinity of the environment was probably normal marine to slightly restricted. Because stenohaline taxa are common, the predominantly “restricted fauna” may reflect quiet, nearly stagnant conditions more than hypersalinity.

Bassler (1932) had made a comprehensive study of the “Cannon” fauna, but Wilson (1949) stated that his reinterpretation of the formational contact between the Cannon and the overlying Catheys Formation was so differ-

ent as to put the current stratigraphic placement of many species in some doubt. Most type specimens described herein from this section were collected during the late 19th century, before Bassler’s or Wilson’s work, so stratigraphic placement of many type specimens is difficult.

*Catheys Formation.*—The Catheys Formation is Shermanian-Edenian in age, correlating with the Clays Ferry Formation and Kope Formation in Kentucky (fig. 5). Wilson (1949, 1962) claimed that the Catheys was unconformable with the underlying Bigby-Cannon Limestone over the central Tennessee high, but that the hiatus was of short duration and the two formations are conformable to the east and west.

The Catheys thickens eastward across central Tennessee from about 25 ft in the eastern Central Basin to nearly 250 ft in the Sequatchie Valley of southeastern Tennessee. The formation consists of six interbedded and intertonguing facies, which are described below (fig. 8).

*Granular phosphatic facies.*—This facies is essentially identical to the like units in the Hermitage and Bigby-Cannon Formations. The massive-bedded, coarse-grained, blue-gray limestone is present in 5- to 10-ft-thick lentils. These lentils are most common in the lower half of the formation, and are most prominent in the westernmost Central Basin. Fossils are mainly very worn and fragmented.

*Dove-colored facies.*—This facies is present as lentils less than 5 ft thick in the basal 25 ft of the formation. The limestone is light gray, fine grained, dense, and brittle. It differs from the like-named facies of the Bigby-Cannon Limestone mainly in its appreciably higher clay and glauconite content. Ostracodes are the most common element of a very sparse fauna.

*Pale-colored facies.*—Nearly half the Catheys Formation is made up of this blue limestone, which weathers to characteristically pale hues. The facies thickens eastward, along with the total formation, from 10 to 125 ft in composite thickness.

The limestone is dark blue on fresh surfaces, fine grained, and dense. Beds range from 3 to 24 in thick, have wavy surfaces, and are separated by blue-gray shale partings that sometimes thicken to several inches. The fauna is moderately diverse and is dominated by brachiopods and bryozoans.

*Shaly facies.*—This blue-gray shale facies is very irregular in its occurrence within the formation and in its thickness. It commonly is present in shale beds about 5 ft thick, but it can reach 20 ft in thickness. It varies from soft, crumbly, clay-shale to fissile, compact, calcareous shale that breaks into flakes.

The most typical fossils in these shales are slender branching bryozoans, particularly *Constellaria*, which in

many places is crowded into beds. Other fossils include brachiopods and lophospirid and bellerophontid gastropods, as well as the gastropod *Cyclonema*.

**Nodular facies.**—This facies makes up about one-third of the formation. It is distributed throughout the unit and throughout the Central Basin, and it interbeds with all the other facies. It thickens from west to east, attaining a maximum composite thickness of 75 ft.

This blue-gray limestone contains the most well preserved fossils of any facies of the formation. The fauna is composed mainly of a brachiopod-bryozoan assemblage. The beds are 3 to 8 in thick, have irregular knobby surfaces, and are separated by thin shale partings.

**Laminated siltstone facies.**—This facies consists of thin laminae of fine-grained, blue-gray limestone uniformly interlaminated with laminae of silt and clay. It is present as a 5- to 10-ft-thick unit near the base of the formation, and grades laterally and vertically into the shaly facies. It is nearly barren of fossils.

#### "EDEN GROUP"

**Inman Formation.**—The Inman Formation varies from 40 to 70 ft in thickness and has a rather limited area of exposure. The formation consists of greenish-gray, calcareous shale, and zones of red shale interbedded with uniformly bedded, greenish-gray to light-gray, fine-grained, dense limestone having fenestral fabric. The fauna is neither abundant nor diverse, and consists mainly of brachiopods and bryozoans. It seems to represent a quiet, shallow, subtidal to intertidal environment of deposition. The red shales might represent the first incursion of the Queenston delta red bed facies into the area. The entire Inman Formation probably is Edenian in age, but the upper part may be early Maysvillian in age (fig. 5).

#### "MAYSVILLE GROUP"

**Leipers Formation.**—The Leipers Formation is generally less than 75 ft thick, but it reaches 175 ft thick in northernmost central Tennessee. The Leipers is late Edenian-Maysvillian in age (fig. 5), although these rocks have traditionally been called the Maysville Group in Tennessee. Wilson (1949, p. 182–190) described three facies.

**Argillaceous facies.**—This variable facies consists of (1) thin-bedded nodular limestone with shale partings, (2) slabby-bedded argillaceous to rather pure blue-gray limestone, (3) massive-bedded argillaceous to silty limestone, (4) blue-gray calcareous shale, and (5) light-gray to bluish-gray mudstone and siltstone. All subfacies except the last contain an abundant brachiopod-bryozoan assemblage.

**Granular facies.**—This massive-bedded, coarse grained, dark-blue limestone is in most places crossbedded or irregularly bedded, but locally it contains lenses of gray calcareous shale. Fossils are generally very broken and abraded. The facies thickens westward, just as do the similar facies of the Bigby-Cannon Limestone and Catheys Formation, to a maximum composite thickness of 75 ft.

**Pale-colored facies.**—This fine-grained, dense limestone is dark blue when fresh, but it weathers to pale blue. The beds are 2 to 24 in thick and are separated by shale partings. The unit may be 25 to 50 ft in composite thickness.

Fossils are not as abundant in this facies as in the previous two, but they are common. The most representative members of the fauna are the brachiopod *Platystrophia ponderosa* and several species of gastropods.

**Summary of Leipers Formation.**—The granular facies dominates the formation in the western outcrop area, the argillaceous facies dominates the lower formation to the east, and the pale-colored facies dominates the upper formation in the east. The pattern is interpreted as a western shoaling area or bank, with a broad lagoon to the east which probably shallowed upward over time.

#### "RICHMOND GROUP"

The group is bounded by unconformities and contains two main formations, the Arnheim Formation and the Fernvale Limestone, with tongues of the Sequatchie Formation entering the section from the east. These rocks have traditionally been called the Richmond Group in Tennessee. The Nashville dome was a positive feature during Richmondian time, and the Arnheim and Fernvale apparently were deposited only around the western and northern flanks of the dome.

**Arnheim Formation.**—This unit probably does not correlate with the type Arnheim Formation of the Cincinnati area. Faunal evidence indicates a somewhat different age for the Tennessee unit (Bassler, 1932, p. 122, 124; McFarlan, 1943, p. 29; Sweet, 1979; Elias, 1982, p. 27, 28). The unit probably is late Maysvillian and early Richmondian in age (fig. 5).

The Tennessee Arnheim varies from 10 to 20 ft thick around the northern and western flanks of the Nashville dome. It consists of four facies, which intergrade laterally and vertically: (1) massive-bedded, argillaceous, rubbly limestone, (2) thin-bedded, nodular, blue-gray limestone, (3) cherty, argillaceous, blue-gray limestone, and (4) gray shale. The unit is very fossiliferous, the fauna being dominated by brachiopods.

In most places the lowermost Arnheim is a basal conglomerate that lies on a red, iron-stained contact with the underlying Leipers Formation. In some areas the



Arnheim is overlain by a massive-bedded, calcareous mudstone tongue of the Sequatchie Formation, rather than by the Fernvale Limestone.

*Fernvale Limestone.*—The Fernvale Limestone typically consists of massive- or irregularly bedded, very coarsely crystalline, gray limestone containing varicolored grains. In some places, thin, wavy, lenticular beds can be discerned within the massive beds. In some areas, the unit becomes ferruginous or phosphatic.

The Fernvale generally overlies either the Arnheim or Leipers unconformably, but it overlies a tongue of the Sequatchie Formation where the latter is present. The formation grades eastward into the Sequatchie Formation. Brachiopods, particularly *Rhynchotrema capax*, dominate the moderately common fossil assemblage. The Fernvale is early Richmondian in age (fig. 5).

#### MIDDLE ORDOVICIAN LITHOSTRATIGRAPHY OF KENTUCKY

The Middle Ordovician strata of Kentucky are exposed around the flanks of the Jessamine dome. The section includes the High Bridge Group (Blackriveran-Kirkfieldian) and the Lexington Limestone (Kirkfieldian-Shermanian). In different areas, the Clays Ferry Formation, Kope Formation, and Lexington Limestone straddle the Middle-Upper Ordovician boundary (Pojeta, 1979, p. A14) (fig. 5). Cressman (1973) and Cressman and Noger (1976) provided comprehensive reviews of the Middle Ordovician lithostratigraphy of Kentucky.

#### HIGH BRIDGE GROUP

The carbonate rocks of the High Bridge Group range from 550 to 700 ft thick. The High Bridge Group is divided into three formations, which are, in ascending order, the Camp Nelson Limestone, Oregon Formation, and Tyrone Limestone. These are the oldest strata exposed in Kentucky. They crop out in the gorge carved by the Kentucky River across the Jessamine dome. The thickest exposed section of the High Bridge Group is in this gorge, and measures 440 ft in thickness. The lower part of the Camp Nelson Limestone is known only from drill cores.

Cressman and Noger (1976) and Kuhnhenh, Grabowski, and Dever (1981) have described the carbonate rocks of the High Bridge Group. They interpreted the depositional environments of the group as being analogous to the shallow subtidal, intertidal, and supratidal facies of the modern Bahama Islands. Peritidal carbonates dominate in a series of shallowing upward cycles resulting from constantly migrating environments on a stable cratonic platform. Cressman and Noger (1976, p. 9–13) compared the High Bridge Group with

other correlative carbonate sequences in Alabama, Arkansas, New York, and Ontario. They concluded that the High Bridge Group was part of a vast complex of tidal flats and associated environments that extended over much of the craton of Eastern North America during Blackriveran-Rocklandian time. The High Bridge Group of central Kentucky is directly correlative with the Stones River Group of central Tennessee (Sweet and Bergstrom, 1976, text-fig. 3; Pojeta and Repetski, 1982, col. 58) (figs. 5, 6).

*Camp Nelson Limestone.*—The Camp Nelson Limestone is the lowermost formation in the High Bridge Group. It unconformably overlies the Whiterockian-age Wells Creek Dolomite in the subsurface (Sweet and Bergstrom, 1976, text-fig. 3) and is conformable with the overlying Oregon Formation. The Camp Nelson is composed of micrite, pelmicrite, and biopelmicrite (Cressman and Noger, 1976, p. 1). Burrows are common throughout most of the unit, and many are dolomitized selectively.

Most of the Camp Nelson represents shallow subtidal environments, with subordinate peritidal deposits. Some biomicrites have a diverse fauna of ostracodes, trilobites, brachiopods, corals (*Tetradium*), bryozoans, pelecypods, and nautiloids. The peritidal carbonates display algal laminae, fenestral fabric, intraformational conglomerates, and mud cracks. The two types of carbonates are arranged in shallowing-upward cycles. These cycles are thicker than those in the two overlying formations.

*Oregon Formation.*—The Oregon Formation ranges from 6 to 65 ft thick. It is composed mainly of a finely crystalline dolomite that is interbedded with micritic limestone. The contacts with the adjacent limestone formations are placed at the base of the lowest dolomite bed and the top of the highest dolomite bed.

Peritidal depositional environments in repeated shallowing-upward cycles characterize the formation. Biopelsparites contain fragments of crinoids, bryozoans, brachiopods, ostracodes, and tabulate corals. Biomicrites have a more restricted fauna of ostracodes, gastropods, and some trilobites and tabulate corals. Peritidal carbonates, which predominate, have cryptogalaminated and thin-bedded dolostones with desiccation features and some intraclastic layers (Kuhnhenh and others, 1981).

Dolomite is much more abundant in the Oregon Formation than in the Camp Nelson or Tyrone Limestone. Kuhnhenh, Grabowski, and Dever (1981, p. 9) suggested that the Oregon sediments were more exposed as parts of low, broad islands. They believed the dolomite is diagenetic in origin, because lithologies in the Oregon do not differ significantly from those of the Tyrone Limestone.

*Tyrone Limestone.*—The Tyrone Limestone is 55 to 155 ft thick, the thickness varying in complement with

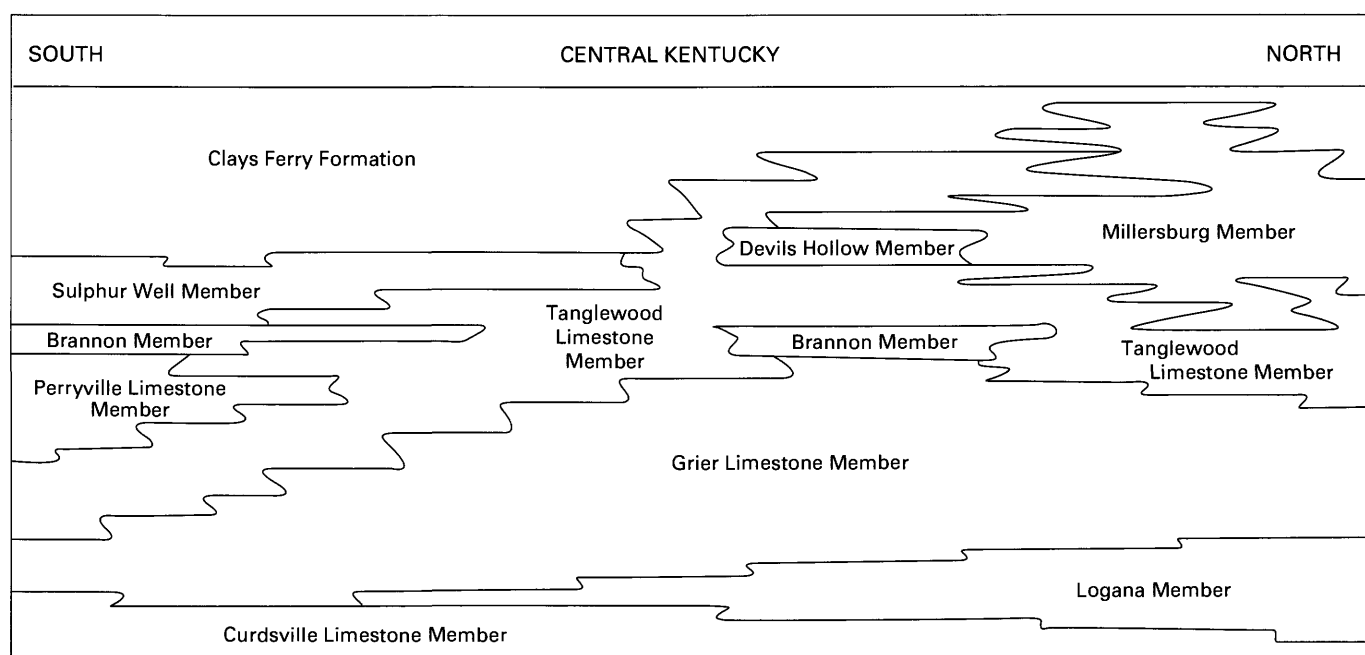


FIGURE 11. — Facies relationships between the major members of the Lexington Limestone and the Clays Ferry Formation in central Kentucky (modified from Cressman, 1973, and his unpublished figure).

the thinning of the Oregon Formation, with which it intertongues in its lower part. The Tyrone is conformable with the underlying Oregon but is disconformable with the overlying Lexington Limestone (Cressman, 1973, p. 12, 13). The limestones of the Tyrone are biopelsparites, biomicrites, and peritidal micrites, similar to the rocks of the underlying Oregon Formation but with less dolomite. Just as in the lower High Bridge strata, the Tyrone carbonates are arranged in shallowing-upward cycles. These cycles become shorter and simpler in the upper part of the Tyrone (Kuhnhehn and others, 1981, p. 5). Greene (1966) listed a mainly molluscan fauna dominated by gastropod species. In addition, the Tyrone contains *Tetradium* thickets and pelecypod, nautiloid, and polyplacophoran mollusks.

#### LEXINGTON LIMESTONE

The Lexington Limestone is a complex facies mosaic of mostly bioclastic and fossiliferous limestones cropping out around the Jessamine dome in central Kentucky (fig. 11). Sweet and Bergstrom (1976, text-fig. 3) and Sweet (1979, p. G13) assigned a Kirkfieldian-Edenian age to the unit (fig. 5).

Black, Cressman, and MacQuown (1965) redefined the formation to include all strata formerly assigned to the Lexington Limestone and the Cynthiana Formation

(McFarlan, 1943; McFarlan and White, 1948; Nosow and McFarlan, 1960), with the exception of the Cynthiana beds placed in the Clays Ferry Formation by Weir, Greene, and Simmons (1965). The mainly bioclastic and fossiliferous limestones of the Lexington contrast greatly with the mainly micritic Tyrone limestones below and the interbedded shales and limestones of the Clays Ferry Formation above.

The Lexington Limestone unconformably overlies the Tyrone Limestone. Cressman (1973, p. 12, 13) demonstrated at least 10 ft of erosional relief on the Tyrone Limestone, over which the Curdsville Limestone Member of the Lexington Limestone transgressed, but he felt that the time gap represented was small.

The contact between the Lexington Limestone and the overlying Clays Ferry Formation is conformable and diachronous because of intertonguing (figs. 5, 11). The Lexington is up to 320 ft thick in its central outcrop area, but it thins to less than 200 ft to the north and south because of intertonguing of the upper members of the Lexington Limestone with the shale and limestone of the Clays Ferry Formation. Silicified fossil horizons are common in the Lexington Limestone, and the majority of silicified fossils studied here were collected from this unit by the USGS. Cressman (1973) presented an excellent detailed lithostratigraphic study of the Lexington Limestone. The following descriptions of the members of the

Lexington Limestone are taken primarily from that report.

*Curdsville Limestone Member.*—The Curdsville Limestone Member is the basal unit in the Lexington Limestone (fig. 11). The contact with the underlying Tyrone Limestone is an erosional unconformity. The member ranges from about 20 to 40 ft thick, thinning westward owing to facies gradation into the Logana Member. The Curdsville is overlain by the Logana Member in the central and northern outcrop areas, and by the Grier Limestone Member to the south.

MacQuown (1967) divided the Curdsville into three informal units, which are gradational at their contacts. The lower 10-ft-thick unit is light-colored bioclastic limestone that consists of calcirudites, and crossbedded and ripple-marked calcarenites. The lower unit is composed of well-sorted, abraded skeletal debris having about 5 to 10 percent quartz sand. The middle unit is present from 10 to 20 ft above the base of the member and consists of bioclastic calcarenite and calcirudite interbedded with calcisiltite and shale. The upper unit consists of medium-gray, irregularly bedded, fossiliferous limestone and bioclastic calcarenite. Cressman (1973, p. 14) interpreted this sequence as recording a marine transgression, with higher energy, shallow-water deposits grading upward into lower energy deposits. The close interbedding between calcirudite, calcarenite, calcisiltite, and minor shales probably represents small migrating bars separated by intervening low areas.

*Logana Member.*—The Logana Member reaches 50 ft thick in the northern outcrop area and thins southward, where it intertongues with the underlying Curdsville and overlying Grier Limestone Members (fig. 11). The member consists of interbedded dark calcisiltite and shale in nearly equal proportions. The calcisiltite is generally argillaceous, is in broad lensing beds about 0.2 to 0.3 ft thick, and in many places has a petroliferous odor. The interbedded shales are brownish gray, fissile, calcareous, and partly dolomitic.

Most beds are unfossiliferous, but silicified mollusks and brachiopods are common in some places. Dalmanellid brachiopods can occur as coquinas, or can coat upper and lower bed surfaces, with pelecypods closely packed in the bed interior. Cressman (1973, p. 17) believed that the Logana was deposited at the height of the initial Lexington transgression, and that its facies relationship with the Curdsville and Grier Limestone Members reflects a deepening of water to the north. The dark color, even tabular bedding, and general sparsity of fossils or burrows in the Logana suggest deeper water, quiet conditions, and poor oxygenation.

*Grier Limestone Member.*—The Grier Limestone Member consists predominantly of thin- and irregularly bedded to nodular-bedded, poorly sorted, fossiliferous

limestone. It ranges in thickness from 100 to 180 ft, the variation resulting mainly from intertonguing of the lower part with the Logana Member and the upper part with the Tanglewood Limestone Member (fig. 11).

Through the northern outcrop area, the Grier conformably overlies the Logana Member, and in the southern area it has a gradational contact through 10 to 15 ft with the Curdsville Limestone Member. Through most of central Kentucky, the Grier is overlain by the calcarenites of the Tanglewood Limestone Member, the two members complexly intertonguing, but in the south-central outcrop area it is overlain by the calcisiltite and shale of the generally unfossiliferous Brannon Member (fig. 11).

The most common bedding assemblage in the Grier Limestone Member consists of sets, about 0.5 ft thick, of nodular-bedded, fossiliferous calcisiltite to very poorly sorted, fossiliferous calcarenite with minor shale partings, alternating with slightly irregular, 0.4-ft-thick beds of poorly sorted, fossiliferous calcarenite. Brachiopods and bryozoans are the most conspicuous fossils, but gastropods are common in some calcisiltites, and ostracodes, crinoids, pelecypods, and trilobites are also present. This member apparently was deposited in shallow, well-aerated, moderately agitated water of normal salinity. The nodular bedding is probably due to the activity of burrowing organisms. Cressman (1973, p. 19) estimated that the member was deposited in water 50 ft or less deep.

*Perryville Limestone Member.*—Cressman (1973, p. 23) defined the Perryville Limestone Member as the beds lying between the calcarenite of the Tanglewood Limestone Member below and the interbedded calcisiltite and shale of the Brannon Member above, in the southwestern part of the Lexington Limestone outcrop area (fig. 11).

The Perryville has been divided into three units. The basal unit, called the Faulconer Bed, consists of 40 ft of brownish-gray, fossiliferous, micritic limestone. Beds are about 0.5 ft thick, have rough surfaces, and show nodular internal structure upon weathering. The fauna of the Faulconer Bed consists of ostracodes, pelecypods, gastropods, brachiopods, bryozoans, crinoids, colonial corals, and stromatoporoids. The fossils show little breakage or abrasion, and no obvious sorting or orientation, and many are coated by encrusting algae (probably *Girvanella*).

The middle unit of the Perryville, called the Salvisa Bed, consists of 10 to 15 ft of interbedded light-gray to light-olive-gray micritic limestone and brownish-gray micritic limestone. Fossils are sparse in most places but may be abundant locally (for example, USGS 5015-CO, appendix); ostracodes are most common, and gastropods and pelecypods are scattered. The matrix is largely pelletal and is burrowed in many places.

The upper unit, the Cornishville Bed, is 2 to 10 ft thick and consists of mostly nodular bedded calcisiltite and fine-grained calcarenite containing abundant brachiopods and some bryozoans. The unit resembles the Grier Limestone Member and may be a tongue of that unit (Cressman, 1973, p. 28).

The Faulconer Bed was deposited in shallow, quiet water of normal marine salinity. The Salvisa Bed was deposited under quiet, perhaps more hypersaline conditions, as indicated by its more restricted fauna. The Cornishville Bed was deposited in an environment similar to that of the Grier Limestone Member (Cressman, 1973).

*Tanglewood Limestone Member.*—The Tanglewood Limestone Member is an extensive irregular body of bioclastic calcarenite that completely intertongues with other members of the upper Lexington Limestone and the Clays Ferry Formation (fig. 11). It is typically a crossbedded, phosphatic, pinkish-gray, medium-grained, well-sorted, bioclastic calcarenite in which whole fossils or large fossil fragments are rather uncommon. The unit ranges in thickness from 60 to 100 ft, the variation due to intertonguing with other members. The calcarenite consists largely of bryozoan, brachiopod, and crinoid fragments that are thought to have been transported from adjacent sites of accumulation of the Grier Limestone and Millersburg Members.

Crossbedding is common in the Tanglewood calcarenites. Harbar, Cressman, and Potter (1971) found these crossbeds to be bimodal, and interpreted them to be the result of tidal currents. Cressman (1973, p. 31, 32) interpreted the Tanglewood calcarenite body as a bank that stood above surrounding areas of the sea floor, with tidal currents producing migrating sandbars.

*Brannon Member.*—The Brannon Member consists of about 30 ft of interbedded calcisiltite and shale. Throughout most of its area of exposure, it is both overlain and underlain by the Tanglewood Limestone Member. In other areas, the Brannon lies on the Grier or Perryville Limestone Member, and is overlain by the Sulphur Well Member (fig. 11).

The interbedded calcisiltite and shale of the Brannon are present in nearly equal proportions, so that the member closely resembles the Logana Member. The calcisiltite is medium to light gray and generally occurs in smooth-surfaced tabular beds about 0.2 to 0.3 ft thick. The shale is calcareous and medium to dark gray. Fossils are sparse in the unit and less abundant than in the Logana Member; however, thin-shelled brachiopods are present on some bedding surfaces.

The Brannon weathers to a clayey soil containing abundant chert. Campbell (1898) placed the Brannon beds in what he called the Flanagan Chert because of the cherty float in residuum derived from this unit. McFar-

lan and White (1948, p. 1636) stated that the Flanagan Chert was mainly included in the Brannon Member. Recognizing what was meant by the term "Flanagan Chert" in the modern stratigraphic scheme is important because numerous type specimens of bellerophontids described by Ulrich and Scofield (1897) were cited as coming from that unit. Apparently, silicified beds at many different stratigraphic levels were erroneously called the Flanagan Chert. No monoplacophorans or bellerophontaceans were present in USGS silicified samples from the Brannon Member.

The Brannon apparently was deposited in an environment similar to that of the Logana Member, that is, in quiet water below wave base, where bottom conditions were generally inhospitable for life (Cressman, 1973, p. 37).

*Sulphur Well Member.*—The Sulphur Well Member consists of about 35 ft of mostly poorly sorted bryozoan calcirudite having a clay and silt-rich, calcitic to dolomitic matrix. Beds are lenticular and irregular, a few inches thick generally, and are separated by thin shale partings. Bryozoans are found throughout the unit, but are most abundant on bedding surfaces. Brachiopods are fairly common in some places.

The Sulphur Well Member in all places has a sharp planar contact with the underlying unit, which may be the Brannon, Tanglewood Limestone, or Grier Limestone Member (fig. 11). It is overlain by the Clays Ferry Formation, this contact being either sharp or gradational. Cressman (1973, p. 37) stated that the Sulphur Well and Grier Limestone Members were deposited under similar environmental conditions, that is, in moderately agitated, normal marine waters slightly below wave base.

*Stamping Ground Member.*—This member consists of about 15 ft of fossiliferous nodular limestone that apparently is entirely surrounded by the Tanglewood Limestone Member. The brachiopod *Rhynchotrema*, which is commonly silicified, is the most conspicuous fossil in the unit. At many localities, stromatoporoids are present directly above the Stamping Ground Member in the basal Tanglewood Limestone Member. Cressman (1973, p. 39) suggested that the environment of deposition was similar to that of the Millersburg Member, that is, shallow, moderately turbulent, normal marine water.

*Greendale Lentil.*—This unit is a 10- to 15-ft thick lentil surrounded entirely by the Tanglewood Limestone Member. It consists of 75 percent limestone and 25 percent shale. Bedding sets 0.2 to 1.5 ft thick consist of olive-gray to light-gray, fossiliferous, argillaceous calcisiltite in nodular beds separated by irregular shale partings and thin shale beds that alternate with 0.2- to 0.5-ft thick irregular beds of light-gray, coarse-grained, fossiliferous calcarenite. This lentil is restricted to parts

of the Georgetown and Lexington West quadrangles, in the area immediately northwest of Lexington, Ky.

*Devils Hollow Member.*—The Devils Hollow Member was described (McFarlan and White, 1948, p. 1640) at its type locality as consisting of 15 ft of coarse-grained, gastropod coquina overlain by 10 ft of micritic limestone containing ostracodes (resembling the Tyrone Limestone). These two rock types intertongue, and at some localities only one of the two types is present. The member is underlain conformably by the Tanglewood Limestone Member, and is overlain conformably by the Tanglewood calcarenites or by the nodular, fossiliferous, shaly limestone of the Millersburg Member (fig. 11).

The gastropod coquina is a coarse biosparite crowded with specimens of such species as *Sphenosphaera troosti*, *Tropidodiscus subacutus*, and *Lophospira medialis* (McFarlan and White, 1948, p. 1637). Locally, the coquina may be composed of brachiopods rather than gastropods; in either instance, the fossils may be silicified. The micritic limestone contains only ostracodes and sparse gastropods and pelecypods, which may be silicified.

The Devils Hollow Member seems to represent very shallow subtidal to intertidal environments of deposition, because sedimentary structures characteristic of tidal flats (that is, mud cracks, intraformational breccia) are not present in the micritic limestones. Cressman (1973, p. 41) suggested that these beds were deposited in shallow restricted lagoons of higher than normal salinity. The gastropod coquinas were bar and (or) beach deposits directly associated with these lagoons.

*Millersburg Member.*—The Millersburg Member is a 0- to 90-ft-thick body of nodular- and irregularly bedded, fossiliferous limestone and shale that completely intertongues with the Tanglewood Limestone Member and the overlying Clays Ferry Formation (fig. 11). The Millersburg limestone is gray to brownish gray and nodular bedded. It consists of whole and broken fossils in a silt- to clay-sized carbonate matrix. Shale makes up about one-third of the member. Characteristically, the Millersburg appears as limestone nodules several inches in diameter aligned along bedding and set in a matrix of calcareous shale. The nodular beds alternate with irregular beds of poorly sorted calcarenite. Both fragments and whole fossils of bryozoans, brachiopods, mollusks, and trilobites are abundant, and scattered stromatopora and colonial corals are present in several horizons.

The Millersburg is similar in lithology, bedding, and gross fossil content to the Grier Limestone Member, but it contains a greater proportion of shale. Both were deposited in shallow, well-aerated, moderately agitated, normal marine waters probably less than 15 m (meters) deep (Cressman, 1973, p. 43). The nodular bedding is probably due to active burrowing. The high shale content

of the Millersburg is the result of the increased supply of terrigenous sediment to the area during latest Middle Ordovician time, which is also reflected in the composition of the intertonguing Clays Ferry Formation.

#### UPPER ORDOVICIAN LITHOSTRATIGRAPHY OF KENTUCKY, SOUTHWESTERN OHIO, AND SOUTHEASTERN INDIANA

The tristate area surrounding Cincinnati, Ohio (Ohio-Indiana-Kentucky), exposes the type section for the Upper Ordovician (Cincinnatian Series) of North America. Traditionally, the Cincinnatian Series has been divided into three groups, which are now considered stages (fig. 12). These are, in ascending order, the Edenian, Maysvillian, and Richmondian Stages. The history of lithostratigraphic nomenclature for this region is extremely complex. Excellent summaries of this history have been given by Gutstadt (1958), Weiss and Norman (1960), and Weir and others (1984).

Throughout much of this century the basic stratigraphic scheme outlined by Patton, Perry, and Wayne (1953) and Caster, Dalve, and Pope (1955) has been used throughout the tristate region (fig. 12). However, more recent work has demonstrated that many of these traditional units were based more on paleontologic parameters than on lithologic parameters. Therefore, numerous new lithostratigraphic names have been proposed. These new classifications apply more or less to the three adjacent geographic areas: central Kentucky, southeastern Indiana, and southwestern Ohio-northern Kentucky (fig. 12). The change in nomenclature from central Kentucky to northern Kentucky and southwestern Ohio seems well warranted because of facies changes. The change in nomenclature in southeastern Indiana is due more to the crossing of State borders than to any change in the character of the strata. The application of some names coined for strata in northern Kentucky to strata in southwestern Ohio has not been satisfactorily confirmed by mapping in Ohio, but the general scheme seems to work (Gordon Weir, written commun., 1977). As is discussed below, some workers do not agree with this extension of the Kentucky nomenclature.

In central Kentucky, Upper Ordovician strata crop out around the perimeter of the Jessamine dome, outlining the Middle Ordovician strata previously discussed. Nearly all of the Ordovician strata to the north in the tristate area are Late Ordovician in age; exceptions are some exposures of the Point Pleasant Tongue of the Clays Ferry Formation along the Ohio River Valley.

The revision of stratigraphic nomenclature in these areas began in the early 1960's. Weiss and Sweet (1964) renamed the Eden Shale of northern Kentucky and

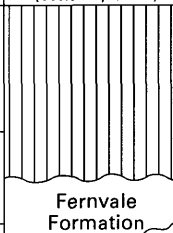
CINCINNATIAN LITHOSTRATIGRAPHIC UNITS												
SERIES	STAGES	OHIO-INDIANA-KENTUCKY (Caster, Dalve, and Pope, 1955)		SOUTHEAST INDIANA (Brown and Lineback, 1966)	SOUTHWEST OHIO (Weiss and Sweet, 1964; Ford, 1967)	NORTHERN KENTUCKY (Peck, 1966)	SOUTH-CENTRAL KENTUCKY (Weir and others, 1965)	CENTRAL TENNESSEE (Wilson, 1949)				
		Formations	Members									
CINCINNATIAN	Richmondian	Elkhorn		Whitewater Formation	Unnamed Units	Drakes Formation	Drakes Formation	Preachersville Member				
		U. Whitewater										
		Saluda				Saluda Formation						
		L. Whitewater										
		Liberty										
		Waynesville	Blanchester	Dillsboro Formation		Bull Fork Formation	Ashlock Formation	Rowland Member		Fernvale Formation		
			Clarkesville									
			Ft. Ancient									
		Arnheim	Oregonia									
		Sunset										
	Maysvillian	McMillan Formation	Mt. Auburn		Grant Lake Limestone			Fairview Formation	Reba Member		"Arnheim" Formation	
			Corryville						Terrill Member			
			Bellevue						Gilbert Member			
		Fairview Formation	Fairmount						Stingy Creek Member			Leipers Formation
			Mt. Hope						Tate Member			
	Edenian	Latonia Formation	McMicken	Kope Formation	Kope Formation	Kope Formation	Garrard Siltstone	Inman Formation				
			Southgate				Clays Ferry Formation	Catheys Formation				
			Economy									

FIGURE 12.—Cincinnatian lithostratigraphic units in Ohio, Indiana, Kentucky, and central Tennessee.

southwestern Ohio, calling it the Kope Formation (fig. 12). They argued that the term Eden has a stadial connotation.

In south-central Kentucky, Weir and Greene (1965) named the Clays Ferry Formation to replace the Edenian faunally based units such as the Cynthiana Formation and Million Shale, and retained usage of the late Edenian Garrard Siltstone. In the same area, Weir, Greene, and Simmons (1965) named the Calloway Creek Limestone, Ashlock Formation, and Drakes Formation for traditional Maysvillian and Richmondian units previously extended from the Cincinnati area on faunal bases (fig. 12).

Peck (1966) studied the Upper Ordovician strata in northern Kentucky along the eastern flank of the Cincinnati arch. He found it difficult to trace rock units above the Fairview Formation (early Maysvillian) from the type sections in the Cincinnati area to the Maysville, Ky., area. He concluded that these post-Fairview units had been previously identified in the Maysville area on faunal bases, and rejected the traditional units. He assigned strata previously called the Bellevue, Cor-

ryville, and Mt. Auburn Members of the McMillan Formation to the Grant Lake Limestone. Also, he assigned strata previously called the Arnheim, Waynesville, Liberty, and Whitewater Formations in that area to the Bull Fork Formation. Finally, Peck extended the Preachersville Member of the Drakes Formation (Weir and others, 1965) from south-central Kentucky to the Maysville area for the uppermost Ordovician strata, which had previously been assigned to the Whitewater and Elkhorn Formations.

Ford (1967) mapped Ordovician strata in the southwestern corner of Ohio, on the western side of Cincinnati. He recognized the Kope Formation, Fairview Formation, Miamitown Shale, and Bellevue Limestone as mappable units in the area (fig. 12). He did not address stratigraphy above the Bellevue Limestone. Pojeta (1979, fig. 2) extended the use of the Bull Fork Formation for post-Bellevue units in southwestern Ohio.

Brown and Lineback (1966) revised the Upper Ordovician lithostratigraphy of southeastern Indiana (fig. 12). They recognized the Kope Formation and proposed the name Dillsboro Formation for "the sequence of highly

fossiliferous argillaceous limestones and calcareous shales that lie between the shale of the Kope Formation and the dolomitic limestone of the Saluda Formation" (p. 1020). They continued recognition of the Saluda Formation and the Whitewater Formation for the latest Richmondian-age strata of the area. Shaver and others (1970) supported this classification, as did Gray (1972), who placed all the Cincinnati units in Indiana in the Maquoketa Group.

Hay, Pope, and Frey (1981) and Tobin (1982, 1986) have proposed Upper Ordovician lithostratigraphic classifications that apply to southwestern Ohio, southeastern Indiana, and adjacent northernmost Kentucky. Both classifications accept the Kope and Fairview Formations, and the Bellevue Limestone and Miamitown Shale as used by Ford (1967). However, the later Maysvillian- and Richmondian-age strata are classified quite differently.

Hay, Pope, and Frey (1981) introduced the Brookville Formation for limestone and shale wedges between the Bellevue Limestone and Whitewater Formation. They recognized four new members, as well as the Waynesville Shale and Liberty Limestone of the traditional classification. However, this classification has been outlined only in a guidebook, and is not valid according to the rules of the Code of Stratigraphic Nomenclature.

Tobin (1982, 1986) disagreed with the approach of most recent workers, who have chosen to combine the traditional stratigraphic units, which they believed to be faunally based, into larger units (for example, Brown and Lineback, 1966; Peck, 1966; Hay and others, 1981). Through references to original descriptions of the traditional stratigraphic units and extensive fieldwork, Tobin concluded that many of the traditional units were indeed valid. Tobin (1982, 1986) recognized three shallowing-upward carbonate sequences in the Cincinnati Series. These sequences are described below in ascending order.

Kope to Bellevue sequence.—In this sequence, the Kope represents an offshore facies, the Fairview a transitional facies, and the Bellevue a shoreface facies.

Corryville to Oregonia sequence.—In this sequence, the Corryville is an offshore facies, the Sunset is a transitional facies which contains the Mt. Auburn offshore bar facies, and the Oregonia is a shoreface facies.

Waynesville to Saluda sequence.—In this sequence, the Waynesville Shale represents an offshore facies, the Liberty Limestone is a transitional facies, the Whitewater Formation is a shoreface facies, and the Saluda Formation dolomite represents restricted lagoonal, intertidal and supratidal facies.

Tobin (1982) recognized all of these facies as formations. He stated that these facies built eastward down the paleoslope toward the Appalachian Basin. The diachronous nature of the Cincinnati units had been dem-

onstrated previously by conodont studies (Sweet, 1979, fig. 3). Viewing the Cincinnati Series in this way is a significant step toward understanding this important type section.

The most modern recognized stratigraphic classifications are used herein (fig. 12). The lithostratigraphy of Weir and Greene (1965) and Weir, Greene, and Simmons (1965) are used for south-central Kentucky. The units of Peck (1966) are used for north-central Kentucky. The units of Ford (1967) and Peck (1966) are used for southwestern Ohio and adjacent northernmost Kentucky. Weir and others (1984) documented and summarized the Upper Ordovician stratigraphy of Kentucky. The classification of Brown and Lineback (1966) is used for southeastern Indiana. The distribution of these stratigraphic units in the tristate area is shown in figure 5.

The revision of the traditional Cincinnati lithostratigraphic classification seems to have been warranted in most cases. However, the complete abandonment of the traditional units seems unwise. The paleontological and paleoecological knowledge accumulated through years of work in this type section is based on the traditional classification. If this wealth of data is to be retained and used effectively in both understanding the type section and extrapolating to other areas, the traditional units must be retained in some form. Therefore, these traditional units are used herein as informal biofacies units. For example, in this paper, *Cyrtolites* (*Cyrtolites*) *hornyi* n. sp. is said to come from the Liberty biofacies of the Dillsboro Formation in southeastern Indiana.

The lithostratigraphy of the tristate region is described in three sections: south-central Kentucky, north-central Kentucky and southwestern Ohio, and southeastern Indiana. Formations are considered in ascending order for each area within the region.

#### UPPER ORDOVICIAN LITHOSTRATIGRAPHY OF SOUTH-CENTRAL KENTUCKY

As a result of the joint U.S. Geological Survey-Kentucky Geological Survey mapping program of the State of Kentucky, Weir and Greene (1965) and Weir, Greene, and Simmons (1965) completely revised the Upper Ordovician lithostratigraphic classification for south-central Kentucky (fig. 12). Weir and others (1984) documented and summarized previous work. Except where noted, the descriptions given below are drawn from those works.

#### CLAYS FERRY FORMATION

The Clays Ferry Formation was named by Weir and Greene (1965) to encompass strata previously included in the Cynthiana Formation, Fulton Shale, and Million Shale as used by Foerste (1906) and Palmquist and Hall



(1961). This 120 to 220 ft of interbedded limestone and shale straddles the Middle-Upper Ordovician boundary (fig. 5). To the south it intertongues with the upper members of the Lexington Limestone, but to the north it becomes younger and intertongues with the shales of the Kope Formation in north-central Kentucky (figs. 5, 11).

Limestone makes up 30 to 60 percent of the Clays Ferry Formation. Beds are even and 1 to 6 in thick. The limestone varies from medium- to dark-gray, argillaceous calcisiltite to medium-gray brachiopodal limestone to medium-gray crinoidal calcarenite. The calcisiltite is sparsely fossiliferous and contains mainly crinoidal fragments and some gastropods. The brachiopodal limestone is characterized by abundant *Rafinesquina*, some of which are shingled, as well as by *Sowerbyella* and *Dalmanella*, all packed in a mud matrix. Bryozoans are also common.

Shale makes up 30 to 60 percent of the formation. It is generally greenish to olive gray, and is present in distinctly laminated sets 1 to 12 in thick. Fossils generally are sparse in these shales, though bryozoans are common at some locations.

Siltstone makes up 5 to 10 percent of the unit, occurring mainly in the upper part. It is present mostly in 1- to 3-in even beds in which fossils are sparse. This lithology resembles the Garrard Siltstone, which overlies the Clays Ferry in south-central Kentucky.

*Point Pleasant Tongue*.—Along the Ohio River Valley, the Lexington Limestone and Kope Formation are separated by 100 ft of limestone and shale interbedded in nearly equal proportions (fig. 5). This unit's even bedding and regular interbedding of limestone and shale are reminiscent of the Clays Ferry Formation, but in the upper part are beds as thick as 10 ft that consist of crossbedded calcarenite.

This unit has a complex nomenclatural history. Until recently it had been assigned to the Cynthiana Formation, but the USGS mapped it as the Point Pleasant Formation (Weiss and others, 1965; Cressman, 1973). Now the unit is considered the Point Pleasant Tongue of the Clays Ferry Formation (Swadley, 1975), and is correlated with the upper Lexington Limestone and lower Clays Ferry (Cressman, 1973; Sweet, 1979, fig. 3). It is overlain by the Kope Formation.

Cressman (1973, p. 45) suggested that the finer grained, less fossiliferous parts of the Clays Ferry Formation were deposited in quiet water at least 80 ft deep, similar to the depositional environments of the Logana and Brannon Members of the Lexington Limestone. The more fossiliferous parts of the formation probably were deposited at shallower depths, but currents were never strong enough to remove fine clastics or to break up the skeletal material effectively. The Point Pleasant Tongue was, at least in its upper portion, a much shallower

facies, with thick crossbeds indicating rather high energy conditions. It is noteworthy that these upper Point Pleasant beds are directly overlain by Kope shales characterized by a trilobite-crinoid fauna. This situation apparently reflects a rapid transgression at the end of Point Pleasant deposition.

#### GARRARD SILTSTONE

The Garrard Siltstone is a 10- to 100-ft-thick unit of chiefly limy siltstone with minor thin lenses of mudstone and limestone. Most beds are 6 to 24 in thick, and many are laminated. Ball-and-pillow structures are common. Fossils, except for brachiopods, are scarce in the thin limestone lenses. Bryozoans are also known in the unit.

The Garrard is late Edenian in age, correlating with the upper Kope Formation to the north (figs. 5, 12). It is conformable with the underlying Clays Ferry Formation and overlying Calloway Creek Limestone. Ford (1968, p. 1784) suggested that the northward decrease in grain size from the Garrard to the Kope implied tectonic control of sedimentation from a southerly source.

#### CALLOWAY CREEK LIMESTONE

This early Maysvillian-age unit ranges from 80 to 130 ft thick in south-central Kentucky. It consists of 70 to 80 percent fine- to medium-grained, thin-bedded, gray limestone, 15 to 25 percent greenish-gray calcareous shale, and about 5 percent calcareous siltstone. Fossils are abundant, with brachiopods and bryozoans most conspicuous.

The Calloway Creek Limestone is transitional with both the underlying Garrard Siltstone and the overlying Ashlock Formation (figs. 5, 12). It grades northward into the Fairview Formation, which is similar in lithologic and faunal character but is much thicker bedded.

#### ASHLOCK FORMATION

The Ashlock Formation is a 125- to 145-ft-thick unit of late Maysvillian and early Richmondian age in south-central Kentucky (figs. 5, 12). Weir, Greene, and Simmons (1965) divided the formation into five members, which are described in ascending order below.

*Tate Member*.—The Tate was originally described by Foerste (1912) as a member of the McMillan Formation. This 30- to 80-ft-thick unit consists of greenish-gray, laminated to thin-bedded, sparsely glauconitic, calcareous to dolomitic mudstone that commonly grades into an argillaceous limestone at the top. Fossils are uncommon, except for a silicified brachiopod-bryozoan assemblage in the Back Bed, a coarse-grained, silty limestone present 5 to 15 ft above the base of the member. This member belongs to Weir and Peck's (1968, p. 168) dolomitic



mudstone lithofacies, which was thought to have been deposited in very shallow, quiet, subtidal to tidal flat environments.

*Stingy Creek Member.*—This term replaced the name “Mt. Auburn Member of the McMillan Formation” in south-central Kentucky. The Stingy Creek is a 5- to 15-ft-thick unit of gray limy siltstone and silty limestone that is obscurely thin bedded and contains an abundance of brachiopods and bryozoans. This member belongs to Weir and Peck’s (1968) nodular-bedded, fossiliferous limestone and mudstone lithofacies, which was deposited under somewhat higher energy conditions than was the Gilbert Member, possibly in wave-agitated shoals on a sloping shelf.

*Gilbert Member.*—The Gilbert was also recognized by Foerste (1912) as a member of the McMillan Formation. It consists of bluish- to olive-gray, fine- to medium-grained limestone occurring in thin, wavy beds. A brachiopod-bryozoan fauna is common and well preserved. The unit is 10 to 20 ft thick. The limestone beds, each a few inches thick, are generally separated by gray limy siltstone partings less than 1 in thick. This member belongs to Weir and Peck’s (1968) micrograined limestone lithofacies, which was deposited in shallow, quiet lagoons.

*Terrill Member.*—This term replaced the name “Sunset Member of the Arnheim Formation.” The unit consists mainly of greenish-gray, laminated, limy or dolomitic mudstone. Bedding surfaces characteristically display ripple marks and mud cracks, and fossils are rare. However, the basal few feet of the 5- to 15-ft-thick member commonly contains a rich brachiopod-bryozoan fauna. The Terrill belongs to Weir and Peck’s (1968) dolomitic mudstone lithofacies, which was probably deposited mainly on broad tidal flats.

*Reba Member.*—This unit was previously known as the Oregonia Member of the Arnheim Formation in south-central Kentucky. The 10- to 25-ft-thick member is made up of a basal micrograined limestone overlain by medium-grained limestones that become more silty and argillaceous near the top. The basal unit is essentially barren of fossils, except for some ostracodes and trace fossils. The overlying thin-bedded limestones contain a fairly abundant brachiopod-bryozoan fauna. This member belongs to the same lithofacies as the Stingy Creek Member.

#### DRAKES FORMATION

Weir, Greene, and Simmons (1965, p. 16) named the Drakes Formation for Richmondian-age strata in south-central Kentucky formerly called the Waynesville, Lib-

erty, and Whitewater beds (fig. 12). The formation consists of 120 to 150 ft of grayish-green, dolomitic or calcareous, silty mudstone to argillaceous, finely crystalline dolomite or dolomitic limestone.

On the southern and eastern sides of the Lexington dome in central Kentucky, the formation is divisible into the Rowland and overlying Preachersville Members. On the western side of the dome, the formation is divisible into (ascending) the Rowland, Bardstown, and Saluda Dolomite Members.

*Rowland Member.*—This member mainly encompasses strata assigned earlier to the Waynesville Limestone. The 40- to 60-ft-thick member consists chiefly of grayish-green, sparsely glauconitic, dolomitic or calcareous, silty mudstone. The mudstone is obscurely bedded, and many of the bedding surfaces are covered by ripple marks and mud cracks. Fossils are rare to absent. The Rowland belongs to Weir and Peck’s (1968) dolomitic mudstone facies, and is thought to have been deposited on extensive tidal flats.

*Preachersville Member.*—Strata included in this member previously were assigned to the Liberty and Whitewater Formations. The 55- to 95-ft-thick unit is similar to the underlying Rowland Member, but it contains 10 to 20 percent argillaceous, finely crystalline dolomite or dolomitic limestone. Locally, the basal 6–8 ft is a limestone rich in colonial corals and stromatoporoids known as the Otter Creek Coral Bed (Simmons and Oliver, 1967). Peterson (1970) correlated these beds with coral-rich layers in the Bardstown Member on the western side of the Cincinnati arch.

*Bardstown Member.*—This 12- to 40-ft-thick member overlies the Rowland Member and underlies the Saluda Dolomite Member on the western side of the Cincinnati arch in Kentucky. It consists of about 90 percent gray to greenish-gray, fine- to medium-grained limestone containing abundant whole or fragmented fossils. These beds are 1 to 8 in thick. About 10 percent of the member is bioclastic to coquinoïd limestone. Peterson (1970) described two to four layers in the middle two-thirds of the member that contain concentrations of colonial corals.

*Saluda Dolomite Member.*—This member reaches a maximum thickness of 75 ft in Kentucky on the western side of the Cincinnati arch. Northward in Indiana, it is as much as 60 ft thick and is recognized as a formation. The Saluda is a dolomite or calcareous dolomite, and is distinguished from the underlying Bardstown Member by the abrupt change from the fossiliferous limestone of the latter to a mainly unfossiliferous dolomite. Hatfield (1968) described the Saluda in Indiana in detail. His work is discussed later, in the section on Indiana Upper Ordovician lithostratigraphy.

UPPER ORDOVICIAN LITHOSTRATIGRAPHY OF  
NORTH-CENTRAL KENTUCKY AND  
SOUTHWESTERN OHIO

It was in this area, particularly in the vicinity of Cincinnati, Ohio, that the stratigraphic units of the traditional classification mainly were originally described (Caster and others, 1955) (fig. 12). The stratigraphic revisions of Peck (1966), Ford (1967), and Pojeta (1979) are used here (fig. 12).

KOPE FORMATION

The Kope Formation is Edenian and locally early Maysvillian in age (fig. 5). It grades southward into the Clays Ferry Formation (fig. 5). It lies conformably on the Point Pleasant Member of the Clays Ferry Formation east and west of Cincinnati, but this contact becomes unconformable northwestward (Rooney, 1966; Gray, 1972). The Kope is overlain conformably by the Fairview Formation in Ohio and Kentucky, and the two inter-tongue in some areas (Sweet, 1979, fig. 3). The Kope ranges in thickness from 150 to 280 ft over the Indiana-Ohio-Kentucky tristate outcrop area.

The Kope Formation is 70 to 80 percent shale, with some shales being more than 3 ft thick. The shales are interbedded with limestones and minor siltstone beds. Kope limestones are thin to medium bedded and generally contain whole or broken fossils in varying numbers. The shales also are fossiliferous in many places. The fauna is dominated by brachiopods and bryozoans, but crinoids, trilobites, and mollusks are characteristic of some parts of the section (Weiss and others, 1965).

The name Kope Formation was proposed by Weiss and Sweet (1964) to replace the term "Eden shales," as "Eden" has stadial connotations. The traditional four-part subdivision of the Eden shales (Nickles, 1902) was rejected by Weiss and others (1965) because the four "members" were based largely on biofacies exposed in the immediate vicinity of Cincinnati and could not be traced consistently into surrounding areas. In this four-part scheme, the basal Fulton beds consist of 5 ft of dark shales characterized by the presence of the trilobite *Triarthrus eatoni*. The overlying Economy Shale was characterized by the trilobite *Cryptolithus* and by crinoids and delicate brachiopods. The upper Southgate and McMicken "members" contained more and thicker bedded limestones, some characterized by ripple marks and by robust brachiopods and bryozoans. This sequence reflects shallowing upward toward higher energy Fairview conditions.

Weiss and others (1965, p. 49, 50) concluded that the Kope and Clays Ferry shales and siltstones were derived from the southeast and east, based on percentage of clastics, grain-size increase, and paleogeography. Ford (1968) suggested a southerly source area.

Weiss and others (1965) postulated that clastic mud accumulated in depressed areas on a sea floor of low, broad relief, while limestones were deposited on the tops and flanks of topographically higher areas, with skeletal debris occasionally being swept into adjacent lows. They estimated an average depth of accumulation of 25 m.

Anstey and Fowler (1969) also studied Kope depositional environments. They estimated, on the basis of bryozoan growth forms, that water depth averaged more than 20 m. They claimed that the Kope limestones formed by the growth of benthonic communities dominated by bryozoans, on slightly elevated areas of the sea floor. They also outlined an upward shallowing of water depth, on the basis of an upward increase in limestone content and fauna abundance, an upward decrease in the wave length of megaripples, and the presence of oncolites and mud cracks in the overlying Dillsboro Formation in Indiana.

FAIRVIEW FORMATION

The Maysvillian-age Fairview Formation ranges from 70 to 110 ft in thickness over southwestern Ohio and northern Kentucky (fig. 12). The formation consists of interbedded limestone, shale, and minor siltstone. Limestone makes up 50 to 60 percent of the unit; it consists of medium- to coarse-grained skeletal limestone in the lower part and fine-grained, silty, sparsely fossiliferous limestone in the upper part. Shale makes up 35 to 40 percent of the formation, occurring as thin beds or partings between the limestones. Siltstone makes up 5 to 15 percent of the unit, occurring as thin to medium beds that become more abundant upward (Peck, 1966).

The Fairview was originally referred to as the "Hill quarry beds" (Pojeta, 1984) in the vicinity of Cincinnati, where it was extensively quarried. Nickles (1902) named the Fairmont (*Dekayia aspera*) beds and the underlying Mount Hope (*Amplexopora septosa*) beds, which were later combined as members of the Fairview Formation by Bassler (1906). Peck (1966, p. B5) felt that these two members were based more on faunal than lithologic characters, and did not favor their use outside the immediate type area.

Ford (1967, p. 935) postulated that the coarse, fragmental limestones of the Fairview were formed around submarine topographic highs. He envisioned a situation in which waves and currents broke and sorted skeletal material on the highs, and deposited progressively finer skeletal debris in progressively deeper surrounding areas, where fine clastics were also settling. The positions of these highs and intervening depressions migrated laterally through time.

The Fairview Formation lies conformably on and intertongues with the Kope Formation (fig. 5), and

locally is as old as Edenian in age. In the Cincinnati area, it is conformably overlain by two local units, the Miami town Shale and Bellevue Limestone. Elsewhere, it is conformably overlain by the Grant Lake Limestone. The Fairview grades westward into the Kope and Dillsboro Formations of Indiana, and southward into the Ashlock Formation of Kentucky (fig. 12).

#### BELLEVUE LIMESTONE

Ford (1967, p. 932-934) redefined the Bellevue Limestone as a sequence of medium- to thin-bedded, coquinoïd limestones, with minor interbedded shales present in the vicinity of Cincinnati (fig. 12). Its maximum known thickness is 25 ft at the type locality.

Ford (1967) noted that the formation had a limited areal extent, and that it thickened south and southeast of Cincinnati. He suggested that the Bellevue might be a northwestward tongue of the Grant Lake Limestone, and Luft (1971) mapped it as such (fig. 5). Tobin (1982) considered the Bellevue to be the top unit of a shallowing-upward carbonate sequence which began with Kope deposition.

#### MIAMITOWN SHALE

Ford (1967) proposed the Miamitown Shale for 5 to 35 ft of shale and mudstone with widely spaced limestone interbeds that conformably overlies the Fairview Formation in the vicinity of Cincinnati (fig. 12). The limestones in this unit are commonly nodular bedded and contain a characteristic gastropod-pelecypod assemblage that includes *Lophospira*, *Cyclonema*, and *Ambonychia*.

Ford (1967) suggested that the Miamitown Shale reflects a return to conditions of Kope deposition. Considering the Miamitown's relatively small areal extent, its position between the rather high energy Fairview and Bellevue limestones, and the presence of a predominantly molluscan fauna, it seems improbable that the Miamitown was deposited in water as deep as Kope sediments. The Miamitown may reflect a period of increased fine clastic influx into a protected lagoonal setting.

#### GRANT LAKE LIMESTONE

The Grant Lake Limestone is Maysvillian-Richmondian in age and is distributed through northern Kentucky and parts of adjacent southwestern Ohio (fig. 12). The Bellevue Limestone of the Cincinnati area is thought to be a northern tongue of the Grant Lake (fig. 5) (Ford, 1967; Luft, 1971). The formation is conformable with the underlying Fairview Formation and overlying Bull Fork Formation. It grades westward into the Dills-

boro Formation of Indiana, and southward into the Calloway Creek Limestone and Ashlock Formation (fig. 5).

Peck (1966) named the Grant Lake Limestone for strata in the Maysville, Ky., area that had previously been assigned to the Bellevue, Corryville, and Mt. Auburn Members of the McMillan Formation. He described the Grant Lake as chiefly irregularly bedded argillaceous limestone and minor interbedded calcareous shale. Limestone makes up 70 to 90 percent of the unit, and is mainly gray with olive-gray mottling, micrograined to medium grained, argillaceous, and very fossiliferous. Some well-sorted, fine- to coarse-grained, bioclastic limestones are present locally. The fauna is dominated by brachiopods and bryozoans, but gastropods, cephalopods, pelecypods, crinoids, trilobites, and ostracodes are common locally.

The formation belongs to Weir and Peck's (1968) nodular-bedded, fossiliferous limestone and mudstone lithofacies, which they regarded as representing a relatively high energy shelf environment, such as wave-agitated shoals (Pojeta, 1979).

#### BULL FORK FORMATION

Peck (1966) named the Bull Fork Formation for strata previously called Arnheim, Waynesville, Liberty, and Whitewater Formations in the Maysville, Ky., area. The unit was mapped in north-central Kentucky on the eastern side of the Cincinnati arch (fig. 12). Pojeta (1979, fig. 2) extended its use into southwestern Ohio to include strata above the Bellevue Limestone that Ford (1967) had left unnamed.

The Bull Fork Formation is 200 ft thick in its type area. It consists of interbedded limestone and shale. The shale content gradually increases from 20 percent near the base to about 80 percent in the upper part, and is mainly calcareous, medium gray to greenish gray, and fissile to poorly fissile. The formation contains three main types of limestone. The most common type, which accounts for 50 to 70 percent of the total limestone, is gray, with some olive-gray mottling, and has fine- to medium-grained matrix encasing medium- to very coarse grained fossil fragments. This type of limestone is evenly to irregularly bedded, with beds 1 to 8 in thick, and in some locations has large ripple marks on upper bed surfaces. The second limestone type, which makes up 5 to 40 percent of the limestone, consists of 1- to 8-inch-thick, even beds composed of olive-gray, microgranular limestone containing sparse fossil fragments. The third limestone type, which makes up 5 to 30 percent of the limestone, is medium- to bluish-gray, fine- to coarse-grained, well-sorted, bioclastic limestone. This limestone type is present in 2- to 18-in-thick, even beds that display

crossbedding in many places. Brachiopods and bryozoans are the dominant faunal elements, but solitary and colonial corals, gastropods, cephalopods, pelecypods, crinoids, trilobites, and ostracodes are common locally.

The Bull Fork belongs to Weir and Peck's (1968) planar-bedded, fossiliferous limestone and mudstone lithofacies. This lithofacies is believed to represent a deeper, more protected environment than the nodular-bedded limestone and mudstone lithofacies (Pojeta, 1979, p. A6).

#### DRAKES FORMATION

The only part of the Drakes Formation present in this area is 25 to 30 ft of the Preachersville Member (fig. 12). The unit thickens southward toward its type area in south-central Kentucky (Weir and others, 1965).

The Preachersville Member in northern Kentucky consists of calcareous to dolomitic mudstone and minor interbedded dolomitic limestone and dolomite. The mudstone makes up 90 percent of the unit. It is mainly grayish green, but it becomes reddish purple locally near the top. It is thin bedded, fissile to blocky, and locally silty. The dolomitic limestone and dolomite are gray to brown, fine to medium grained, and argillaceous to silty, and occur as thin lenses and irregular beds. Megafossils are sparse and poorly preserved (Peck, 1966, p. B22).

The Preachersville is generally overlain unconformably by the Lower Silurian Brassfield Formation, or by even younger units, in different areas.

#### UPPER ORDOVICIAN LITHOSTRATIGRAPHY OF SOUTHEASTERN INDIANA

The Point Pleasant Tongue of the Clays Ferry Formation is exposed at a few localities along the Ohio River in southeastern Indiana (Brown and Anstey, 1968) and across the river in Kentucky (Swadley, 1969), where it is directly overlain by the Kope Formation. The contact is well defined by the change from the mud-free bioclastic limestone of the Point Pleasant to the argillaceous limestones and shales of the Kope.

Rooney (1966) described an erosional unconformity at the top of the "Trenton" in all but extreme southwestern Indiana. He delineated a northeast-southwest hinge line that ran from the Findlay arch in Ohio to the Ozark dome in Missouri. Uplift of the area northwest of this hinge line at the end of "Trenton" deposition culminated in the emergence of a broad plateau, while deposition remained continuous southeast of the hinge line (Rooney, 1966, figs. 1-9). The plateau was transgressed in Edenian time by Kope muds. The unconformable contact is marked by truncation of "Trenton" beds, karst solution features, and concentrations of pyrite, angular chert, phosphatic grains, and carbonate breccia.

The Kope Formation was discussed previously, so a detailed description is not necessary here. However, some local features are noted below. Discussed in more detail are the younger Ordovician units recognized in Indiana: the Dillsboro, Saluda, and Whitewater Formations.

#### KOPE FORMATION (INDIANA)

Brown and Lineback (1966, p. 1020) extended the use of this formational name into Indiana from the type section in the Maysville area of Kentucky and Ohio, which was described by Weiss and Sweet (1964) (fig. 12).

The Kope thickens northward in southeastern Indiana from 220 ft in outcrop to 550 ft in the subsurface in Wayne County. It overlies the Point Pleasant Tongue conformably in extreme southeastern Indiana (Swadley, 1969), where the pre-Kope thins northward in concert with the Kope thickening (fig. 5). Brown and Lineback (1966) suggested that this might reflect a facies relationship.

In Indiana, the Kope Formation consists mainly of bluish- to brownish-gray clay-shale, with only 5 percent limestone, most of which is present in the upper one-third of the unit. The limestone generally is fossiliferous and occurs as rather discontinuous beds. The Kope is overlain conformably by the Dillsboro Formation in Indiana. The contact is marked by a much lower percentage of limestone in the Kope.

#### DILLSBORO FORMATION

Brown and Lineback (1966, p. 1020) named the Dillsboro Formation for "the sequence of highly fossiliferous argillaceous limestones and calcareous shales that lie between the shales of the Kope Formation and the dolomitic limestone of the Saluda Formation" in southeastern Indiana (fig. 12). The formation is Maysvillian and early Richmondian in age. It was proposed to take the place of the biofacies units of traditional usage (Patton and others, 1953). The replaced units were, in ascending order, the Mount Hope, Fairmount, Bellevue, Corryville, Mount Auburn, Arnheim, Waynesville, and Liberty Formations. It is recommended here that these units continue to be cited as informal biofacies units within the Dillsboro, in order to retain paleontological information for paleoecological and biostratigraphic purposes.

The Dillsboro contains about 30 percent limestone and 70 percent shale. Shale becomes more predominant southward in the lower part of the formation. Limestones are variable, but are mainly argillaceous and contain an abundant fossil fauna. Brachiopods and bryozoans are most conspicuous, but various mollusks, arthropods, and echinoderms are common locally.

Pojeta (1979, p. A7) noted that much of the Dillsboro is lithologically and faunally similar to the Bull Fork Formation. The Bull Fork is a direct lateral equivalent of the upper Dillsboro (Sweet, 1979, fig. 3), but the name changes going across State borders from Ohio-Kentucky to Indiana (fig. 5).

#### SALUDA FORMATION

The Richmondian-age Saluda Formation is a broad, lens-shaped unit distributed through southeastern Indiana and extending into adjacent southwestern Ohio and northern Kentucky (figs. 5, 12). In Indiana it lies conformably between the Dillsboro and Whitewater Formations, although where the Whitewater has been removed by erosion the Lower Silurian Brassfield Formation lies on the Saluda unconformably. In Ohio the Saluda has generally been considered a thin (6-ft-thick) member of the Whitewater Formation, separating the upper and lower members of that formation (Caster and others, 1955). In Kentucky, Weir, Greene, and Simmons (1965) made the Saluda a member of the Drakes Formation along the western flank of the Cincinnati arch (see discussion of lithostratigraphy of central Kentucky). The Saluda Formation of Indiana has been described in detail by Hatfield (1968). The formation is composed mainly of dolomitic mudstone, but it also contains a coral-rich zone at the base and a coral-stromatoporoid-rich zone just above the top of the formation.

The basal coral zone is composed of large heads of the colonial corals *Tetradium* and *Favistella* in a matrix of dolomitic limestone, skeletal-micritic limestone, or calcareous shale. The zone ranges from 2 to 12 ft thick and may be present within either the Saluda or Dillsboro formation or may overlap the boundary between them. An upper *Tetradium*-stromatoporoid zone lies just above the Saluda in the lowermost Whitewater Formation.

The Saluda itself is mainly calcitic dolomite that in many places exhibits laminations, mud cracks, and small ripple marks. Ostracodes are the only common fossils. Beds of more bioclastic limestone or shales are present locally.

Hatfield (1968) concluded that the Saluda was deposited in a broad, shallow lagoon enclosed by broad, low banks of corals. Dolomite content increases toward the interior of this lagoon. Hatfield interpreted bioclastic limestones and shales as storm deposits washed into the lagoon. Evidence suggests that water depth in the lagoon was usually a few inches to a few feet, and that salinities were above normal.

#### WHITewater FORMATION

The Whitewater Formation was originally named by Nickles (1903). As currently recognized, the formation

includes the Elkhorn Formation of other classifications (Utgaard and Perry, 1964; Brown and Lineback, 1966; Shaver and others, 1970).

The Whitewater is the youngest Richmondian-age formation in the Cincinnati type section (fig. 12). It conformably overlies the Saluda Formation, and is unconformably overlain by either the Lower Silurian Brassfield Formation or the Middle Silurian Osgood Formation. In general, the Whitewater contains a higher percentage of limestone than do the strata beneath the Saluda.

The Whitewater consists of various types of limestone interbedded with calcareous shales. The limestones include thin-bedded, argillaceous, fossiliferous limestone, thin-bedded ostracodal limestone, medium-bedded, relatively unfossiliferous limestone, medium-bedded limestone containing burrows, and rubbly-weathering, argillaceous limestone (Brown and Lineback, 1966, p. 1022). Because the Whitewater thickens in concert with Saluda thinning, the two are thought to be facies of one another. The Whitewater is generally believed to reflect the shallowing upward associated with the Ordovician-Silurian unconformity. The fauna of the Whitewater is dominated by a brachiopod-bryozoan assemblage, and locally is also rich in mollusks.

#### MATERIAL AND PRESERVATION

The silicified collections that constitute the core of this study were made mostly between 1961 and 1972 as part of the joint geologic mapping project of the State of Kentucky undertaken by the U.S. Geological Survey and the Kentucky Geological Survey. Nearly 1,100 fossil collections were made during the mapping project, of which more than 200 contained silicified fossils. Altogether, almost 36,000 pounds of limestone containing silicified fossils were collected. The Lexington Limestone was found to have the most widespread silicification, both stratigraphically and geographically, and this unit accounts for 116 of the silicified fossil collections. Twenty-five silicified collections were made from the High Bridge Group, and 64 silicified collections were made from rock units above the Lexington Limestone. Pojeta (1979, p. A15-A19) described these collections and the methods by which the silicified fossils were etched from the bulk limestone samples.

Other specimens described herein came primarily from museum collections. Examined were collections from the U.S. National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.; the American Museum of Natural History (AMNH), New York, N.Y.; the University of Chicago (UC) Walker Museum (collections now at the Field Museum of Natural History,

Chicago, Ill.); and the geology museums of the University of Cincinnati (UCGM), Cincinnati, Ohio, and Miami University (MU), Oxford, Ohio. The type materials for most of the species described herein were examined, and many were photographed for the first time. A small proportion of specimens studied were new collections made by the author.

The symmetrical univalved mollusks described herein occur in five different modes of preservation: (1) internal molds (pl. 3, figs. 4–6), (2) external molds (pl. 2, figs. 4, 5), (3) composite molds (pl. 24, figs. 1–5) (McAlester, 1962), (4) calcitic casts or replicas (pl. 7, figs. 11–16), some apparently coated by micrite envelopes (Bathurst, 1966), and (5) silicified casts or replicas (pl. 25, figs. 1–14). The first four of these modes of preservation are prevalent in the interbedded shales and limestones of the Cincinnati Series. However, the vast majority of specimens known from the limestones of the Lexington Limestone and High Bridge Group in central Kentucky and the Stones River and Nashville Groups of central Tennessee are silicified replicas.

Generally, the aragonitic shells of mollusks are dissolved soon after burial, leaving only internal and (or) external molds. Therefore, calcitic replicas were the least common preservational mode encountered. However, these aragonitic shells occasionally were replaced by calcite. Probably more common are calcitic specimens preserved by micrite envelopes (Bathurst, 1966) produced by algal borings into the mollusk shells after the death of the individuals. After the algal filaments died and decayed, micritic aragonite filled the borings, forming a micrite envelope that preserved the outer form of the original shell.

Many internal molds of mollusk fossils also retain the markings of the shell exterior. McAlester (1962) proposed that such composite molds resulted from the early dissolution of the aragonitic mollusk shells while the enclosing matrix was still in a plastic state. After dissolution, compaction of the sediment imprinted the external mold on the surface of the internal mold. The interpretation of internal and composite molds must be done with care. Many molds are distorted by compaction, and their size is generally much smaller than the original shell, with shrinkage of up to 40 percent of original size known (McAlester, 1962; Basan and Frey, 1982).

As noted above, nearly all fossil mollusks from the Middle Ordovician strata of the Cincinnati arch province described herein are silicified. The source of silica for these silicified fossil horizons may have been volcanic ash falls or siliceous skeletal material in the sediment. Laufeld and Jeppson (1976) made conclusions of broad application in their study of bentonites and silicified fossil horizons in the Silurian strata of Gotland. They reported that the Gotland silicified fossil horizons were generally

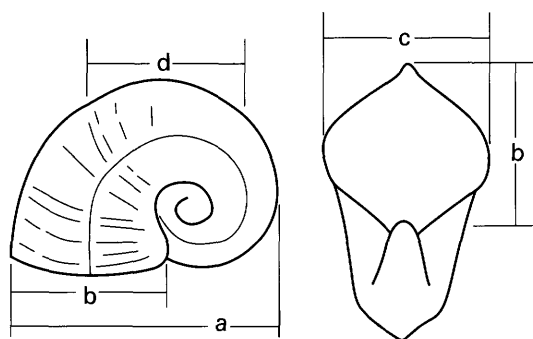
restricted to fairly thin stratiform levels. They found that in most silicified horizons only the skeletal material was silicified, not the matrix. They noted that many of these silicified fossil horizons almost certainly were caused by bentonite layers that were deposited in adjacent quieter water environments. Finally, they agreed generally with other studies of silicified faunas about the sequence of silicification by taxonomic groups and shell mineralogy (Hintze, 1983; Newell and others, 1953; Dapples, 1967; Cooper and Grant, 1972). The low-Mg calcite skeletons of bryozoans, brachiopods, and corals are most susceptible to replacement by silica, followed by high-Mg calcite groups, such as crinoids and ostracodes, and aragonite groups, such as gastropods and pelecypods.

The distribution, taphonomy, and diagenesis of the Cincinnati arch Middle Ordovician silicified fossil horizons have not yet been analyzed in detail, but some generalizations from observations are possible. As noted for many other such occurrences (Laufeld and Jeppson, 1976), the Kentucky silicified fossil horizons appear to be restricted to fairly thin stratiform levels. However, most silicified fossil horizons are not known to be associated with bentonite seams. There are various grades of silicification among the Kentucky specimens. Some, particularly those that weathered out of the limestones naturally, are hard and durable; others are brittle and fragile, and still others are coarsely crystalline and friable. Among symmetrical univalved mollusks, correlation between taxa and grade of preservation was observed, and it is concluded that the preservational differences are strictly diagenetic. Some specimens seem to have layers of silicification that peel away like an onion skin. This might reflect differential silicification of shell layers. Detailed analyses of these different patterns of silicification are needed, such as those of Permian silicified fossil assemblages from Wyoming by Boyd and Newell (1972) and Schmitt and Boyd (1981).

## MEASUREMENTS

When sufficient material was available, series of measurements were made. These measurements are listed with the descriptions of the individual species in the section on "Systematic Paleontology." The orientations of the most common measurements are shown in figure 13. These measurements were shell length, aperture length, aperture width, and umbilical diameter. Other common measurements were ventral width, posterior width, and dorsal width. These latter measurements recorded the width of the body whorl at points evenly spaced around the coiled shell in order to assess rate of whorl expansion.

There is bound to be some error in many of the measurements because of the nature of the fossil mate-



## EXPLANATION

- a — Shell length  
b — Aperture length  
c — Aperture width  
d — Umbilical diameter

FIGURE 13.—Common measurements made on fossil specimens.

rial. Many of the specimens measured were fragmentary or were embedded in rock, and thus were difficult to measure; nevertheless, the measurements listed will give the reader an appreciation for the sizes and relative dimensions of the individual species. When measurements were sufficiently accurate to have important bearing on the differentiation of species, bivariate plots were drawn and regression analyses carried out.

### STRATIGRAPHIC DISTRIBUTION OF ORDOVICIAN MONOPLACOPHORA AND BELLEROPHONTACEAN GASTROPODA IN THE CINCINNATI ARCH REGION

In the accompanying tables (tables 1–4) are listed the stratigraphic distributions of monoplacophorans and bellerophon-taceans in the Middle and Upper Ordovician lithostratigraphic units of the Cincinnati arch region.

### PALEOECOLOGY OF SYMMETRICAL UNIVALVED MOLLUSKS

#### INTRODUCTION

Paleontologists have generally regarded bellerophon-taceans, and those Paleozoic taxa now recognized as monoplacophorans, as algal grazers that mainly inhabited nearshore shallow subtidal and intertidal marine environments. This general conclusion has been based on common paleoenvironmental occurrences and faunal associations in the fossil record, as well as on comparison with some modern archaeogastropods (mainly limpets). However, data on fossil archaeogastropods and monoplacophorans show this conclusion to be an oversimplification.

TABLE 1.—Distribution of bellerophon-taceans in the Stones River Group of central Tennessee

[Data are based on museum collections and species listed in Wilson (1949). MF = Murfreesboro Limestone; PL = Pierce Limestone; RL = Ridley Limestone; LL = Lebanon Limestone; CL = Carters Limestone. X = present]

Species	MF	PL	RL	LL	CL
<i>Bucania emmonsii</i>	X				
<i>Phragmolites grandis</i>				X	
<i>Pterotheca expansa</i>	X				
<i>P. saffordi</i>				X	
<i>P. undulata</i>					X
<i>Tetranota bidorsata</i>	X	X	X	X	
<i>T. sexcarinata</i>				X	

#### AUTECOLOGY OF MONOPLACOPHORANS

All modern monoplacophorans, such as *Neopilina*, live at water depths of 200 m or more, are limpet shaped, and are thought to be deposit feeders (Cesari and Guidastri, 1976). In contrast, Paleozoic taxa here interpreted to be monoplacophorans inhabited a relatively shallow subtidal shelf and had limpet shaped (pls. 1–4), convolute (pl. 9, figs. 1–4), involute (pl. 5, figs. 5–7), and evolute (pl. 6, figs. 19–22) isostrophically coiled shells. Detailed paleoecological data on these Paleozoic monoplacophorans are scarce, and at present their life habits can only be speculated on. Lemche and Wingstrand (1959, p. 63) stated that the modern monoplacophoran *Neopilina* was taken from abyssal, dark, muddy, clay sediment where there were no suitable objects for the animal to creep on.

TABLE 2.—Distribution of monoplacophorans and bellerophon-taceans in the Nashville Group of central Tennessee

[Data are based on museum collections and species listed in Wilson (1949). X = present]

Species	Hermitage Formation	Bigby-Cannon Limestone			Catheys Formation
		Bigby facies	Cannon facies	Dove-colored facies	
<i>Archinacella depressa</i>			X		
<i>A. patelliformis</i>		X			
<i>A. valida</i>	X				
<i>Bucania frankfortensis</i>					X
<i>B. lindsleyi</i>			X		X
<i>B. nashvillensis</i>		X	X	X	
<i>B. peracuta</i>			X		
<i>B. singularis</i>					X
<i>Bucania</i> sp.		X			
<i>Bucanopsis carinifera</i>			X		
<i>Carinaropsis cumulae</i>			X		
<i>Cyrtolites (Cyrtolites) retrorsus</i>	X	X		X	
<i>Phragmolites cellulosus</i>	X				
<i>Sphenosphaera clausus</i>		X	X	X	
<i>S. troosti</i>			X	X	
<i>Sphenosphaera</i> sp.					X
<i>Tropidodiscus cristatus</i>			X	X	
<i>T. subacutus</i>				X	
<i>Undulabucania punctifrons</i>	X				



TABLE 3.—Distribution of species of monoplacophorans and bellerophonacean gastropods in the Tyrone Limestone of the High Bridge Group, the members of the Lexington Limestone, and the Clays Ferry Formation of central Kentucky

[Data are based on the U.S. Geological Survey silicified collections and on museum collections. Note that Middle Ordovician stratigraphic units in the central Kentucky area from which no taxa are known are not included in the table. TY = Tyrone Limestone; CF = Clays Ferry Formation; members of the Lexington Limestone are designated: CL = Curdsville Limestone; LO = Logan; GL = Grier Limestone; PL = Perryville Limestone; DH = Devils Hollow; TL = Tanglewood Limestone; and ML = Millersburg. X = present; interrogation points indicate uncertainty of occurrence]

Species	TY	CL	LO	GL	PL	DH	TL	ML	CF
<i>Micropileus variabilis</i>		X							
<i>Vallatothera unguiformis</i>		X			X				
<i>Archinacella simulatrix</i>	X	X	X	X					
<i>A. cingulata</i>		X							X
<i>A. alta</i>									X
<i>Cyrtolites (Cyrtolites) retrorsus</i>		X	X	X	X		X	?	
<i>C. (Cyrtolites) claysferryensis</i>									X
<i>C. (Paracyrtolites) subplanus</i>			X	?					
<i>C. (Paracyrtolites) parvus</i>									X
<i>Sinuities pervoluta</i>	X	X							
<i>S. obesus</i>		X	X						
<i>S. cancellatus</i>		X			?				X
<i>Tropidodiscus subacutus</i>	X	?	?		X	X			
<i>Phragmolites compressus</i>	?								
<i>Temnodiscus nitidula</i>									X
<i>Bucania halli</i>		X		X					
<i>B. subangulata</i>		X		X					
<i>B. nashvillensis</i>				X	X				
<i>B. frankfortensis</i>						X			
<i>B. sublata</i>				X	X	X			
<i>B. micronema</i>					?				
<i>B. rugatina</i>									X
<i>Tetranota obsoleta</i>		X							
<i>Salpingostoma kentuckyense</i>	X	X							
<i>Bucanopsis carinifera</i>				X	X		X		
<i>B. diabloensis</i>						X			
<i>Sphenosphaera ausus</i>			X	X	X	X	X	X	X
<i>Sphenosphaera</i> sp. indet.		X							
<i>S. troosti</i>				X	X				
<i>S. subglobulus</i>	?								
<i>S. bilineatus</i>						X			
<i>Carinaropsis acuta</i>		X	X						
<i>C. cymbula</i>			X	X	X		X		
<i>C. explanata</i>									X
<i>Pterotheca saffordi</i>	X								
<i>P. expansa</i>	X	X							
<i>P. angusta</i>		X							

However, Lowenstam (1978) reported that specimens of *Vema*, another modern monoplacophoran, were found clinging to phosphate pebbles in dredge samples from bathyl depths. He observed these living monoplacophorans in a tank for nearly a month, and noted a maximum linear movement of only 10 cm (centimeters). Similarly, many Paleozoic limpet-shaped monoplacophorans were probably also clingers.

The cap-shaped to conical tryblidiid monoplacophorans in the Ordovician strata of the Cincinnati arch are distributed throughout a spectrum of depositional envi-

ronments (tables 1–4). In the USGS silicified collections, *Archinacella simulatrix* (pl. 2, figs. 7–12) occurs in such varied facies as the Tyrone Limestone, and the lowermost Curdsville Limestone and Grier Limestone Members of the Lexington Limestone. One common factor in these occurrences is that all of these facies probably were deposited in less than 15 m of water (Cressman, 1973).

Other species of *Archinacella* cited herein are found in various Middle and Upper Ordovician formations, many of which contain multiple facies of different depositional origins. Most of these occurrences are known from museum specimens, and the sedimentological and faunal associations generally are unknown. Therefore, correlation between taxa or morphotypes and depositional environments is not possible at present.

There are some consistent environmental distributions for other tryblidiid genera in the USGS silicified collections. *Vallatothera unguiformis* (pl. 1, figs. 12–31) and *Micropileus variabilis* (pl. 1, figs. 1–7) are known only from very shallow water facies. *V. unguiformis* is known only from the Salvisa Bed of the Perryville Limestone Member and the basal meter of the Curdsville Limestone Member of the Lexington Limestone. The fine-grained limestones of the Salvisa Bed were deposited in water 2 m or less deep and are characterized by an ostracode fauna and some mollusk shell beds (Cressman, 1973, p. 30). The lower part of the Curdsville Limestone Member consists of crossbedded bioclastic limestone deposited above wave base in a transgressive sea (Cressman, 1973, p. 14). *V. unguiformis* most likely was an algal grazer. *M. variabilis* was found only in the basal 2 ft of the Curdsville Limestone Member of the Lexington Limestone. Its unsculptured low, conical shell, and its apparent possession of a continuous muscle ring, suggest that it led a limpetlike existence, clinging to and rasping algae from exposed lithified surfaces of the Tyrone Limestone along the shoreline of the transgressing Curdsville sea.

The common bryozoan encrustation of tryblidiid shells in the fauna under study suggests that these mollusks lived exposed lives in firm-bottom depositional environments. Such encrustations are known on the shells of *Archinacella simulatrix* (pl. 2, figs. 7, 8), *A. indianensis* (pl. 3, figs. 16–18), *Helcionopsis striata* (pl. 2, figs. 1–5), *Vallatothera unguiformis* (pl. 1, figs. 30, 31), and *V. manitoulini* (pl. 1, figs. 8–11). The highly sculptured dorsal shells of genera such as *Vallatothera* and *Helcionopsis* also argue against the deposit-feeding habit, in which the shell is often at least partly submerged in soft sediment. All of these taxa were probably algal grazers in shallow-water habitats.

Some smooth-shelled tryblidiids occur in more shale-rich facies, for example, *Archinacella arca* (pl. 3, figs. 7–10) from the Bull Fork Formation and *A. alta* (pl. 3, figs. 4–6) from the Clays Ferry Formation. Hurst (1979)



TABLE 4.—Distribution of species of monoplacophorans and bellerophonacean gastropods in the Upper Ordovician stratigraphic units of the Cincinnati arch region

[Stratigraphic units in southeastern Indiana are designated: KO = Kope Formation, DO = Dillsboro Formation, SA = Saluda Formation, and WW = Whitewater Formation. Units in southwestern Ohio and north-central Kentucky are designated: KO = Kope Formation, FV = Fairview Formation, BL = Bellevue Limestone, GL = Grant Lake Limestone, BF = Bull Fork Formation, and DR = Drakes Formation. Unit in south-central Kentucky is designated: AS = Ashlock Formation. Units in central Tennessee are designated: LP = Liepers Formation, and AR = Arnheim Formation (as used by Wilson, 1949). X = present; interrogation points indicate uncertainty of occurrence]

Species	SE. Indiana				SW. Ohio-N. Kentucky						S. Ky.	Tenn.	
	KO	DO	SA	WW	KO	FV	BL	GL	BF	DR	AS	LP	AR
<i>Vallatothera manitoulini</i>									X				
<i>Helcionopsis striata</i>													X
<i>Archinacella davis</i>					?								
<i>Archinacella</i> cf. <i>patelliformis</i>						X							
<i>A. rugatina</i>									X				
<i>A. arca</i>									X				
<i>A. indianensis</i>		X		X					X	X			
<i>Cyrtolites (Cyrtolites) ornatus</i>		X	X	X		X	X	X	X	X			
<i>C. (Cyrtolites) cf. C. (C.) retrorsus</i>					X								
<i>C. (Cyrtolites) claysferryensis</i>					X								
<i>C. (Cyrtolites) minor</i>					X	X							
<i>C. (Cyrtolites) hornyi</i>		X											
<i>C. (Paracyrtolites) carinatus</i>	X				X								
<i>Sinuities cancellatus</i>									?				
<i>S. planodorsatus</i>					X								
<i>S. granistriatus</i>					X								
<i>S. globularis</i>					X								
<i>S. subcompressus</i>		X											
<i>Tropidodiscus magnus</i>				X									
<i>Phragmolites bellulus</i>						X							
<i>P. elegans</i>									X				
<i>P. dyeri</i>		X	X	X					X	X			
<i>Undulabucania gorbyi</i>		X											
<i>Bucania pojetai</i>												X	
<i>B. simulatrix</i>				X					X	X			
<i>B. crassa</i>				X									
<i>Kokenospira costalis</i>					X								
<i>Tetranota bidorsata</i>					X								
<i>Salpingostomarichmondensis</i>				X					X	X			
<i>Sphenosphaera recurvus</i>								X					
<i>S. subangularis</i>				X									
<i>S. capax</i>						X					X		
<i>S. mohri</i>		X	X	X					X	X			
<i>Pterotheca harviei</i>					X								

cited *Archinacella* sp. and indeterminate monoplacophorans from offshore shale facies in the British Caradocian Series. These monoplacophorans may have been deposit feeders. However, it must be noted that archinacellids have a continuous muscle ring, which is generally thought to be characteristic of clinging molluscan univalves.

Species of the cyrtoneid monoplacophoran genera *Cyrtolites* (pl. 6) and *Sinuities* (pl. 9) were highly successful during the Middle and Late Ordovician and are found in most Ordovician formations in the Cincinnati arch region (tables 2–4). Species of both genera were probably sluggish vagrant benthos. In many cases they occur together, but one genus is usually clearly dominant over the other in any single collection. They are often found in shaly and silty rocks. In fact, they are the dominant symmetrical univalved mollusks in both the Logana

Member (Kirkfieldian) of the Lexington Limestone and the Kope Formation (Edenian), which are the deepest water units in the Kentucky-Indiana-Ohio Ordovician section. However, *Cyrtolites retrorsus* (pl. 5, figs. 1–26) is also common throughout shallow-water facies of the Lexington Limestone, and *C. ornatus* (pl. 6, figs. 1–18) is common throughout most of the Cincinnati section. *C. ornatus* is commonly encrusted by bryozoans (pl. 6, figs. 12–14), and the encrustation can be shown to have occurred both during the life of the animal and after death (see later section on encrustation). Such encrustation suggests that the animal lived exposed on firm substrates under normal marine conditions. In contrast, few specimens of *Sinuities* are encrusted. The absence of encrustation may be attributable to their smoother shell surfaces, their occupation of more turbid environments, some aspect of their mode of life, or a combination of

these factors. *Sinuities* seems to be more dominant than *Cyrtolites* in deeper water facies. The highly irregular apertural margin in *Sinuities* also seems better adapted to the efficient channeling of water through the shell than to clamping onto a firm surface (see section on "Functional Morphology"). It appears that *Sinuities* may have been a deposit feeder on soft bottoms, whereas *Cyrtolites* was more likely an algal feeder in predominantly firm bottom areas.

#### AUTECOLOGY OF BELLEROPHONTACEANS

Bellerophontaceans are often allied closely with pleurotomariaceans because of their common possession of a median labral emargination along the apertural margin (Knight, 1952) and their common association in Paleozoic fossil assemblages. Unfortunately, ecological comparison of bellerophontaceans with modern pleurotomariaceans is nearly fruitless, because today the latter group is represented by only a small number of relict species living in deeper water environments (Vermeij, 1978, p. 221). A more fruitful ecological comparison can be made between bellerophontaceans and those modern archaeogastropods that occupy the same shallow subtidal environmental regime. These modern groups are mainly algal grazers. They either rasp algae (mainly blue-green algae) from hard surfaces, like many patellaceans, or feed on the thalli of erect green algae, like other patellaceans and most trochaceans (Morton, 1967, p. 96–98).

Steneck and Watling (1982) and Steneck (1983) have discussed morphological limitations on the feeding capabilities of herbivorous mollusks. They concluded that bellerophontaceans and Paleozoic monoplacophorans were probably restricted to feeding on delicate filamentous and microscopic algae (browsing habit), as are most recent nonlimpet archaeogastropods. These modern archaeogastropods, and modern monoplacophorans, have radulae with organic teeth that are too soft to excavate calcareous substrata. This morphological feature is thought to have restricted their feeding on calcareous algae. However, patellacean archaeogastropods have strong buccal muscles and uniquely designed radular teeth that are strengthened by silicate and iron mineral coatings, which allow them to excavate calcareous substrates effectively and even to feed on crustose red algae (Steneck and Watling, 1982; Steneck, 1983). Hickman (1984b) and Harasewych and others (1988) demonstrated that the rhipidoglossate radula can be used to feed on sponges, in addition to browsing on algae.

As pointed out by Peel (1977b, p. 41–43), there are some notable exceptions to the algal feeding habit in modern archaeogastropods. Some fissurellids feed on sponges (Morton, 1967), and the deep-water pleurotomariacean *Mikadotrochus* includes sponges in its

microphagous scavenging habit (Fretter, 1964). Fretter (1964) also found foraminifers, diatoms, algal fragments, and organic detritus in the stomach of *Mikadotrochus*. Woodward (1901), Matsumoto and others (1972), Yonge (1973), and Hickman (1976, 1984a) have inferred or observed carnivory (particularly on sponges) by modern pleurotomariaceans. Harasewych and others (1988) presented evidence from in situ observations and analyses of gut contents showing that the modern pleurotomariids *Petrotrochus midas* and *P. amabilis* feed predominantly and selectively on sponges. Fretter (1975) has even observed ciliary suspension feeding in the modern trochid *Umbonium*. Morton (1967) has discussed the minor anatomical modifications needed for the adaptation of archaeogastropods to these alternative feeding habits. Because the necessary anatomical evolution allowing the carnivorous, the microphagous deposit-feeding (scavenging), and the ciliary suspension-feeding habits is present in modern archaeogastropods, there is no reason to assume such adaptations did not also take place in Paleozoic forms.

Some exceptions to the algal browsing habit in Paleozoic archaeogastropods have been demonstrated. For example, Bowsher (1955) showed that many platycerids were coprophagous on crinoids. The common Upper Ordovician platycerid genus *Cyclonema* is commonly associated with camerate crinoids (Thompson, 1970, p. 222–224). McKerrow (1978, p. 80–82) claimed that Ordovician bellerophontaceans, which he considered to be monoplacophorans, were bottom-dwelling detritus feeders and scavengers, but he offered no evidence to support this conclusion. Yochelson (1971) and Peel (1975b) interpreted open-coiled Paleozoic gastropods as sedentary ciliary suspension feeders on the basis of comparison with modern forms. Runnegar (1983, p. 128) has also suggested that macluritid and euomphalid archaeogastropods were suspension feeders, from analysis of the "living fossil" *Neomphalus* (McLean, 1981), a modern filter-feeding limpet interpreted to be a euomphalid. Peel (1977b, p. 47) suggested that explanate bellerophontaceans were epifaunal deposit feeders on soft substrates, micromorphic bellerophontaceans were grazers among algal foliage, and other shell forms led one or the other of these life styles. However, Peel emphasized that although other life habits have been demonstrated for modern archaeogastropods (as cited above), sufficient evidence of such alternative habits is usually lacking in the fossil record.

Batten (1958) noted the common association of pleurotomariaceans and sponges in shallow, muddy-bottom paleoenvironments in the Permian strata of the Southwestern United States. Batten (1958) and Finks (1960) cited four instances when one or more specimens of the pleurotomariacean *G. (Glyptotomaria) marginata* were

found within the cloacas of the demosponge *Heliospongia vokesi*. Batten (1958) suggested that the gastropods may have fed on algal material collected on the cloacal walls. However, because some modern fissurellids (Morton, 1967), and possibly some pleurotomariaceans (Fretter, 1964), feed on sponges, it is possible that some Paleozoic archaeogastropods also did so.

Yonge (1947) claimed that archaeogastropods were restricted to firm substrates in relatively clean water environments because their bipectinate aspidobranth gills are prone to clogging by fine sediment particles. However, evidence from the fossil record amply demonstrates the common occurrence of archaeogastropods, and bellerophonaceans, in muddy sediments. Peel (1977b, p. 41–46) has discussed this problem at some length; he emphasized two important points. First, the general absence of modern archaeogastropods adapted to life on a soft bottom may be a result of post-Paleozoic competition with the more advanced caenogastropods, whose monopectinate ctenidia and anterior siphon enabled them to cope more easily with soft-bottom conditions. Second, some Paleozoic forms now included in the Archaeogastropoda may actually be caenogastropods, or may even be of a now-extinct organizational grade. More recently, Gilinsky (1984) compared rates of oxygen consumption by Holocene archaeogastropods and caenogastropods living in turbid water. He found no significant differences in oxygen consumption between the two groups. He concluded that his data cast doubt on Yonge's (1947) hypothesis, and suggested that other physical and biotic factors might play roles in controlling gastropod distribution and should be investigated.

Assuming Yonge's (1947) assessment of the bipectinate gill has merit, there are at least three ways to explain the presence of archaeogastropods in muddy sediment deposits. First, the gastropods might have been supported on algal films that bind and cover the muddy sediment surface. Gebelein (1969) cited gelatinous films of algal mucilage from modern carbonate environments in Bermuda, where they stabilized substrates and passively trapped carbonate muds. Peel (1977b, p. 45) cited examples of modern caenogastropods living on such films and pointed out that these films would also furnish an abundant food source. Ferguson (1962) described an assemblage of small bellerophonaceans (generally less than 10 mm (millimeters) in diameter) from British Mississippian-age shales of intertidal to shallow subtidal environments in a transgressive sequence. He postulated that the small snails could survive on the muddy bottom because the rate of sedimentation was very slow and the sediment surface may have been loosely bound by organic slime.

The second possibility is that the snails lived on drifting masses of algae comparable to the modern

*Sargassum* (Peel, 1977b, p. 44). Ruedemann (1934) explained the presence of benthic faunas in Paleozoic black shales in this way. However, it is unlikely this is an important mechanism explaining the widespread occurrence of archaeogastropods in normal marine shales deposited in shallow aerobic settings.

The third and most common explanation is that the snails were algal foliage dwellers, living above the turbid mud bottoms in stands of erect algae (Chronic, 1952; Johnson, 1962, 1964; Gromaczakiewicz-Lomnicka, 1972; Bowen and others, 1974; Peel, 1977b; Goldring and Langenstrassen, 1979). Johnson (1961, p. 5, 6) claimed that Ordovician seas supported a rich algal flora of noncalcareous and slightly calcified marine algae. The mild climates and widespread areas of shallow marine carbonate deposition of the Ordovician were an ideal setting for the development of calcareous marine algae. Johnson believed that the floors of Ordovician shallow shelf areas were covered by an algal flora as populous and diverse as those of modern seas, and he envisioned these algae as the basic food supply for the teeming marine invertebrate communities of the period.

The late Middle Ordovician radiation of archaeogastropods could be linked to the early Middle Ordovician radiation of marine algae. Blue-green algae, in the form of stromatolites and oncolitic encrustations, dominated pre-Middle Ordovician marine algal floras, but during the Middle Ordovician, a radiation of green (Codiaceae and Dasycladaceae) and red (Solenoparaceae) algae occurred (Johnson, 1961; Wray, 1977, fig. 161). Moore (1977, p. 18) reported an abundant and diverse marine algal flora composed of both calcareous and noncalcareous components from the early Middle Ordovician (Chazyian) limestones of eastern Tennessee, and described an algal ecologic zonation comparable to that of recent shallow marine environments. Moore found green and red algae to be most abundant in the broad shelf-lagoon environment and its contained patch reefs, but absent in shelf margin shoal and reef environments. Tidal flats and associated environments showed the influences of stromatolite growth.

There are also some fairly well preserved erect noncalcareous algae known from Ordovician strata. Arbey and Koeniguer (1979) reported casts of small seaweeds from the Ordovician of the Sahara Desert which are similar to the well-known Devonian-age *Protaxites* (Koeniguer, 1974; Jonker, 1979). Also, Fry (1969, 1983) described collections of noncalcareous marine algae made by G. Winston Sinclair from the dolomites of the Late Ordovician (Richmondian) Red River Formation of Manitoba. He recognized numerous erect morphotypes that most closely resemble modern red, green, and brown algae.

Numerous authors discussing Paleozoic marine benthic communities have cited bellerophontaceans as common inhabitants of nearshore delta front shales and siltstones (Johnson, 1962; Sturgeon, 1964; Bretsky, 1969; Sutton and others, 1970; West, 1972; Bowen and others, 1974; Thayer, 1974; Goldring and Langenstrassen, 1979; Linsley, 1979; Rollins and others, 1979; MacLeod, 1982). Bowen and others (1974) suggested that their *Bellerophon* Community from the Devonian of New York was located near delta channel mouths during periods of active progradation, when outflowing nutrients would provide for the most prolific growth of marine plants. Johnson (1962) likewise associated Pennsylvanian gastropod assemblages in the Illinois Basin with areas of prolific plant growth in delta front areas. Likewise, MacLeod (1982, p. 172) cited a bellerophontid community in delta front and interdistributary bay environments in the Upper Pennsylvanian of north-central Texas and suggested that they fed on benthic algae. It should be noted that these delta front areas must have also been sites of active fine clastic sedimentation and accordingly would have been turbid.

Peel (1977b, p. 43–46) has pointed out some possible shortcomings of the algal-foliage-dweller hypothesis. In modern seas, the dominant types of vegetation on soft sediment in shallow water are sea grasses, whereas algal stands are more characteristic of modern rocky shoreline areas. However, sea grasses did not appear in the fossil record until the Tertiary (Brazier, 1975), and therefore it is necessary to suggest that during the Paleozoic algae dominated marine areas in which they are now subordinate.

Peel (1977b, p. 44) further pointed out that the supporting ability of algal foliage restricts the size of gastropods that can live on it. Most modern algal-foliage-dwelling gastropods are quite small. Warmke and Almodovar (1963) found that 99 percent of the mollusks associated with algae in Puerto Rico were gastropods, but they were mainly less than 2 mm in diameter. Brazier (1975) cited the presence of small gastropod faunas as a possible way to recognize former grass beds in the Tertiary fossil record. Johnson (1964, p. 123) claimed that a modern gastropod assemblage dominated by a few species in fine-grained sediments generally indicates the presence of plants. Diverse diminutive molluscan faunas have also been interpreted as algal-foliage-dwelling faunas in the Upper Ordovician Maquoketa Formation (Bretsky and Birmingham, 1970) and the Lower Silurian Brassfield Formation (Harrison and Harrison, 1975). Peel (1978, p. 302) suggested, in his study of the gastropod faunas of the Silurian Arisaig Group in Nova Scotia, that many of the smaller forms of 5 mm or less in diameter were probably algal foliage dwellers, and that those in the 10–15-mm size range may

also have been. However, he doubted that the high proportion of Arisaig gastropods attaining 20 mm or more in size could have lived in algal foliage. However, large and small species of archaeogastropods are commonly found together in Paleozoic fine-grained deposits. Sturgeon (1964, p. 193) stressed the cooccurrence of gastropods ranging in size from 5.5 to 35 mm in the Pennsylvanian shales of Ohio. Chronic (1952, p. 109–111) claimed that small, finely ornamented delicate snails of the fine-grained Permian Kaibab Limestone of Arizona lived in “seaweed forests” above calcareous mud substrates, while contemporary thick- and smooth-shelled large forms lived on the sea floor beneath. Heuer (1973, p. 527, 528) suggested that bellerophontaceans lived on soft, muddy bottoms in Late Pennsylvanian delta front settings in Texas, while most associated pleurotomariaceans lived above the sea floor on erect algae, crinoids, bryozoans, and sponges. Peel (1977b, p. 43) cited examples of modern stratified gastropod faunas in algal foliage habitats, and noted that their death would result in ecologically mixed assemblages made up of forms from different foliage levels, as well as forms that had lived among the holdfasts and at the sediment surface.

It therefore appears that the algal-foliage-dwelling habit may partly explain small Paleozoic archaeogastropods in muddy sediments, but they are generally associated with other species thought to be too large to have been supported by algal foliage. Apparently, at least some Paleozoic archaeogastropods had adaptations that allowed them to cope with soft substrates, and it is likely that feeding habits were much more varied than is generally supposed.

#### PREVIOUS ORDOVICIAN PALEOECOLOGICAL STUDIES

There are very few published studies focusing on Ordovician bellerophontacean-monoplacophoran paleoecology. However, a small number of genera are commonly cited in more general Ordovician community studies. These studies can be conveniently divided into those concerned with clastic depositional environments and those dealing with carbonate depositional environments. A brief review of these studies documents that monoplacophorans and bellerophontaceans occupied a wide variety of Paleozoic habitats.

#### ORDOVICIAN CLASTIC ENVIRONMENTS

Bretsky (1969, 1970b) studied marine benthic communities in Upper Ordovician clastic depositional environments along the Queenston delta front in the Central Appalachians. He reported *Plectonotus* sp. and *Bucania* sp. from shallow subtidal and intertidal silt and fine-sand bottom environments. They are present in Bretsky's

*Orthorhynchula-Ambonychia* assemblage, and are associated with rhynchonellid and linguloid brachiopods and with modiomorphid, ambonychiid, and nuculoid bivalves. Although the bellerophontaceans are found in sediments of the same texture as pleurotomariaceans, the two groups do not commonly co-occur, the bellerophontaceans occupying more nearshore areas adjacent to cross-bedded sand and organic-rich mud depositional environments. *Plectonotus* sp. was by far the more abundant of the two bellerophontaceans, and was commonly found in clumps of numerous specimens in sediment stained with more organic matter than were surrounding sediments. These specimens likely were concentrated on a common food source, probably algal.

Brenchley and Cocks (1982) recognized ten faunal associations in the latest Ordovician regressive sequence in Norway. Unidentified bellerophontaceans were present in three of these associations. All three occurrences were in mudstones, but the three were in deep-shelf, midshelf, and inner-shelf environments, respectively. None were reported from nearshore or onshore facies.

Pickerill and Brenchley (1979) described benthic marine communities in the clastic rocks of the Caradocian Series in North Wales. They recognized four communities, all of which were believed to have been deposited in offshore shelf areas 30 m or less deep. *Cyrtolites* sp., *Sinuities* sp., *Bucania* sp., *Bucanopsis* sp., and indeterminate bellerophontaceans were found in fine-sand, silt, and mud bottom environments 25 m or less deep. *Cyrtolites* sp. was also found in coarse sands deposited in less than 10 m, and *Sinuities* was also found in brachiopod-bryozoan-trilobite assemblages originating in water deeper than 25 m.

Hurst (1979) described the succession of benthic marine faunas of the type Upper Caradocian Series of England, a transgressive clastic sequence ranging from coarse onshore sands to deep-water, organic-rich, laminated shales. Bellerophontaceans were rare in nearshore sand and silt facies, but they composed up to 8.1 percent of the total fauna in stable offshore silt facies, and were locally common in deeper mud environments. In a gradient of 14 depositional facies (1=onshore sands, 14=deep offshore bioturbated and laminated muds) and faunal assemblages, bellerophontaceans and monoplacophorans were common faunal elements (2 to 8 percent of total fauna) in only facies 10 through 13 (offshore silts to muds). Taxa cited were indeterminate bellerophontaceans (facies 6–13), *Sinuities* sp. (facies 8–13), *Cyrtolites* sp. (facies 11), *Temnodiscus* sp. (facies 10–12), *Cymbularia* sp. (facies 11–13), *Archinacella* sp. (facies 12, 13), and indeterminate monoplacophorans (facies 12, 13). It is noteworthy that *Archinacella* sp. and indeterminate monoplacophorans were found in only the deepest water

assemblages. *Sinuities* was the most wide ranging taxon in the sequence, while *Cyrtolites* and recognizable bellerophontaceans were concentrated in facies 10 through 12 that occurred in offshore silt bottom environments. Hurst (1979, p. 239) noted that, as in the successional faunal stages from the Upper Ordovician of Quebec described by Bretsky and Bretsky (1975), *Temnodiscus* sp. and *Sinuities* sp. are characteristic of early diversification faunas succeeding a *Nuculites*-trilobite fauna that colonized barren fine-mud bottoms. It seems likely that these mollusks were dependent on the establishment of some member or members of a pioneer community that may have served as a food source and (or) a supporting structure above the mud bottom.

Horny (1963a) described Middle and Upper Ordovician bellerophontaceans from Bohemia and briefly discussed their paleoecology. The Bohemian Ordovician section consists predominantly of shales, siltstones, and sandstones, with scattered limestones. His data showed that bellerophontacean genera are generally distributed through two or more facies, but that individual species are restricted to a single facies. He observed that while few clay-shales contained bellerophontaceans, many calcareous shales contained abundant specimens. He further observed that while some explanate bellerophontacean species (*Grandostoma grande*, *Pterotheca consobrina*) were found only in shaly sediments, other explanate morphotypes (*Grandostoma bohemicum*, *Bucanopsis calypso*) were found in both shales and sandstones, and still others (*Cyclothea bohémica*, *Tremanotus tuboides*) were found only in coarse-grained bioclastic-tuffaceous limestones around volcanic islands. His data suggest that the explanate shell form was not adapted to any special substrate conditions.

McKerrow (1978, p. 78, 83, 89) cited undetermined bellerophontaceans from three Ordovician communities: the *Dinorthis* Community of shallow shelf, coarse clastic bottoms; the Diverse Brachiopod Community of the middle to deep shelf environment; and the *Christiania-Sampo* Community of the deep shelf.

In summary, Ordovician bellerophontaceans living on clastic sediment substrates seem to be most common in siltstones and somewhat less common in calcareous shales, and are found only occasionally in sandstones. However, the environmental settings of these substrate types can be quite variable. Bretsky (1969, 1970b) cited bellerophontaceans as nearshore silt-bottom inhabitants in a progradational delta front setting, similar to the occurrences in Devonian and Pennsylvanian strata cited above. Conversely, Pickerill and Brenchley (1979) and Hurst (1979) cited their silt-bottom-dwelling bellerophontaceans and monoplacophorans from relatively deep offshore environments in a transgressive setting. This apparent discrepancy is clarified when the character and

composition of the faunas from the two settings are considered. Bretsky's delta front fauna contained only two species, with *Plectonotus* sp. being clearly dominant. That species may have been an opportunist, capable of surviving the relatively unstable delta front conditions with eurytopism and a high rate of fecundity (see Levinton, 1970). Moreover, trilobation of the shell, as in *Plectonotus* sp., has been convincingly interpreted as a modification of the entrance to the mantle cavity to increase the efficiency of water circulation (Peel, 1974, p. 249), and thereby to assist in keeping the gills unfouled in turbid delta front conditions. On the other hand, the monoplacophoran-bellerophontacean assemblages cited from the British Caradocian Series are much more diverse (at least 10 genera), as is expected in more stable offshore environmental settings (see Sanders, 1968). Moreover, a diversity of general shell forms is present in the Caradocian, including cap-shaped, involute, convolute, and explanate morphotypes, probably representing the occupation of a variety of niches.

#### ORDOVICIAN CARBONATE ENVIRONMENTS

Berry (1974, p. 159) cited nautiloid cephalopods and bellerophontaceans and macluritacean archaeogastropods as the dominant fauna of the extensive tidal flat environments of the Late Cambrian-Early Ordovician carbonate platforms in North America. He interpreted all three groups as algal grazers. He (1974, p. 161) claimed that this nautiloid-bellerophontacean-macluritacean fauna continued to dominate intertidal and adjacent shallow subtidal carbonate environments through the end of the Ordovician, while orthid-strophomenid brachiopod faunas came to dominate essentially all other subtidal carbonate environments.

Walker (1972), who studied the community ecology of the Black River Group (Blackriveran) of New York State, cited only one bellerophont, *Plectonotus* sp., that being from his wave-baffle margin community. This community occupied the front and back flanks of *Tetradium* coral banks and was dominated (80 percent of total biovolume) by the byssate pelecypod *Cyrtodonta* and the high-spined gastropod *Loxoplocus*.

There was a distinct increase in abundance and diversity of molluscan univalves in post-Blackriveran strata in Eastern North America. In their work on communities of the lower Trenton Group (Rocklandian-Shermanian) of New York State, Titus and Cameron (1976) cited *Phragmolites compressus*, *Sinuities bilobatus corrugatus*, *Sinuities cancellatus*, and *Sinuities cancellatus acutus* as common elements in the *Triplesia* community of the lagoonal facies and in the *Liospira* community of the nearshore shoal facies. *Phragmolites compressus* was also a member of the *Encrinurus* community of the

foreshoal shallow shelf facies. Titus (1982) continued this work on the communities of the middle Trenton Group (Shermanian) of New York State. He reported *Sinuities cancellatus liratus* from the *Liospira* community in the nearshore shoal facies, *Sinuities cancellatus* from the *Encrinurus* community in the foreshoal shallow shelf facies, and *Sinuities bilobatus corrugatus* from the *Trematis* community in the offshore open shelf facies.

Byers and Galvin (1979) studied two contemporaneous communities from normal marine shallow subtidal deposits of the Platteville Formation (Rocklandian) in Wisconsin. *Sinuities* sp. and *Phragmolites* sp. were found to make up 11 and 2 percent of the first community, respectively. The second community, which contained the same common taxa but in different percentages, had *Sinuities* sp. and *Phragmolites* sp. making up 26 and 1 percent of the community, respectively, with *Sinuities* sp. being the most abundant fossil in the total assemblage. *Sinuities* sp., which was considered to be an algal-browsing archaeogastropod, was in many places found alone covering bedding planes, and the authors suggested that it might have been an opportunistic species.

The scant data on molluscan univalves from studies of communities on carbonate strata of the Champlainian Series give a deceptive impression of low diversities. The monoplacophoran-bellerophontacean faunas of the Lexington Limestone covered herein show that these mollusks could be abundant and diverse. The apparent abundance of species of *Sinuities* and *Phragmolites* in Middle Ordovician studies from New York and Wisconsin cannot be readily explained, as these genera are not dominant in the Middle Ordovician strata of the intervening Cincinnati arch region but are more common in the more shale rich Late Ordovician strata of that area.

In summary, it appears from examination of Middle and Upper Ordovician benthic marine community studies that only a small number of bellerophontacean and monoplacophoran taxa were associated with onshore environments; rather, most were distributed throughout nearshore and offshore normal marine shelf environments.

#### POST-ORDOVICIAN PALEOECOLOGICAL STUDIES OF NOTE

In a general study of Silurian-Devonian communities, Boucot (1975, p. 13-18) charted six benthic assemblages. His only mention of bellerophontaceans was his *Homolonotid-Plectonotus* community, which characterized the most nearshore assemblage zone (Benthic Assemblage 1). Berry (1975, p. 49, fig. 15) interpreted this community as occupying a quiet-water, high intertidal environment.

Peel (1975a, c, 1977b, 1978) contributed greatly to the understanding of the paleoecology of Paleozoic gastropods through his studies of the faunas of the Silurian Arisaig Group of Nova Scotia. The morphotypic composition of these Silurian monoplacophoran-bellerophontacean faunas is similar to the compositions of Middle and Late Ordovician faunas, so Peel's observations apply to the present investigation. The Arisaig Group is a 1,300-m-thick siltstone-dominated sequence that provides a nearly continuous faunal record of shallow marine communities throughout the Silurian and Early Devonian Periods. Watkins and Boucot (1975) and Bambach (1969) have studied the brachiopods and pelecypods of the Arisaig Group, respectively. Watkins and Boucot (1975) concluded that most of the Arisaig could be referred to nearshore Benthic Assemblage 2 of Boucot (1975), with offshore Benthic Assemblages 3 and 4 in some parts of the group. Peel's (1977b, 1978) observations on bellerophontacean paleoenvironmental distributions are summarized below.

1. The hard-bottom shallow marine platform fauna was characterized by trochiform pleurotomariaceans, with the small, globose bellerophontacean *Bucanopsis* sp. making up 12 percent of the gastropod fauna.
2. The soft-bottom shallow marine platform fauna was dominated by high-spined murchisoniids and loxonomataceans, with the trilobed *Tritonophon trilobata* and the explanate *Phragmosphaera globata* making up 14–25 and 12 percent of the gastropod fauna, respectively.
3. The soft-bottom open lagoon fauna typically was heavily dominated by trochiform holopeids. With a decrease in water depth, the holopeids were replaced by a fauna of small bellerophontaceans, including trilobed plectonotinids, and by lenticular pleurotomariaceans and some high-spined gastropods.

Peel (1975a, c, 1978) suggested that explanate bellerophontaceans in the Arisaig, such as *Phragmosphaera globata*, were adapted to life on soft substrata, the broadly expanded apertures serving to support the shell on top of the sediment. He further reasoned (1978, p. 302, 303) that gastropods ranging up to 10–15 mm in diameter, including species of *Tritonophon*, *Tropidodiscus*, *Pharetrolites*, and *Cymbularia*, could have been algal foliage dwellers.

Heuer (1973, p. 510–541) discussed the paleoecology of Upper Pennsylvanian gastropods from the Wolf Mountain Shale (Canyon Group, Missourian Series) of north-central Texas. The Wolf Mountain Shale was deposited in a prodeltaic shallow shelf setting. The formation contains a diverse gastropod fauna, including 13 genera and 24 species of pleurotomariaceans, and 3 genera and 4 species of bellerophontaceans, as well as less common

euomphalaceans, murchisoniaceans, and subulitaceans. Heuer (1973, p. 527–530) concluded that the bellerophontaceans were deposit feeders that lived on the sea floor, while the pleurotomariaceans mostly dwelled above the sea floor on erect organisms such as algae, crinoids, bryozoans, and sponges. He proposed that the pleurotomariaceans either fed directly on their supporting hosts or fed on epizoans and organic detritus on the surfaces of the hosts. Heuer claimed that the morphology of the bellerophontaceans was better adapted to life on soft substrates, as indicated by (1) generally shorter labral slits than in the cooccurring pleurotomariaceans, reflecting shallower mantle cavities that could be more easily flushed of fouling detritus by rapid contractions of the shell muscles, (2) a symmetrical shell with a low center of mass due to the weighting of thick parietal deposits, which would give greater stability during movement through soft sediments, and (3) the presence of broad to explanate apertural margins in three of four bellerophontacean species (*B. (Bellerophon)* sp., *B. (Pharkidonotus) percarinatus*, and *Knightites (Cymatospira) montfortianus*) in the fauna, reflecting a broad foot that would prevent sinking into soft sediment.

A survey of a complete spectrum of Paleozoic community studies gives the impression that bellerophontaceans were most abundant during the Devonian and Pennsylvanian Periods, and most commonly occurred in communities associated with delta front environments (as previously discussed). It should be noted that in such occurrences a single species is usually dominant and probably represents opportunistic situations. More significantly, most bellerophontacean genera have been cited from Paleozoic communities throughout the marine environmental spectrum. Linsley (1968, p. 360) found bellerophonts in environments associated with Devonian coral-stromatoporoid biostromes. Moore (1964, p. 339–341) cited bellerophontaceans as being scattered throughout most marine facies in Kansas Pennsylvanian–Lower Permian cyclothems, but they were most abundant in nearshore limestones containing algal (*Osagia*)-molluscan assemblages. Stevens (1965, 1966) and Yancey and Stevens (1981) cited bellerophontaceans (Euphemitid community) as characterizing Middle Pennsylvanian to Lower Permian communities inhabiting the subtidal to lower intertidal zone of large bays or sounds, where sedimentation was rapid and salinity was variable, though generally normal. Yochelson (1969) and Imbrie and others (1964) cited bellerophontaceans from firm-substrate “shelly facies” from Mississippian and Pennsylvanian carbonates, respectively. Ausich and others (1979, p. 1191–1193), who studied Mississippian Borden delta communities in Indiana and Kentucky, noted bellerophontaceans in prodelta slope and basin siltstones and shales deposited in up to 500 ft of water. They



speculated that these patchy basinal communities, which were dominated by gastropods, survived at these depths by feeding on plant debris channeled down submarine canyons. Interestingly, some modern pleurotomariaceans lead a similar mode of life in deep western Atlantic waters (Abbott, 1968, p. 52).

Monoplacophorans are generally so rare in Paleozoic communities that they are not even cited in paleoecological studies. Notable exceptions are species of the isostrophically coiled Ordovician genera *Sinuities* and *Cyrtolites*, both of which are locally abundant in Ordovician mollusk-dominated assemblages discussed in the following sections.

In summary, from this review it appears that Paleozoic monoplacophorans and bellerophontaceans were not uniformly nearshore algal grazers as generally assumed, but occupied a wide range of depositional environments and probably led a number of different modes of life. Most probably fed on marine algae and therefore occupied those shallow-water depositional environments where plant growth was most prolific. Some must have grazed on algal mats and rasped algal coatings from hard surfaces. Others, particularly those taxa characterized by small, lightweight shells, dwelled within and fed upon the foliage of erect benthic algae. Those taxa occurring in deeper soft-bottom facies, as well as many of those that were so abundant in turbid delta front areas, were most likely detritus feeders and scavengers. Some taxa having disjunct coils, or other features that seem to indicate an essentially immobile existence, may have been suspension feeders. The common occurrence of bellerophontaceans in fine-grained soft-bottom facies does not lend support to Yonge's (1947) conclusion that the presumed aspidobranch gill of primitive mollusks is intolerant of turbid conditions. Bellerophontaceans thought to be too large and too heavy to have been supported in algal foliage are commonly found in "muddy" rocks, and probably dwelled on the soft bottoms. Many bellerophontaceans were euryhaline and were able to build large populations in such unstable environments as delta fronts, bays, and restricted lagoons. In fact, low-diversity bellerophontacean assemblages dominate the faunas of many such depositional environments, particu-

larly in Devonian though Permian strata. However, at least in Ordovician strata, higher diversity assemblages of bellerophontaceans and monoplacophorans occur in more normal marine settings but are much less abundant in number of specimens.

#### PALEOECOLOGY OF SYMMETRICAL UNIVALVED MOLLUSKS OF THE TYRONE LIMESTONE AND THE LEXINGTON LIMESTONE OF CENTRAL KENTUCKY

The USGS silicified fossil collections from the Middle Ordovician limestones of Kentucky were taken as bulk samples that were precisely located both stratigraphically and geographically. Such collections afford a potential for paleoecological analyses never before available. Most previously existing collections of fossils from these strata were gathered around the turn of the century and generally are accompanied by vague locality data which are difficult to use because of changes in stratigraphic nomenclature and geographic markers.

Of the 200 silicified collections from the Ordovician strata of Kentucky and adjacent States (Pojeta, 1979), 87 contained approximately 2,700 specimens of monoplacophorans and bellerophontacean gastropods classifiable to species. In attempting to analyze the paleoenvironmental distribution of these data, it was found that data regarding mere presence or absence in the various stratigraphic units reveal little of paleoecological significance (table 3). Many taxa were distributed through numerous stratigraphic units, and therefore through many depositional environments. However, upon constructing histograms of relative abundance of taxa by percentage of the total monoplacophoran-bellerophontacean fauna in a stratigraphic unit, the dominance of certain species in different paleoenvironmental settings became obvious. Tables 5-13 display the distribution and relative abundance of individual species in the USGS silicified collections from the Tyrone Limestone, various members of the Lexington Limestone and the Clays Ferry Formation.

#### TYRONE LIMESTONE

Three silicified samples from the Tyrone Limestone contained 40 specimens of monoplacophorans and bellerophontaceans. Two of these samples each contained only a single specimen of one of two species, *Tropidodiscus* cf. *T. subacutus* and *Archinacella* cf. *A. simulatrix* (table 5). The third sample (6034-CO) contributed 96 percent of the Tyrone specimens—two explanate species, *Salpingostoma kentuckyense* (pl. 25, figs. 1-14) and *Pterotheca expansa* (pl. 40, figs. 5-7). The low diversity of the Tyrone fauna may be partly the result of the small number of samples. The apparent abundance of the two explanate species might demonstrate support for Peel's

TABLE 5.—Relative abundance of species in USGS silicified samples from the Tyrone Limestone  
[Total number of samples = 3; total number of specimens = 40]

Species	Percentage of fauna	No. of samples
<i>Salpingostoma kentuckyense</i>	68	1
<i>Pterotheca expansa</i>	28	1
<i>Tropidodiscus</i> cf. <i>T. subacutus</i>	2	1
<i>Archinacella</i> cf. <i>A. simulatrix</i>	2	1



TABLE 6.—Relative abundance of species in USGS silicified samples from the Curdsville Limestone Member of the Lexington Limestone

[Total number of samples = 13; total number of specimens = 263]

Species	Percentage of fauna	No. of samples
<i>Sinuities obesus</i>	41	9
<i>Cyrtolites</i> cf. <i>C. (Cyrtolites) retrorsus</i>	24	3
<i>Salpingostoma kentuckyense</i>	9	2
<i>Carinaropsis acuta</i>	6	5
<i>Salpingostoma</i> sp. indet.	4	2
<i>Pterotheca expansa</i>	4	2
<i>Micropileus variabilis</i>	3	2
<i>Sphenosphaera</i> sp. indet.	2	2
<i>Bucania</i> cf. <i>B. halli</i>	1.5	2
<i>Tropidodiscus</i> sp. indet.	1.5	2
<i>Archinacella</i> cf. <i>A. simulatrix</i>	1	1
<i>Bucania</i> sp. indet.	1	4
<i>Cyrtolites</i> sp. indet.	1	2
<i>Tetranota</i> cf. <i>T. obsoleta</i>	1	1
<i>Vallatotheca</i> cf. <i>V. unguiformis</i>	1	1
<i>Pterotheca angusta</i>	1	1
<i>Bucania subangulata</i>	1	1

(1978) hypothesis that explanate shell forms were an adaptation for soft substrates, as the Tyrone is characterized by very fine-grained limestone lithologies representing mainly lime mud deposited in shallow lagoon and tidal flat environments. However, collection 6034-CO is from a shell bed within a calcarenite surrounded by fine grained limestone lithologies.

## LEXINGTON LIMESTONE

The distribution of monoplacophoran-bellerophon-tacean assemblages in the members of the Lexington Limestone seems to reflect three stages of faunal dominance. Different taxa groups dominate (1) the Curdsville Limestone and Logana Members (tables 6, 7), (2) the Grier Limestone Member (table 8), and (3) the upper Lexington limestone members and the intertonguing Clays Ferry Formation (tables 9–13). It should be noted that these three stages are stratigraphically distributed through the lower, middle, and upper parts of the Lexington Limestone.

TABLE 7.—Relative abundance of species in USGS silicified samples from the Logana Member of the Lexington Limestone

[Total number of samples = 8; total number of specimens = 534]

Species	Percentage of fauna	No. of samples
<i>Sinuities obesus</i>	77	6
<i>Cyrtolites (Cyrtolites) retrorsus</i>	11	4
<i>Cyrtolites</i> cf. <i>C. (C.) retrorsus</i>	11	5
<i>Carinaropsis cymbula</i>	1	1
<i>Cyrtolites (Paracyrtolites) subplanus</i>	1	1
<i>Carinaropsis</i> cf. <i>C. acuta</i>	1	1

TABLE 8.—Relative abundance of species in the USGS silicified samples from the Grier Limestone Member of the Lexington Limestone

[Total number of samples = 18; total number of specimens = 541]

Species	Percentage of fauna	No. of samples
<i>Carinaropsis cymbula</i>	25	11
<i>Sphenosphaera clausus</i>	19	6
<i>Bucanopsis carinifera</i>	13	6
<i>Cyrtolites (Cyrtolites) retrorsus</i>	9	6
<i>Sphenosphaera</i> cf. <i>S. buriginensis</i>	8	3
<i>Sphenosphaera</i> cf. <i>S. troosti</i>	7	3
<i>Cyrtolites (Paracyrtolites) subplanus</i>	4	1
<i>Archinacella simulatrix</i>	3	4
<i>Bucania</i> cf. <i>B. nashvillensis</i>	3	2
<i>Bucania</i> sp. indet.	2	4
<i>Bucania subangulata</i>	1	2
<i>Cyrtolites</i> sp. indet.	1	3
<i>Sphenosphaera</i> cf. <i>S. clausus</i>	1	2
<i>Sphenosphaera</i> sp. indet.	1	2
<i>Carinaropsis</i> sp. indet.	1	2
<i>Bucania</i> cf. <i>B. sublata</i>	1	1
<i>Tropidodiscus</i> sp. indet.	1	1
<i>Sinuities</i> sp. indet.	1	1

The lowest members of the Lexington, the Curdsville Limestone and Logana Members, were dominated by two species, these being, in order of decreasing abundance, *Sinuities obesus* (pl. 9, figs. 1–12) and *Cyrtolites (C.) retrorsus* (pl. 5, figs. 1–4, 13), with *Salpingostoma kentuckyense* (pl. 24, figs. 10–12) continuing to be a common element from the Tyrone Limestone into the transgressive deposits of the lower portion of the Curdsville Limestone Member (tables 6, 7). The Curdsville has a high species diversity (17 species), probably reflecting the variety of depositional environments represented in the unit, from shallow transgressive bar and interbar deposits in the lower part of the unit to deeper subtidal environments in the upper part where it intertongues with the Logana Member. The three species cited above constitute 74 percent of the Curdsville fauna. The

TABLE 9.—Relative abundance of species in USGS silicified samples from the Perryville Limestone Member of the Lexington Limestone

[Total number of samples = 5; total number of specimens = 217]

Species	Percentage of fauna	No. of samples
<i>Sphenosphaera clausus</i>	47	4
<i>Bucanopsis carinifera</i>	12	4
<i>Bucania</i> cf. <i>B. sublata</i>	7	2
<i>Vallatotheca unguiformis</i>	6	3
<i>Carinaropsis cymbula</i>	6	1
<i>Bucania</i> cf. <i>B. nashvillensis</i>	5	3
<i>Sphenosphaera</i> cf. <i>S. buriginensis</i>	4	1
<i>Sphenosphaera</i> sp. indet.	4	2
<i>Tropidodiscus subacutus</i>	3	3
<i>Cyrtolites (Cyrtolites) retrorsus</i>	2	1
<i>Sphenosphaera</i> cf. <i>S. bilineatus</i>	1	1

TABLE 10.—Relative abundance of species in USGS silicified samples from the Devils Hollow Member of the Lexington Limestone  
[Total number of samples = 4; total number of specimens = 187]

Species	Percentage of fauna	No. of samples
<i>Tropidodiscus subacutus</i>	70	2
<i>Bucania</i> cf. <i>B. frankfortensis</i>	11	1
<i>Bucanopsis diabloensis</i>	7	2
<i>Sphenosphaera</i> sp. indet.	5	1
<i>Tropidodiscus</i> sp. indet.	4	2
<i>Sphenosphaera</i> cf. <i>S. clausus</i>	2	1
<i>Bucania</i> cf. <i>B. sublata</i>	1	2
<i>Sphenosphaera clausus</i>	1	1

Logana Member represents the height of the initial Lexington transgression, and may represent the deepest water environments in the formation. Although the Logana is a much more homogeneous lithologic unit of deeper water origin compared with the Curdsville Limestone, it is dominated by two of the same species. *S. obesus* makes up 77 percent of the low-diversity Logana fauna and is present in six of eight silicified samples. The *C. retrorsus* group makes up 22 percent of the Logana fauna (table 7). It is noteworthy that the monoplacophoran-bellerophontacean fauna of the Edenian Kope Formation, which consists of relatively deep water shales at the base of the Cincinnati Series, is also dominated by species of *Sinuities* and *Cyrtolites*. The Logana fauna is low in diversity, having only five species in three genera, and three of those species accounting for only about 1 percent of the symmetrical univalved fauna.

The Grier Limestone Member represents the most enduring, widespread, and uniform environmental conditions during Lexington deposition. Its monoplacophoran-bellerophontacean fauna is somewhat transitional in composition, and its high diversity (18 species) and even distribution of species relative abundance (table 8) apparently reflect the stability of the Grier environment. The nodular wackestones of the Grier indicate a soft-bottom environment with shell beds, and the abundance and variety of a normal marine fauna indicate a very favorable habitat. The three dominant symmetrical univalved molluscan species in the Grier are, in order of descending abundance, *Carinaropsis*

TABLE 11.—Relative abundance of species in USGS silicified samples from the Millersburg Member of the Lexington Limestone  
[Total number of samples = 5; total number of specimens = 80]

Species	Percentage of fauna	No. of samples
<i>Sphenosphaera clausus</i>	68	5
<i>Cyrtolites</i> ( <i>Cyrtolites</i> ) <i>retrorsus</i>	19	2
<i>Archinacella</i> sp. indet.	9	1
<i>Cyrtolites</i> sp. indet.	4	2
<i>Sphenosphaera</i> sp. indet.	1	1

TABLE 12.—Relative abundance of species in USGS silicified samples from the Tanglewood Limestone Member of the Lexington Limestone  
[Total number of samples = 5; total number of specimens = 89]

Species	Percentage of fauna	No. of samples
<i>Sphenosphaera</i> cf. <i>S. clausus</i>	65	3
<i>Sphenosphaera clausus</i>	15	1
<i>Bucanopsis carinifera</i>	13	1
<i>Sphenosphaera</i> sp. indet.	5	1
<i>Carinaropsis cymbula</i>	1	1
<i>Carinaropsis</i> sp. indet.	1	1

*cymbula* (25 percent) (pl. 38, figs. 1-12), *Sphenosphaera clausus* (19 percent) (pl. 31, figs. 7-10), and *Bucanopsis carinifera* (13 percent) (pl. 27, figs. 8-12). All have rapidly expanding shell forms, but only the first can be considered truly explanate. The abundance of morphotypes having broadly expanded apertures is comparable to Peel's (1977b, 1978) soft-bottom shallow-marine platform fauna from the Silurian Arisaig Group discussed earlier. It should be noted that the intrageneric species diversities are higher than in any other member of the Lexington Limestone. *Cyrtolites*, *Bucania*, and *Sphenosphaera* all have more than one species in the Grier, probably attesting to environmental stability and greater partitioning of niches.

The upper Lexington Limestone is a complex facies mosaic of interfingering carbonate depositional environments which intertongues upward with the more shaly deposits of the Clays Ferry Formation. Except for the Devils Hollow Member, all members of the upper Lexington Limestone, as well as the intertonguing Clays Ferry Formation, are dominated by *Sphenosphaera clausus*, with species of *Bucanopsis*, *Cyrtolites*, and *Carinaropsis* distributed throughout (tables 9-13). Whereas the *S. clausus* group makes up nearly 70 percent of the upper Lexington monoplacophoran-bellerophontacean fauna, it is nearly absent from the Devils Hollow Member, which is dominated by 70 percent *Tropidodiscus subacutus*, a species that is rare in other members. This discrepancy might be explained by the small number of samples from the Devils Hollow

TABLE 13.—Relative abundance of species in USGS silicified samples from the Clays Ferry Formation  
[Total number of samples = 12; total number of specimens = 419]

Species	Percentage of fauna	No. of samples
<i>Sphenosphaera clausus</i>	73	7
<i>Cyrtolites</i> ( <i>Cyrtolites</i> ) <i>claysferryensis</i>	16	10
<i>Sphenosphaera</i> cf. <i>S. clausus</i>	8	3
<i>Sphenosphaera</i> sp. indet.	2	3
<i>Bucania rugatina</i>	1	2
<i>Bucania</i> sp. indet.	1	2

Member. Only one sample accounts for the apparent dominance by *T. subacutus* in the unit; however, if this sample is ignored, *Sphenosphaera* spp. is still subordinate to other species in the Devils Hollow. Cressman (1973, p. 41) suggested that the Devils Hollow represents very shallow restricted lagoon and bar deposits. Most other upper Lexington members represent more normal shallow marine conditions, possibly accounting for the faunal differences.

The marked dominance of *S. clausus* through such varied depositional environments as the Perryville Limestone, Millersburg, and Tanglewood Limestone Members of the upper Lexington Limestone, as well as the relatively shale rich Clays Ferry Formation, is difficult to explain. It can only be assumed that there was some unifying environmental factor, such as a food source, in these varied environments that allowed the species to flourish during this period. In any case, *S. clausus* must have been an ecological generalist. When the paleosynecology of the entire Lexington fauna is analyzed, explanations for the distribution of individual taxa may become more clear. It is interesting that while most of the members of the upper Lexington Limestone are moderately shallow water facies and would seem to be adequate habitats for symmetrical molluscan univalves, diversities generally are relatively low. The Perryville Limestone Member is most diverse with 11 species; next is the Devils Hollow Member with 8 species. The Millersburg and Tanglewood Limestone Members, as well as the Clays Ferry Formation, contain only 5–6 species each. The Millersburg, which is similar to the Grier Limestone Member in lithology, bedding style, and overall fauna (Cressman, 1973, p. 43), would especially be expected to contain a more diverse fauna. This apparent anomaly can probably be explained by there being only 5 samples from the Millersburg, compared with 18 samples from the Grier Limestone Member.

#### COMMENTS ON THE PALEOECOLOGY OF THE STONES RIVER GROUP OF CENTRAL TENNESSEE

The bellerophon-taceans from the Blackriveran-Kirkfieldian-age Stones River Group of central Tennessee are listed in table 1. Data are derived from Wilson (1949) and museum specimens examined in the present study. No relative-abundance data or any other significant paleoecological data on the fauna are available, and except for a few observations made below, the available data do not permit detailed analyses. No monoplacophorans are listed in Wilson (1949).

The apparent low diversity of the Stones River fauna may be the result of a scarcity of collections. Only four genera and seven species are known (table 1). However, both the Stones River and High Bridge Groups represent

shallow subtidal-intertidal environments that are generally thought to be ideal habitats for the animals under discussion, and the low-diversity assemblages may truly reflect a paucity of species during that time.

*Tetranota bidorsata* is distributed throughout the Stones River Group (table 1). Both *Pterotheca expansa* and *P. saffordi* (pl. 39, figs. 1, 2) occur in thin-bedded limestones in association with abundant leperditicoid ostracodes, suggesting that these species were adapted to tidal flat and restricted lagoonal environments (pl. 39, figs. 5, 12 13; pl. 40, figs. 8, 9). Such occurrences are also known from the correlative High Bridge Group of Kentucky.

#### COMMENTS ON THE PALEOECOLOGY OF THE NASHVILLE GROUP OF CENTRAL TENNESSEE

The occurrences of monoplacophoran and bellerophon-tacean taxa in the Nashville Group are listed in table 2. Data are from museum specimens examined in this study and from faunal lists by Wilson (1949). No relative-abundance data are available.

#### HERMITAGE FORMATION

The monoplacophoran-bellerophon-tacean fauna of the Hermitage Formation is apparently of low diversity and abundance. Wilson (1949) reported species from only two members, *Phragmolites cellulosus* (pl. 43, figs. 4–12) from the Curdsville Limestone Member and *P. cellulosus* with *Cyrtolites retrorsus* from the "Ctenodonta member." Other species identified from museum collections in this study were *Archinacella valida* (pl. 2, figs. 15, 16) and *Undulabucania punctifrons* (pl. 23, figs. 1–9). Museum labels on these specimens do not allow more precise placement within the members of the formation. One noteworthy point is that both of the species listed by Wilson (1949) were reported from the two shallowest subtidal facies of the Hermitage Formation.

#### BIGBY-CANNON LIMESTONE

It is unfortunate that currently only presence-absence data are available for species from the Bigby-Cannon Limestone. That formation seems to be an ideal unit for paleoecological analysis, as it consists of a high-energy subtidal shoaling facies (Bigby facies), a low-energy shelf lagoon facies (Cannon facies), and a restricted lagoon-tidal flat facies (dove-colored facies). Nevertheless, some trends are discernible. Table 2 shows the distribution of monoplacophoran-bellerophon-tacean taxa in these three facies, as well as in the overlying Catheys Formation. Data are derived from both Wilson's (1949) species lists

and specimens in museum collections examined during the present study.

The Cannon facies contains nine species of monoplacophorans and bellerophontaceans, approximately twice the number reported from either of the other facies of the Bigby-Cannon Limestone. Alberstadt (1973, p. 630) cited preliminary work showing that most Cannon communities were dominated by bellerophontid and lophospirid gastropods and leperditicoid ostracodes. He suggested that the dark, organic-rich, muddy wackestone-packstone of the Cannon indicates quiet, nearly stagnant lagoonal conditions. Alberstadt (1973, p. 626) attributed much of the organic material in the Cannon to marine algae. Blue-green algal encrustations are common, but the rock also contains an appreciable amount of crushed, dark-orange and brown fragments of unidentifiable organic fossils, which probably are of algal origin. One such fragment illustrated by Alberstadt (1973, fig. 5D) resembles a small plumose growth of blue-green algae. It seems likely that the abundant gastropods and other fauna lived above the fetid mud bottom on such algal masses. Considering the moderately large shells of some of the Cannon bellerophontaceans (for example, *Bucania* sp. and *Sphenosphaera* spp.), if the animals were indeed algal foliage dwellers, the algae may have formed low, thick bushes or mats capable of supporting their weight. It seems the algae not only would have been a food source for the gastropods, but also might have baffled and stabilized the muddy sediment, effectively reducing turbidity. If the Cannon bellerophontaceans were not algal foliage dwellers, they must have been able to cope with muddy substrate conditions much better than predicted by Yonge (1947). In fact, the abundance of bellerophontaceans in such organic-rich fine sediments might lend support to the interpretation that they were bottom-dwelling detritus feeders and scavengers.

Each facies of the Bigby-Cannon Limestone contains a variety of general bellerophontacean morphotypes, and without relative-abundance data, no patterns are obvious. The high-energy shoals of the Bigby facies and the lagoonal-tidal flat muds of the dove-colored facies each supported approximately the same number of monoplacophoran-bellerophontacean species, three of which are common to both facies. Four of the species in the dove-colored facies are also found in the Cannon facies, but only two of the five Bigby species also are found in the Cannon.

#### COMMENTS ON THE PALEOECOLOGY OF UPPER ORDOVICIAN FAUNAS

Data on the paleoecology of the molluscan univalve taxa in the Upper Ordovician of the tristate area are scant. Previous paleoecological studies have focused on

TABLE 14.—Relative abundance of species in USGS silicified samples from the Dillsboro Formation in Indiana

[Total number of samples = 2; total number of specimens = 337]

Species	Percentage of fauna	No. of samples
<i>Sphenosphaera mohri</i>	74	2
<i>Cyrtolites (Cyrtolites) hornyi</i>	13	1
<i>Archinacella indianensis</i>	12	1
Bellerophontacean sp. indet.	1	1

the prolific brachiopod and bryozoan faunas of these strata, and gastropods generally are mentioned only as a general grouping (Fox, 1962, 1968; Hatfield, 1968; Richards, 1972; Richards and Bambach, 1975; Harris and Martin, 1979). Mollusks usually are abundant only in sparse, mollusk-rich beds scattered through the section. Pojeta (1971) has discussed the autecology of Upper Ordovician pelecypods, but the synecology and environmental distribution of entire molluscan communities remain unstudied.

Silicified beds and fossils are uncommon in the Upper Ordovician of the tristate area, and only a few collections were made by the USGS. Most specimens examined here were from existing museum collections. The current data base does not allow detailed paleoecological analysis. The USGS silicified samples from the Liberty biofacies of the Dillsboro Formation (Richmondian) of southeastern Indiana (6139-CO, 6140-CO) were the only Upper Ordovician USGS collections containing abundant well-preserved and silicified specimens (table 14). These samples contained specimens of *Cyrtolites hornyi* (pl. 8, figs. 1–12), *Sphenosphaera mohri* (pl. 36, figs. 1–12), and *Archinacella indianensis* (pl. 3, figs. 19, 20). The only other common genera in Upper Ordovician rocks of the area are species of *Sinuities* (pl. 10, figs. 1–13) and *Salpingostoma* (pl. 26, figs. 1–8).

By far the most abundant taxa in the Cincinnati section are species of *Sinuities* and *Cyrtolites*. Specimens of these two genera are locally abundant in mollusk-dominated beds, in many places occurring together, generally with one or the other clearly dominant. Such mollusk beds generally are thin limestone beds or lenses in interbedded limestone and shale sections. Adjacent strata are commonly dominated by brachiopod-bryozoan assemblages. The mollusk beds are generally considered to represent special environmental conditions, such as nearshore areas having abnormal marine salinities, but at present there are few sedimentological data to support such interpretations. Before interpretations can be made with confidence, detailed sedimentological and paleoecological analyses of thick stratigraphic sections are needed. One such section is locality KY-1 (see appendix), near Carrollton, Ky., where the well-exposed Kope Formation contains a number of such isolated mollusk beds. The small slab shown on plate 8, figure 21, is from

this locality and demonstrates the diversity of mollusks that can be present in such beds.

At locality OH-1 (Bear Creek Quarry), an argillaceous, mollusk-rich limestone lens surrounded by gray shale was found in the lower Kope Formation, about 10 ft above the Point Pleasant Tongue of the Clays Ferry Formation. This small lens was only a few feet across and a maximum of about 3 in thick. The surrounding shale and overlying and underlying limestone beds were dominated by trilobite-crinoid-brachiopod assemblages. Excavation of about 4 ft<sup>2</sup> (square feet) of the lens produced more than 100 well-preserved specimens of *Sinuities planodorsatus*, 5 specimens of *Tetranota bidorsata* (pl. 21, figs. 1–8), 1 specimen of *Cyrtolites claysferryensis*, and sparse othoconic nautiloids, lingulid brachiopods, small loxonometacean gastropods, crinoid ossicles and *Cryptolithus* trilobite fragments (pl. 4, fig. 17; pl. 21, fig. 1). This great concentration of symmetrical molluscan univalves is puzzling, as the surrounding strata apparently are barren of the taxa; perhaps it can be attributed to a localized food source. Petrographic analysis has not yielded any significant clues as to the nature of this possible food source. Another possible interpretation is that the mollusks were not the feeders, but rather the meal. Could such a concentration of shells be the “nest” of predatory nautiloids? It should be noted that the monoplacophoran and bellerophonacean shells are exceedingly well preserved and show no breakage. But then, there is no evidence for the presence of an operculum in these early forms that would have required forced entry by predators. Other such occurrences should be watched for, in the hope that clues to their origin can be found.

A third field occurrence, from the Clays Ferry Formation of north-central Kentucky, was a mollusk bed dominated by *Cyrtolites claysferryensis* and also containing lophospirid gastropods and sparse pelecypods (pl. 4, figs. 15, 16). Of particular interest is a specimen of *C. (Cyrtolites) claysferryensis* with an apparent borehole through its dorsum (pl. 4, fig. 15). Fenton and Fenton (1931), Carriker and Yochelson (1968), and Sohl (1969) have reviewed the occurrence of Paleozoic borings, which are common in brachiopods in the Upper Ordovician. Although Fenton and Fenton (1931) and most other early authors assumed that these borings were made by predatory gastropods, reviews of more recent authors have concluded that there is little evidence to support this interpretation. Sohl (1969) believed that the predatory boring habit common to many Holocene snails did not arise until Late Cretaceous time. He further agreed with Carriker and Yochelson (1968) that Paleozoic borers probably were mainly unknown soft-bodied organisms that employed a purely chemical means of boring. The boring shown here is believed to be the first reported in

a monoplacophoran shell. It is interesting that this boring is in the approximate position of the shell muscles.

The possible sources of nutrition and modes of feeding for primitive gastropods and monoplacophorans were discussed earlier, and it was stressed that evidence in the fossil record is scarce indeed. One approach to solving this puzzle is to draw conclusions from repeated associations. For example, the repeated occurrence of species of *Pterotheca* with leperditiid ostracodes in restricted lagoonal to intertidal environments in the Stones River and High Bridge Groups could be viewed as evidence of an algal grazing habit (pl. 39, figs. 3–5, 12, 13; pl. 40, figs. 8, 9).

Another association that has been observed repeatedly in Upper Ordovician strata is the occurrence of species of *Phragmolites* with small sticklike bryozoans. *Phragmolites* was never observed in mollusk-dominated beds, but was seen only in predominantly bryozoan-brachiopod assemblages. *P. dyeri* is shown on plate 45, figure 11, with abundant sticklike bryozoans. Specimens in the original type suite of *P. elegans* (pl. 45, fig. 10) are preserved with the aperture attached to sticklike bryozoans. The evidence is far from conclusive, but it is suggested that *Phragmolites* may have grazed on these bryozoans. The shells of most species of *Phragmolites* are small and thin enough to have been supported in bryozoan thickets. Note also the specimen of the related species *Undulabucania punctifrons* preserved with its aperture clamped over a massive bryozoan colony (pl. 23, figs. 2, 3).

*Sphenosphaera mohri* (pl. 35, figs. 1–14) and *Salpingostoma richmondensis* (pl. 26, figs. 1–8) have been observed in the rubbly, higher energy deposits in the Richmondian-age Whitewater Formation of southeastern Indiana. These relatively large, massive-shelled species are commonly associated with massive bryozoans and brachiopods in transported shell-debris deposits, where much of the skeletal material is broken and worn. *S. mohri* is commonly found encrusted by massive bryozoans. Apparently these taxa inhabited higher energy environments either on or surrounding shoaling areas.

#### SHELL SCULPTURING AND ENCRUSTATION AS DEFENSES AGAINST PREDATION

As noted in the “Systematic Paleontology” section under the appropriate species, shell sculpturing might be an adaptation for camouflage against predators. Most notable examples are the reticulate patterns on the shells of species of *C. (Cyrtolites)* (pls. 4–7) and the fine wavy patterns on the shells of species of *Undulabucania* (pl. 23, figs. 1–15).

Of even greater advantage for camouflage is encrustation by epizoans. Carrier shells (gastropods that cement

skeletal debris to their surface for camouflage) are known from the Devonian (Linsley and Yochelson, 1973) to the Holocene. McNamara (1978) has discussed the encrustation of Late Ordovician gastropods by bryozoans, and suggested a symbiotic relationship. The gastropod was afforded protection from predators, while the bryozoan benefited by having a perch from which to suspension feed. Benefit to the bryozoan was enhanced by currents created by the movement of the gastropod, as well as by the movement of currents through the shell of the gastropod.

Bryozoan-encrusted shell debris of all kinds abounds in many Upper Ordovician beds of the tristate area, and is usually easily attributable to postmortem encrustation. Many of the shells illustrated on the plates herein have bryozoan encrustations. Judging from the positions of many of the encrustations, or their extremely massive character, most of these encrustations took place after the animal died (pl. 1, figs. 9–11; pl. 30, fig. 19; pl. 32, figs. 6–9; pl. 34, figs. 4, 6; pl. 37, figs. 18, 19; pl. 41, figs. 4, 5). However, other encrustations thinly cover both sides of a coiled shell, but not the outer apertural lip. Such cases are particularly common in species of *Cyrtolites* (pl. 6, figs. 1, 12–16; pl. 7, figs. 5–7). Morris and Rollins (1971, figs. 4, 5) illustrated another such specimen of *Cyrtolites* cf. *C. ornatus* that is completely encrusted by bryozoans but also has further encrustation by *Cornulites* worm tubes. Of particular significance is the symmetrical attachment of these *Cornulites* on the upper umbilical regions of both sides of the shell, and the mutual adapertural orientation of the worm tubes. This occurrence is strong evidence for encrustation of the *Cyrtolites* shell while still occupied by a living animal. These encrustations not only would serve to camouflage the shell, but also would strengthen it against crushing, by predators such as nautiloids, and thicken it so as to make entry by drilling more difficult. The borehole in a shell of *C. (Cyrtolites) claysferryensis* (pl. 4, fig. 15) demonstrates the presence of drilling predators.

Signor and Brett (1984) proposed that bellerophontaceans and other invertebrate groups showed an increase in the frequency of predation-resistant morphologic features during the mid-Paleozoic in response to the rapid radiation of durophagous (shell-crushing) predators (primarily crustaceans and fishes). They pointed out that among mid-Paleozoic bellerophontaceans, there is a decrease in the frequency of phaneromphalous genera and an increase in the frequency of genera having sculptured shells. Vermeij (1975, 1978) has demonstrated that modern gastropods having phaneromphalous shells or unsculptured shells are more susceptible to durophagous predation. It should be noted that a trend toward reduction of the umbilicus in Ordovician bellerophontaceans is thought here to have facilitated the

transport of the bellerophontiform shell, but apparently this more mobile shell form was also preadapted to deal with durophagous predators (see "Functional Morphology" section).

## FUNCTIONAL MORPHOLOGY

### INTRODUCTION

The primary functions of the shell in molluscan univalves are to house and protect the animal from the dangers of its external environment and to provide sites for muscle attachment. The ancestral monoplacophoran univalve is generally assumed to have had a simple low conical shell reflecting the form of the animal's visceral hump (Stasek, 1972). As evolution progressed and the visceral mass and its containing shell became larger and more elongate, the shell coiled in order to maintain balance. The factors that seem to have had the greatest control over coiled shell morphology are the balancing of the shell itself and the efficient channeling of water currents through the shell for respiration and, sometimes, feeding.

In a symmetrically coiled monoplacophoran, which has not undergone the larval process of torsion, the head of the animal is under the coil (exogastric). In a symmetrically coiled bellerophontacean gastropod, which has undergone torsion, the head is toward the outer apertural margin and the shell coils posteriorly away from the head (endogastric). These opposite orientations should be reflected in the functional aspects of shell morphology (Peel, 1987, p. 326). Herein, morphological evidence for each orientation in bellerophontiform shells is discussed.

Raup (1966) presented four parameters that can be used in the description and functional analysis of coiled shells: the shape of the generating curve (whorl shape), the rate of whorl expansion (W), the distance of the generating curve from the axis (D), and the movement of the generating curve along the axis (whorl translation=T). In planispiral shells, T always equals zero. Raup (1967, text-fig. 3) illustrated cephalopod shell forms under a continuum of varying W and D values. This approach is also useful in picturing the effects of these parameters on bellerophontacean-monoplacophoran shell forms. These W and D values are referred to repeatedly in the following functional analyses (Peel, 1987, p. 322).

### MONOPLACOPHORA

#### TRYBLIDIIDA

The shells of monoplacophorans of the order Tryblidiida grade from cap shaped to conical in form, and are

generally considered more primitive morphotypes than the coiled shells of the Cyrtoneillida. However, Pojeta and Runnegar (1976, p. 29) pointed out that relatively tall shells are the first to appear in the Tommotian fossil record, and that limpet-shaped shells seem to have developed from them. They suggested that the limpet-form shells may not represent the ancestral stock, but rather were secondarily adapted for benthic grazing. Indeed, the morphological similarities of the typical cap-shaped tryblidiid shell and the shell of the patelliform gastropods, which are probably secondarily adapted for clinging and grazing, suggest a common mode of life for the two groups. In fact, Lowenstam (1978, p. 231) has reported the modern monoplacophoran *Vema* clinging to phosphorite nodules in dredge samples and noted that the animals were nearly stationary during a month of laboratory observation. On the other hand, Lemche and Wingstrand (1959, p. 63) cited *Neopilina*, whose shell is essentially identical to that of *Vema*, as a deposit feeder from abyssal, dark, muddy sediment where, they claimed, there was an absence of suitable hard substrata for clinging. It remains uncertain whether the monoplacophoran cap-shaped shell is adapted secondarily to a clinging mode of life, like that of the patellacean gastropods, or simply reflects the primitive condition.

The encrustation of many Ordovician tryblidiid shells by bryozoans suggests that the animals led an exposed life, such as that of an algal grazer, rather than the often partially covered life of a bottom-dwelling deposit feeder. Furthermore, the highly sculptured shells of some genera, such as *Helcionopsis* (pl. 2, figs. 1–3) and *Vallatotheca* (pl. 1, figs. 8–31), argue against a deposit-feeding habit. Vermeij (1978, p. 33) pointed out that gastropods living under wave-energy stress generally have lower shells, many with smoother surfaces, and a relatively larger aperture and foot than animals living in more sheltered surroundings. These observations probably also hold true for Paleozoic monoplacophorans living in shallow-water habitats. However, at present, detailed paleoecological data on the distribution of tryblidiid taxa are insufficient to test this model.

Through studies of the anatomy of *Neopilina galathea* by Lemche and Wingstrand (1959), tryblidiid monoplacophorans are known to have a poorly developed head, and to have numerous pedal muscles and five or six pairs of gills distributed around the lateral and posterolateral shell margins. Pojeta and Runnegar (1976, fig. 10) confidently adapted this morphology to the Cambrian genus *Scenella*. They traced the probable path of water flow through the shell as entering anterolaterally, running along the lateral mantle cavity, and exiting posterolaterally (figs. 14A, B). In side view, the lateral margins of Ordovician tryblidiid shells can be straight (pl. 2, figs. 3, 8, 20), convex (pl. 1, figs. 27, 28), or concave (pl. 3,

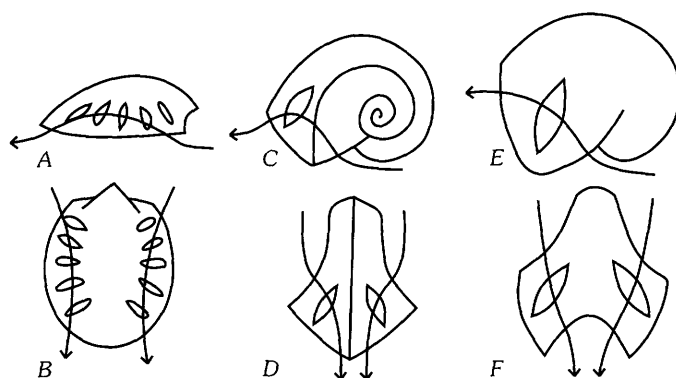


FIGURE 14.—Paths of water currents through the shells and mantle cavities of monoplacophorans. Fusiform-shaped structures represent the gills. A, B, Right-lateral and dorsal views of a tryblidiid, which had multiple pairs of gills in a lateral to posterolateral mantle cavity. C, D, Right-lateral and dorsal views of *Cyrtolites*, which had a single pair of gills in a posterior mantle cavity. Water currents enter around the lateral angulations of the diamond-shaped aperture and exit through the dorsal angulation, which is sinuate in some species. E, F, Right-lateral and dorsal views of *Sinuites*, which had a single pair of gills in a posterior mantle cavity. Water currents enter through apertural reentrants in the lobate aperture and exit through a deep dorsal sinus.

figs. 9, 22). It seems likely that these different lateral apertural margin profiles were designed to channel currents more efficiently through the mantle cavity. However, it is at this time impossible to say what significance these different lateral apertural profiles had to possibly varied modes of life.

#### CYRTONEILLIDA

The Cyrtoneillida is generally believed to be the more advanced of the two monoplacophoran orders. Because of the mechanical requirements of a coiled shell, the isostrophic cyrtoneillids had fewer pedal retractor muscle scars than the tryblidiids. These scars typically form anterior, posterior, and lateral pairs arranged in a ring well within the aperture (Rollins, 1969). Stasek (1972, p. 21) proposed that this migration of the muscle insertions deeper into the shell suggests the concomitant development of a larger posterior mantle cavity and the ability of the animal to draw into it. Peel (1980) also suggested that circumumbilical muscle attachment in sinuitids represents the ability to retract into the shell and reflects a monoplacophoran morphological grade that may have first undergone torsion. Stasek (1972) further claimed that the enlarged mantle cavity was accompanied by a reduction in the number of the gills, but an increase in their size. Finally, Stasek claimed that the steep anterior slope of the coiled shell might indicate the development of a distinct head in the organisms.

Such anatomical modification could explain the success of the cyrtoneillid genera *Cyrtolites* and *Sinuites* during



the Middle and Late Ordovician. Features of the shell morphology of these two successful Ordovician genera demonstrate adaptations in the exogastric shell for more efficient water flow through the mantle cavity. Linsley (1978a, b) pointed out that the obstruction of anterior inhalant passages into the shell by the coil and the fleshy stalk leading from the foot to the visceral mass made it necessary for the inhalant ducts to the posterior mantle cavity to be concentrated laterally. Typically, species of *Cyrtolites* have diamond-shaped apertures (pl. 5, figs. 11, 14; pl. 8, figs. 1, 5, 8; figs. 14C, D). Starobogatov (1970) and Linsley (1978b, p. 437) have interpreted the lateral angulations of these apertures as inhalant canals, and the dorsal angulation, which is sinuate in Middle Ordovician species of *Cyrtolites*, as the exhalant canal. It should be noted that not all species of *Cyrtolites* have such angulated apertures. *C. (Cyrtolites) retrorsus* shows a complete gradational series in apertural outlines, from diamond shaped to nearly circular (pl. 5, figs. 3, 5, 8, 11, 14, 18, 22). However, the marked lateral angulations of the apertures in *C. (C.) claysferryensis* (pl. 8, figs. 11, 15) and *C. (Paracyrtolites) carinatus* (pl. 7, figs. 18-25), which occupied the clay-rich environments of the Clays Ferry and Kope Formations, might indicate a need for more efficient channeling of currents, and thereby support Linsley's conclusions.

Starobogatov (1970) noted grooves along the sides of the final whorl in the Devonian cyrtoneid *Sinuities* that he interpreted as inhalant channels, with the posterior sinus acting as an exhalant canal. He claimed that the narrow streams of water that would be channeled through these lateral grooves into the posterior mantle cavity could probably bathe only one pair of posterolateral gills efficiently. This sinuitid hydrodynamic design is also demonstrated well by Ordovician species of *Sinuities* illustrated herein (figs. 14E, F). Water would be drawn into the shell anterolaterally through umbilical reen-trants along the inner apertural margin (pl. 9, figs. 3, 4, 12; pl. 11, figs. 3, 7, 9). After passing over the gills, the deoxygenated water and waste products would be expelled through the posterior apertural sinus (pl. 11, figs. 1, 2, 6, 10, 11). The lateral apertural lobes of *Sinuities*, which project downward to varying degrees in different species, probably protected the single pair of large gills. These lobes also could have acted as struts, supporting the shell while the animal was inactive yet still allowing movement of water through the shell. Such supportive struts are known in the shells of living and fossil gastropods (Linsley and others, 1978).

Although the apertural margins of *Sinuities* and *Cyrtolites* have been modified for the same purpose, the general shell morphologies of the two genera are quite different. Species of *Cyrtolites* are loosely coiled and widely umbilicate (pl. 5, figs. 6, 9, 12; pl. 6, figs. 1, 6, 18)

(high D value of Raup, 1966), and even become disjunctly coiled in *C. (C.) disjunctus* (pl. 6, figs. 19-22). The plane of the aperture in *Cyrtolites* is tangential to the coil, enabling the animal to clamp down onto hard substrata. Middle Ordovician species, such as *C. (C.) retrorsus*, had a shallow apertural sinus (pl. 5, figs. 7, 13) that would have prevented a complete seal around the clamped-down aperture, but would have enabled more efficient expulsion of water from the mantle cavity. This apertural sinus is not present in Late Ordovician species, such as *C. (C.) ornatus* (pl. 6, figs. 7, 10), so that the entire apertural margin was in the same plane and the clamped-down shell would be more completely sealed off. Perhaps such protection was of more benefit to the survival of species of *Cyrtolites* than was the sinus and its exhalant function.

In contrast, species of *Sinuities* have more tightly coiled shells (pl. 9, figs. 4, 8; pl. 11, figs. 3, 8) (low D value), which are nonumbilicate or nearly so, have rounded whorls, and have very irregular apertural margins. As discussed above, the inhalant umbilical reen-trants, the jutting posterolateral lobes, and the pronounced posteromedian sinus (pl. 11, figs. 6-11) are all clear adaptations for efficient channeling of water through the shell, but such irregularities of the apertural margin would surely preclude efficient clamping down on firm substrates. In the faunas studied here, species of *Sinuities* are most common and diverse from the deeper water, muddy environments of the Logana Member of the Lexington Limestone and the Kope Formation. Living in these soft-substrate environments must have made efficient channeling of water through the shell (in order to prevent fouling of the bipectinate gills by fine sediment) more important to survival than the ability to clamp down. Also, the tightly coiled shell of *Sinuities* most likely indicates a more vagrant mode of life than that of *Cyrtolites*. Of possible significance to this point is the fact that specimens of *Cyrtolites* commonly are encrusted by epizoans, whereas specimens of *Sinuities* are rarely encrusted.

## BELLEROPHONTACEA

### SHELL COILING

Linsley (1977, 1978a, b) discussed the benefits and problems resulting from the coiling of the shell in the Gastropoda. Shell coiling lowers the center of gravity and the pressure point, reduces the total surface area of the shell subject to fluid drag, reduces the shearing effect, and thus reduces the energy necessary to move the shell forward. In other words, shell coiling enables the animal to be more mobile, an obvious advantage for feeding and self protection.



An anisotropically coiled shell, such as that of the vast majority of gastropods, is naturally unbalanced. Shell balance must be restored by positioning the center of gravity over the midline of the foot (Linsley, 1977). This is done through the tipping up of the shell (inclination) and the twisting of the coil toward the rear so that torsion is effectively reduced (regulatory detorsion). On the other hand, the isotropically coiled gastropod shell, such as that of a bellerophontacean, is naturally balanced. Its axis of coiling is parallel to the substrate, and its center of gravity is automatically positioned over the midline of the foot. Nevertheless, a loosely coiled isotropic shell can also be difficult to balance, as it affords broad areas of resistance from all sides. Just as in an anisotropically coiled form, a loose coil hinders movement, makes the animal more prone to predation, and probably restricts it to either algal grazing or sedentary suspension feeding in a quiet-water environment. Bellerophontaceans adopted three adaptive strategies to reduce resistance of their planispiral shells to movement and (or) currents: (1) lateral compression of the whorl shape, (2) tightening of the coiling radius (decrease in D), which increased whorl overlap and reduced the size of the umbilicus, and (3) increase in the rate of whorl expansion (W) (Linsley, 1977).

In the early evolution of the Bellerophontacea, there is a clear trend from primitive loose shell coiling toward tighter shell coiling (decrease in D value) or reduction of the coil altogether (fig. 15). All of the earliest bellerophontaceans are loosely coiled (high D value). The Upper Cambrian *Chalarostrepsis* is actually disjunctly coiled in adulthood (Knight and others, 1960, fig. 94). Yochelson (1971) and Peel (1975b) have interpreted disjunct coiling in gastropods as representing a sedentary suspension-feeding mode of life. The descendants of *Chalarostrepsis*, the Ordovician genera *Tropidodiscus* (pl. 41, figs. 6–13) and *Phragmolites* (pl. 44, figs. 1, 5, 8), have loose but contiguous coils, leaving a wide-open umbilicus. Their laterally compressed shells are generally thin and light, probably to make balancing easier. These forms must have inhabited only quiet-water areas (Linsley, 1978b) and were probably algal grazers or algal foliage dwellers.

The progressive trend toward tighter coiling is exemplified within the genus *Bucania* (fig. 15). The earliest appearing and more morphologically primitive members of the genus, those species in Ulrich and Scofield's (1897) *B. sulcatina* group (pl. 12, figs. 1–9), have wide umbilici (high D values) and deep, narrow slits like the tropidodiscids, but have broad, depressed whorls (with low W values). Members of the new genus *Undulabucania* (pl. 23, figs. 1–15) are of the same morphological grade. From this level, there is a complete morphological gradation within the genus *Bucania* to the more advanced *B.*

*nashvillensis* group (pl. 14, figs. 1–14), which is characterized by tighter coiling (lower D values), smaller umbilici, longer apertures (higher W values), more rounded whorls, and, in many cases, thicker shells. These features lowered the shell's center of gravity, reduced its surface area, and streamlined its form, thus making it easier to balance and transport. The thickening of the shell suggests migration of some specimens into new, higher energy environments. The lengthening of the aperture, and presumably the foot, indicates a trend toward faster movement. The rounding of the whorls served to streamline the shell, reducing resistance against movement. These modifications indicate an increase in the mobility of species of *Bucania* during the Middle Ordovician. The broad, bulky shells of the *B. sulcatina* group probably represent sluggish grazers. The more compact and streamlined shells of the *B. nashvillensis* group must have allowed a greater variety of life habits. Most species of both groups have moderately large to large shells, and must represent bottom-dwelling animals. *Bucania micronema* (pl. 19, figs. 1–6) may have been small and lightweight enough to have been an algal foliage-dweller.

This progression went still further in more advanced Middle Ordovician bellerophontaceans. The bucanopsids and bellerophontids have still more tightly coiled shells (low D values), and most species have completely or nearly closed umbilici. The rate of whorl expansion (W) in the shells also increases, resulting in a more compact coil. The compact, rounded shells at this level of development are thought to represent the most mobile of the Ordovician bellerophontaceans. This interpretation could partly account for the wide distribution and large numbers of species, such as *Sphenosphaera clausus* (pl. 30, figs. 1–23; pl. 31, figs. 1–13) and *Bucanopsis carinifera* (pl. 27, figs. 1–16), in the Middle Ordovician deposits of Kentucky and Tennessee (see section on paleoecology). These species apparently occupied a variety of depositional environments and may have had a wide range of life habits.

The next step in this morphological sequence was toward specialization through reduction of the coil and development of a broadly expanded aperture (very high W values), as seen in the carinaropsids and pterothecids. *Sphenosphaera* showed the incipient stages of apertural platform evolution in the lineage (pl. 30, figs. 2, 9, 17). In *Carinaropsis*, the apertural platform evolved to cover approximately one-third of the aperture opening (pl. 37, figs. 3, 4, 18, 19). The platform's function must have been to support the animal's visceral mass, a function the reduced coil could no longer serve in the adult animal. This specialized shell form probably represents a mobile, but sluggish creature. The extreme of this trend is seen in *Pterotheca* and its relatives. They exhibit a reduced

MORPHOLOGICAL AND ECOLOGICAL TRENDS IN ORDOVICIAN BELLEROPHONTACEANS							
ECOLOGICAL TREND	Increase in mobility →						
	Probable decrease in mobility →						
MORPHOLOGICAL TRENDS	Increase in rate of whorl expansion (W) →						
	Tightening of coiling (decrease in D) →			Reduction of coil →			
	Decrease in size of umbilicus →			Development of inner aperture platform →			
	-----						
		Slit generally deep and narrow	Slit generally short and wide			Slit as open keel	
TYPICAL							
SHELL							
FORMS							
	<i>Bucania sulcatina</i>	<i>Bucania nashvillensis</i>	<i>Sphenosphaera clausus</i>	<i>Carinaropsis cymbula</i>	<i>Pterotheca saffordi</i>		

FIGURE 15.—Morphological and corresponding ecological trends in Middle Ordovician bellerophontaceans. Five general levels of development are recognized. Dashed line indicates early beginning of inner apertural platform. *Level 1* (a, b) Left-lateral and ventral views of *Bucania sulcatina*. Typical of this level of development are a wide, open umbilicus and a deep labral slit up to a half-whorl deep. Species of *Bucania* and *Undulabucania* in this group have broad, depressed whorl forms; however, the tropidodiscids, most of which have high, narrow, laterally compressed whorl forms, also belong in this group. *Level 1* taxa probably were sluggish vagrant benthos. *Level 2* (c, d) Left-lateral and ventral views of *Bucania nashvillensis*. Note the increase in the rate of whorl expansion, the decrease in the coiling radius, the lengthening of the whorl form, and the shortening of the labral slit. Similar shell forms such as those of *Tetranota bidorsata* also belong to this group. *Level 2* taxa probably were moderately mobile vagrant benthos. *Level 3* (e, f, g): Left-lateral, anterodorsal, and ventral views of *Sphenosphaera clausus*. Note the closing of the umbilicus through continued increase in the

rate of whorl expansion and decrease in the radius of coiling. Note also the increase in the flaring of the aperture lips and the incipient outbuilding of an inner apertural platform. Species of *Bellerophon* and *Bucanopsis* also belong to this group, which is thought to be the most mobile of the Ordovician bellerophontaceans. *Level 4* (h, i, j) Left-lateral, anterodorsal (with dorsum partly cut out to show apertural platform), and ventral views of *Carinaropsis cymbula*. At this level, the rate of whorl expansion has increased to the point where the coil is nearly completely reduced in the adult animal. The coil can no longer support the visceral mass in the adult animal, and an inner apertural platform evolved and served the same support function. *Level 4* taxa probably were sluggish vagrant benthos. *Level 5* (k, l, m) Left-lateral cross-sectional transverse cross-sectional, and ventral views of *Pterotheca saffordi*. At this specialized level of development, the coil is completely reduced, and the apertural platform evolved so as to cover approximately two-thirds of the aperture. *Level 5* taxa probably were very sluggish, nearly sedentary animals. W, rate of whorl expansion; D, distance of generating curve (whorl) from axis.

vestigial coil and an interior apertural platform that covered more than one-half of the aperture opening (pl. 40, figs. 4, 6). This more highly specialized animal was probably nearly sedentary, living in shallow nearshore areas and possibly suspension feeding, like morphologically similar *Crepidula* of modern seas, or sluggishly grazing on algal mats.

In summary, there was a trend toward tighter coiling of the shell and the decreasing size of the umbilicus (decreasing D values) in Ordovician bellerophontaceans. This trend was in many cases accompanied by an increase in the rate of whorl expansion (W). These trends allowed easier balance and transport of the shell, and thereby permitted greater mobility. This greater mobility

enabled the bellerophontaceans to live in higher energy habitats and to adopt new modes of life. The greater mobility is regarded as an important factor in the Middle Ordovician radiation of the bellerophontaceans. The very high W values seen in carinaropsids resulted in nearly immobile animals.

These conclusions differ slightly from those of Rollins (1967, p. 54–64), who postulated three forms of bellerophontaceans: clingers, creepers, and ploughers. Clinging forms were thought to be sluggish in their habits and to have clamped their shells vertically down over the foot against firm substrates in limpetlike fashion for protection. Typically, Rollins' clingers had rapidly expanding, even explanate, apertures with flat margins. Ordovician genera in this group are *Carinaropsis*, *Pterotheca*, and possibly *Salpingostoma* (pl. 25, figs. 1–14). However, only the last of these genera was found associated with firm substrates in the present study. *Salpingostoma kentuckyense* is present in bioclastic beds of the Tyrone Limestone and the lower Curdsville Limestone Member of the Lexington Limestone, and *S. richmondensis* is present in Upper Ordovician bioclastic beds. *Carinaropsis* and *Pterotheca* are more common in fine-grained limestones in the Middle Ordovician rocks of Kentucky and Tennessee. Peel (1977b, p. 47) has proposed that low, explanate shell forms were adapted to life on soft substrates, where their broad shells would act like snowshoes to prevent the animal from sinking into the soft sediment. "Clinger" is probably a poor term for this group, as they were more likely sluggish vagrant, benthonic animals. Horny (1963a) reported explanate shells of similar morphology from both soft, muddy paleoenvironments and firm bioclastic paleoenvironments. It may be that the explanate shell form was not adapted to any specific substrate conditions.

Rollins' (1967) second group, the creepers, was thought to include more mobile types and to be capable of total retraction of the head-foot mass into the shell like most conspiral gastropods. He included in this group such Ordovician genera as *Bellerophon* (pl. 18, figs. 10–17), *Kokenospira* (pl. 20, figs. 9–12), *Tetranota* (pls. 21, 22), *Tropidodiscus* (pl. 41, figs. 6–13), *Phragmolites* (pls. 43, 44), and *Temnodiscus* (pl. 42, figs. 3–6). I would add to the group the genera *Sphenosphaera* (pls. 29–36), *Bucanopsis* (pl. 27, figs. 1–20), and *Bucania* (pls. 12–20), which Rollins considered clingers. The relative mobility of individual species in this group was probably quite variable. Mobility should have increased with an increase in the whorl overlap (decrease in D), a decrease in the size of the umbilicus, and an increase in the rate of whorl expansion (W) to a point where the coil was small and lightweight but still large enough to support of the visceral mass. Other important considerations in esti-

inating relative mobility are shell thickness and whorl cross-sectional area and shape.

Rollins' (1967) third group, the ploughers, included only such late Paleozoic forms as *Euphemites*, which has extensive inductural deposits over much of the body whorl. They were believed to have ploughed through soft sediment in search of food much like the modern gastropod *Polinices*. Such forms must have been either deposit feeders or predators, like *Polinices*.

Linsley (1978a) attempted to estimate bellerophontacean locomotion rates from shell forms and used generic morphotypes for examples. He concluded that low explanate shells belonged to sluggish grazers or deposit feeders. He thought the form of *Tropidodiscus*, with its laterally compressed whorls, indicated considerable mobility, but that its high center of gravity must have restricted it to quiet-water environments. He considered the tightly coiled *Bellerophon* and *Euphemites* morphotypes to be the most mobile of the bellerophonts. Finally, he considered *Knightites*, which is a moderate-sized shell having a small umbilicus and a slightly flaring aperture, a sluggish grazing animal because of its high development of ornamentation. I generally agree with Linsley's conclusions, but I tend to disagree with the last. I doubt that the shell ornamentation of *Knightites* would have hindered its mobility. In fact, I believe the general shell form to have the potential of a least moderate locomotion. The same general morphotype also characterizes many other taxa, the most notable here being the *Bucania nashvillensis* group and species of *Tetranota*, such as *T. bidorsata* and *T. wisconsinensis*.

#### FUNCTIONAL ASPECTS OF SELECTED BELLEROPHONTACEAN SHELL FORMS

##### EXPLANATE SHELLS

An explanate shell is one in which the rate of whorl expansion increases markedly during maturation, so that in maturity the aperture is broadly expanded and oriented tangential to the coil and the substratum. Many unrelated bellerophontacean genera are characterized by this adult expansion of the shell. Notable examples among the fauna included in this study are *Salpingostoma* (pls. 24, 25) and *Carinaroposis* (pls. 37, 38).

Before expansion, the shell of *Salpingostoma* (pl. 24, figs. 8, 14) closely resembles shells of members of the *Bucania sulcatina* group, except that it apparently has a nearly radial aperture. Linsley (1977, p. 197) defined a radial aperture as one whose apertural plane passes through the axis of coiling, rather than being tangential to the body whorl. Linsley claimed that modern gastropods having radial apertures typically are nearly sedentary and live with the apertural plane perpendicular to the substrate, rather than parallel to the substrate as in

tangential forms. The adult expanded aperture of *Salpingostoma* is tangential to the coil. Using this criterion, it seems that juvenile *Salpingostoma* may have led an essentially sedentary existence, like most gastropods having radial apertures (Linsley, 1977, p. 198), but became more capable of mobility with the development of the tangential aperture in maturity. Furthermore, the expanded bell-shaped aperture of the adult is in many cases quite thickened and, of course, has the long, open slit characteristic of the genus. The apparently sedentary juvenile may have lived through suspension feeding in more sheltered microhabitats. The adult, with its tangential and thickened aperture, could sluggishly move its broadly umbilicate shell into more current swept areas, where its expanded foot would cling to firm substrates. The long adult slit probably served an enlarged single pair of gills and furnished a large exhalant area, making it possible to move a larger amount of water through the mantle cavity. This would have been of particular advantage if the animal were a suspension filter feeder. The modern suspension-feeding caenogastropod *Siliquaria* has a long, open slit that serves a single large food-collecting gill.

In *Carinaropsis* the coil is nearly lost, and in *Pterotheca* it is completely lost. In both genera, the shell is thin and lightweight. In these forms, the visceral mass is supported within a broadly expanded body whorl by an internal platform similar to that of the modern slipper limpet *Crepidula fornicata*, which is a nearly sedentary suspension feeder.

Explanate shells have often been interpreted as being adapted to a clinging mode of life. Concomitant with the development of an expanded explanate aperture is the expansion of the foot. Vermeij (1978, p. 33) has reported that modern marine gastropods living in higher energy settings generally have lower shells and a relatively larger aperture and foot than gastropods living in adjacent more sheltered settings. Of course, the expanded foot would give a broader, more powerful base for clinging. On the other hand, Peel (1975a, c, 1977b, 1978) has suggested that the expanded aperture and foot of explanate bellerophontaceans was an adaptation for life on soft substrates, acting like snowshoes to prevent submergence of the animal into the sediment, as in the modern deposit-feeding gastropod *Aporrhais*. He supported this conclusion by citing occurrences of the explanate bellerophontacean genera *Anapetopsis* and *Phragmosphaera* in soft-bottom environments in the Silurian Arisaig Group of Nova Scotia. A comparable association was reported by Gromaczakiewicz-Lomnicka (1972) from a Carboniferous black shale in Poland, where the explanate bellerophontacean *Patellilabia* is the only large gastropod in a fauna of otherwise diminutive algal-foliage-dwelling gastropods. However, Horny (1963a, p.

66, 67) cited bellerophontaceans having explanate apertures and similar shell morphologies from soft-bottom, muddy facies and from firm-bottom facies of tuffaceous and skeletal debris rocks in the Ordovician-Silurian of Bohemia.

Perhaps the broadly explanate aperture of bellerophontaceans was an adaptation that could serve different functions. Other morphological characteristics of the shells, such as shell size and thickness, must also be taken into account in functional analyses. For example, *Carinaropsis* generally has a very thin, lightweight shell, and among the faunas described herein was most common in the Grier Limestone Member of the Lexington Limestone, an apparently soft bottom facies. Conversely, those explanate shells adapted for powerful clinging in higher energy conditions would be expected to be thicker and heavier. One such example might be *Salpingostoma richmondensis*, which is common in deposits of broken and worn skeletal debris in the Richmondian Whitewater Formation of Indiana and Ohio.

#### TRILOBED SHELLS

Peel (1974) reported at least five genera of bellerophontaceans having trilobate shells in Lower Ordovician through Devonian strata. The appearance of the trilobate whorl form in unrelated stocks can be explained through its functional attributes. Peel (1974, p. 248, 249) interpreted the trilobate dorsum as a modification of the shape of the mantle cavity and its openings to separate inhalant streams of clean water from the exhalant current of fouled and deoxygenated water. Such a modified design would increase the efficiency of water flow through the mantle cavity and would therefore be a likely functional adaptation in unrelated stocks.

Peel (1977b, 1978) has noted the common occurrence of trilobate bellerophonts in nearshore fine-grained sediments in Ordovician and Silurian-Devonian deposits. He cited *Tritonophon* as common in soft-bottom, shallow marine platform facies in the Arisaig Group of Nova Scotia, but absent from contemporary firm-bottom faunas. He considered the genus to be a probable algal foliage dweller. Likewise, Bretsky (1970b) cited the trilobate *Plectonotus* sp. from delta front silts and shales of the Upper Ordovician Queenston delta of the Central Appalachian region. He also speculated that this form was an algal foliage dweller.

Of the fauna studied here, *Tetranota* (pl. 21) is the only trilobed bellerophontacean. In the Middle Ordovician Stones River Group of Tennessee, the genus occurs in fine-grained limestones. It also is present in the offshore shales of the Upper Ordovician Kope Formation in Kentucky and Ohio. Both occurrences reflect soft-bottom

environments. It may be that the increased efficiency of water flow through the mantle cavity of the trilobate shell allowed these animals to inhabit fine-sediment, soft-bottom facies.

#### PALLIAL SYSTEM AND LABRAL EMARGINATION

The mantle cavity is one of the most characteristic features of the Mollusca. In gastropods, it is primarily a respiratory chamber housing the ctenidia (gills) and the associated osphradia and hypobranchial glands, which together form a functional unit (Yonge, 1947). The osphradia, which are situated near the entrance to the cavity, "estimate" the sediment influx. The hypobranchial glands secrete mucus to consolidate the invading sediment particles, so that they do not foul the ctenidia and are easier to expel. The ctenidia are cilia-covered featherlike structures that exchange gases and sometimes collect food from water passing through the mantle cavity. Also, in gastropods, the alimentary, renal, and reproductive systems open into the upper exhalant portion of the mantle cavity, so that their discharged materials can be carried outward by the exhalant pallial currents.

Yonge (1947) thoroughly described and analyzed the structure and function of the organs housed in the mantle cavity in aspidobranch Gastropoda. The term "aspidobranch" refers to the presence of bipectinate ctenidia, which characterize the Archaeogastropoda and are considered the most primitive of known gastropod gill types. Yonge (1947) recognized four aspidobranch arrangements in modern archaeogastropods: (1) asymmetrical shell with two asymmetrical ctenidia (all Zeugobranchia except the Fissurellacea), (2) secondarily symmetrical shell with two symmetrical ctenidia (Fissurellacea), (3) asymmetrical shell with loss of one ctenidium (Neritacea, Valvatacea, Trochacea), and (4) secondarily symmetrical shell with loss of one or both ctenidia (Patellacea, Cocculinacea, some Neritacea).

In the zeugobranchiate mollusks (arrangements 1 and 2), Yonge (1947) reported, inhalant currents created by ctenidial cilia are drawn into the mantle cavity on both sides and above the animal's head. After passing over the ctenidia, the deoxygenated currents pass upward and out of the cavity through a dorsal labral slit or emargination (as in the Pleurotomariidae, Scissurellidae, and some Fissurellidae, for example, *Emarginula*), through a single apical trema (as in some Fissurellidae, for example, *Diodora* (Fissurella)), or through a series of tremata (as in the Haliotidae, for example, *Haliotis*). Such shell emarginations and perforations are morphological adaptations to prevent the mixing of fresh incoming currents and deoxygenated and fouled exiting currents in zeugo-

branchiate forms. Cox (1960, p. 1130) defined emarginate gastropods as those "with margin of outer lip notched or variously excavated."

In gastropods having only one ctenidium, such as the more advanced archaeogastropods and the caenogastropods, inhalant currents enter the mantle cavity on one side of the head and exhalant currents are expelled on the other side of the head. Therefore, there is no need for a slit type of labral emargination. A few highly specialized caenogastropods do bear labral slits, such as the Siliquariidae, which are sessile suspension feeders having a single enlarged food-gathering ctenidium. In 1843, de Konnick noted the similarity between the labral slit emargination of *Bellerophon* and that of the modern fissurellid *Emarginula*. Meek (1866) supported this comparison and further noted the similarity of the tremata of the Silurian bellerophon *Tremanotus*. These comparisons convinced these early authors, and most subsequent authors, of the close phylogenetic relationship between the pleurotomariacean archaeogastropods and bellerophonaceans. Knight (1952) used Yonge's (1947) analysis of the zeugobranchiate pallial system to reconstruct the soft anatomy of bellerophonts. He diagramed bellerophonts as having a zeugobranchiate pallial system, with a pair of bipectinate ctenidia receiving anterolateral inhalant currents from either side of the head, these currents moving upward and inward through the mantle cavity, converging near the top, and being expelled through a dorsal slit. Such a reconstruction is also supported here.

It should be noted that some genera formerly considered bellerophonaceans, but currently interpreted as monoplacophorans because of their muscle scar patterns (for example, *Sinuities*, *Sinuitopsis*, and *Cyrtolites*), may also have a distinct labral sinus. This is not surprising, as these forms are also believed to have one or more pairs of bipectinate gills arranged on either side of the body. Even though the path of currents through the posterior mantle cavities of these forms would be quite different from that of a gastropod, with inhalant currents entering at the opposite end, the zeugobranchiate condition would still be served by an exhalant sinus. Thus far no species having a well-defined slit-selenizone complex has been accepted as a monoplacophoran, but such homeomorphy would not be impossible.

In the Pleurotomariacea and the Bellerophonacea, the characteristic labral emargination can be in the form of a sinus or a slit. A sinus is a simple U-shaped to V-shaped reentrant of the apertural margin. A slit is a parallel-sided reentrant varying from a short notch (pl. 14, fig. 14) to a deep fissure as much as a half-whorl in extent (pl. 23, figs. 10-13; pl. 44, figs. 3, 6). A slit is generally located at the apex of a shallow sinus, and generates a slitband or selenizone. A selenizone (pl. 16, fig. 15; pl. 18,

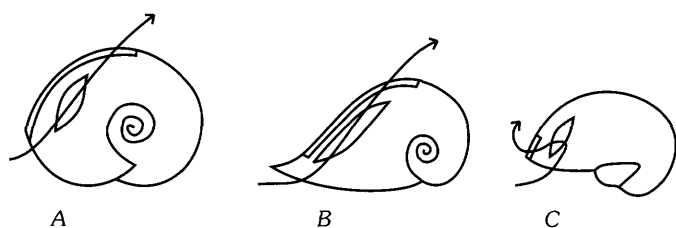


FIGURE 16.—Paths of water currents through the shells and mantle cavities of some Ordovician bellerophontacean gastropods. Fusiform-shaped structures represent the gills. A, *Tropidodiscus*, left-lateral view; water currents entered shell anteriorly and exited through the deep slit posterodorsally, which is similar to such living pleuromariaceans as *Entemnotrochus*. B, *Salpingostoma*, left-lateral view; water currents entered the broad aperture anterolaterally, passed over an enlarged pair of gills, and exited posterodorsally through the deep slit. C, *Sphenosphaera*, left-lateral view; water currents entered shell anterolaterally and curved around to exit dorsally through a short slit, which is similar to such living pleuromariaceans as *Perotrochus*.

fig. 5; pl. 28, fig. 5; pl. 30, fig. 6; pl. 31, fig. 6) is a spiral band tracing the path of the slit around the shell, and is best expressed when marked by a series of concentric growth lines (lunulae) bordered by a pair of spiral threads. If the selenizone is not well defined by lunulae and bordering threads, it may be expressed as a simple, generally slightly elevated band often referred to as a "pseudoselenizone." Horny (1963a, p. 68) has pointed out that there seems to be a complete morphological gradation from the U-shaped sinus to the narrow, channellike slit. Regardless of its form, a median labral emargination, with few exceptions, indicates the presence of a dibranchiate pallial system.

The labral emargination can occur in Paleozoic symmetrical molluscan univalves in five general forms: (1) a V-shaped to U-shaped sinus, as in *Sinuities* (pl. 11, figs. 1, 6, 11), (2) a short, relatively broad notch or slit, as in advanced bucaniids and bellerophontids (pl. 38, fig. 16), (3) a deep, narrow slit that may extend up to one-half whorl back from the apertural margin, as in tropidodiscids and primitive bucaniids (pl. 23, fig. 10; pl. 44, figs. 3, 6, 12), (4) a long, open slit closed off at the anterior margin, such as in *Salpingostoma* (pl. 24, figs. 1–3), and (5) one or a series of discrete openings, such as the tremata of *Tremanotus*, which according to Peel (1972) are repeated closings of a deep labral sinus.

Linsley (1978b, p. 438, 439) concluded that broad, shallow slits were generally associated with broad shell forms, such as *Bellerophon*, illustrated here by *Sphenosphaera* (fig. 16C). The breadth of the outer lip of the shell allowed inhalant currents to be spread to the anterolateral extremities. In these forms, he envisioned a shallow mantle cavity in which anterolateral inhalant currents were effectively separated, by virtue of the shell's width, from the exhalant currents exiting through

the dorsomedian slit. In contrast, in narrow shell forms, such as *Tropidodiscus* (fig. 16A), Linsley (1978b) pointed out, the separation of inhalant and exhalant currents would be difficult. The solution was a greatly deepened slit and mantle cavity. In such a form, currents could enter anteriorly into the mantle cavity, bathe the ctenidia, and continue on in nearly the same line to exit posteriorly at the back of the deep slit. This arrangement in effect created a posteriorly placed anus.

There are some exceptions to Linsley's astute observations concerning the association of a deep slit with only narrow shell forms. Some bellerophonts having broad, depressed whorls, such as species of the *Bucania sulcata* group (pl. 12, figs. 1–3) and *Undulabucania* spp. (pl. 23, figs. 5, 11), also apparently had deep slits. As discussed elsewhere, all of these broadly umbilicate forms with deep slits, regardless of the whorl shape, are considered morphologically primitive. None of the more advanced genera have deep slits, and therefore the structure's functional advantages for respiration must have been overshadowed by some disadvantages, such as weakening of the shell and increased exposure of the animal to predation.

The homeomorphic explanate genera *Salpingostoma* (pl. 24, figs. 1–3; pl. 25, fig. 1; fig. 16B) and *Tremanotus* (Peel, 1972) also bear deeply inset shell openings in the form of a deep slit that is closed off anteriorly and a line of open tremata, respectively. It is suggested here, in the discussion of explanate shell forms, that these genera may have been suspension feeders. The deep emarginations would be useful in allowing more water to move through an enlarged set of ctenidia. As noted, this situation is known in the modern caenogastropod family Siliquariidae.

#### PARIETAL DEPOSITS

Knight (1952) and Rollins and Batten (1968) argued that parietal deposits and long trails near the apertural side of a curved or coiled shell would impede the maneuverability of a protracted head in a monoplacophoran, and therefore one would not expect to find these features in that class of mollusks. Parietal deposits are secondary shell layers laid down on the inner lip of the aperture. Trails are shelly extensions of the outer lip of the aperture away from the coil, as in *Salpingostoma* (pl. 25). Pojeta and Runnegar (1976, p. 32) disagreed with these authors, pointing out that cowries and other gastropods secrete secondary shell layers over the entire shell, and that there was no valid reason why parietal deposits could not be secreted by epithelium near the head. This point is well taken; however, I agree with Harper and Rollins (1982, p. 228) that the crux of the problem is not the capability of secreting secondary



deposits in any certain region of the shell, but rather the functional utility of secreting massive secondary deposits in the parietal region.

*Sinuities granistriatus* and related species are generally accepted as monoplacophorans, and are known to have a thin swash of secondary deposits in the parietal region and over the ventral coil (pl. 45, figs. 1, 2). However, these deposits are so thin that they do not mask the original morphology of the covered areas.

In contrast, many bellerophontaceans have strongly thickened inner apertural margins and parietal areas. Rollins (1966) has described thick, padlike parietal deposits in *Ptomatis*, an explanate Devonian genus. *Salpingostoma kentuckyense* (pl. 25, figs. 2, 8, 10), *Bucania nashvillensis* (pl. 13, fig. 19; pl. 14, figs. 1-5), *Bucania peracuta* (pl. 16, figs. 5-8), *Bucania crassa* (pl. 19, figs. 7-10), and other species in the present study clearly demonstrate the common thickening of the parietal lip in bellerophontaceans. Specimens of *Sphenosphaera clausus* show the marked thickening of the entire parietal region by secretion of rather massive secondary shell layers over the medial region (pl. 30, figs. 2-5, 8, 9; pl. 31, figs. 2, 3, 8).

Thickened parietal regions in bellerophontacean gastropods seem to serve two functions. First, such deposits add considerable weight to the part of the shell that lies on the central portion of the foot, thereby creating a fulcrum for balancing the shell. The added weight would also serve to stabilize the shell under higher energy conditions. Considering the difficulty of balancing large umbilicate shells such as some of those cited above, the added weight in a low central position would be of obvious advantage. Second, thickened parietal deposits may modify the design of the parietal region. This is particularly noticeable in *S. clausus*. Such modification of the parietal region in *S. clausus* would provide a broader, more stable area for the shell to rest on when the foot was extended.

The outbuilding of the parietal region, evident in the figures of *S. clausus* cited above, was taken to its maximum development in species of *Carinaropsis* (pl. 37, figs. 3, 4, 18, 19). In *Carinaropsis*, the coil has been reduced to the point of no longer being able to support the visceral mass of the mature animal. The extensive outbuilding of the parietal region in this specialized case was for the support of the visceral mass. The apertural platform of the modern gastropod *Crepidula* is clearly analogous in its morphology and function to that of *Carinaropsis*.

In summary, it is concluded that thickened parietal regions furnish greater weight over the central area of the gastropod, for better balance and stabilization of the shell. It is further concluded that such deposits may assist in supporting the shell on the extended foot, and

may even provide a better surface over which to move the foot in and out of the shell. Such thickened deposits would overlie the head region in an untorted monoplacophoran, and would not seem to serve any reasonable function. In fact, massive deposits in such a position would seem to be impractical and would probably hinder the balancing of the shell in a monoplacophoran. Therefore, it is here considered highly doubtful that monoplacophorans would secrete thickened secondary parietal deposits. Harper and Rollins (1982) went so far as to claim that the development of a thickened parietal inductura is the single most reliable criterion for distinguishing fossil gastropods from monoplacophorans among Paleozoic isostrophic shells.

#### MUSCLE SCARS AND THEIR FUNCTIONAL SIGNIFICANCE

Muscle patterns in fossil univalved mollusks are central to the continuing debate over the class-level affinities of Paleozoic bilaterally symmetrical isostrophic shells. These muscle patterns occasionally are discovered through fortuitous preservation of muscle scars. Calcification of the shell material is inhibited over the sites of muscle attachment on the shell interior, and as a result there develops a slight depression—the muscle scar (Fretter and Graham, 1962, p. 142). In some fossil specimens, these muscle scars are preserved as raised fillings of the original scar depression on internal molds of the shell.

The modern monoplacophoran *Neopilina* has six pairs of discrete muscle scars arranged around the interior periphery of the shell (Lemche and Wingstrand, 1959). A number of Early to Middle Paleozoic limpetlike shells, the Tryblidiida, have five to eight pairs of discrete scars in a form and arrangement similar to that of *Neopilina*, and therefore have been interpreted as monoplacophorans (Wenz, 1940; Knight, 1952). Pojeta and Runnegar (1976, p. 29) have convincingly reconstructed the musculature of the Middle Cambrian genus *Scenella* using *Neopilina* as a model.

Pairs of discrete dorsal muscle scars have also been found in some isostrophically coiled early Paleozoic genera. Wenz (1940) first described such a muscle scar pattern in *Cyrtionella* from the Devonian of Michigan. On the basis of that single occurrence, he proposed that all bilaterally symmetrical isostrophic Paleozoic molluscan univalves were untorted, and were not gastropods as generally believed. A number years later, Horny (1963c) described symmetrical pairs of muscle scars in the Late Ordovician *Cyrtolites ornatus*. Rollins and Batten (1968) then found monoplacophoranlike muscle scars in the Middle Devonian *Sinuities acutilira*, and more recently Runnegar (1981) and Peel (1980) recognized

TABLE 15.—*Examples of post-Cambrian bellerophontiform molluscan univalves for which muscle scars have been described*

Species	Age	Area	Author(s)
Monoplacophoran-type muscle scars—Multiple discrete pairs			
<i>Cyrtionella mitella</i>	Devonian	Michigan	Wenz (1940)
<i>Cyrtolites ornatus</i>	Ordovician	New York	Horny (1965a)
<i>Simulopsis acutilira</i>	Devonian	New York	Rollins and Batten (1968)
<i>Sinuities cancellatus</i>	Ordovician	New York	Runnegar (1981)
<i>Sylvestrosphaera lemchei</i>	Silurian	Britain	Peel (1980)
? <i>Bucania christiana</i>	Ordovician	Norway	Runnegar (1981)
Gastropod-type muscle scars—Single symmetrical pair, columellar, circumumbilical			
<i>Bellerophon gibsoni</i>	Mississippian	Indiana	Knight (1947a)
<i>Bellerophon</i> sp.	Pennsylvanian	Indiana	Knight (1947a)
<i>Bellerophon</i> cf. <i>B. gibsoni</i>	Mississippian	Indiana	Rollins (1967)
<i>Bellerophon</i> sp.	Pennsylvanian	Missouri	Rollins (1967)
<i>Pharkidonotus labioreflexus</i>	Pennsylvanian	Ohio	Rollins (1967)
<i>Sinuitina brevilineata</i>	Devonian	New York	Rollins (1967); Rollins and others (1971)
<i>Tremanotus alphaeus</i>	Silurian	Illinois	Peel (1972)
<i>Salpingostoma buelli</i>	Ordovician	Wisconsin	Peel (1972)
<i>Bellerophon</i> sp.	Pennsylvanian	U.S.A.	Peel (1972)
	Carboniferous	Ireland	Peel (1972)
<i>Megalomphala taenia</i>	Silurian	Gotland	Peel (1976)
<i>Bellerophon reticostatus</i>	Carboniferous	Ireland	Peel (1982)

similar scars in two other sinuitid species, the Late Ordovician *Sinuities cancellatus* and the Late Silurian *Sylvestrosphaera lemchei*, respectively.

The muscle scars in limpet-form monoplacophorans, and in some isostrophically coiled taxa, are located in a ring just inside the apertural margin. Such an arrangement indicates that the animal could not retract into the shell, but rather must have clamped the shell down over the body for protection. In contrast, muscle scars in the sinuitids are inset more deeply into the shell opening and in some cases are even located at the umbilical shoulder a half-whorl back, suggesting that these forms were probably capable of retracting into the shell (Peel, 1980, p. 95, 96). Considering the widespread use and success of retractability in the gastropods, it is not surprising that the Monoplacophora also evolved this ability as a protective strategy.

The shell, or columellar, muscles in coiled gastropods attach to the inner surface of the shell at the columella. Most prosobranch gastropods have only a single columellar muscle as the result of larval reduction of the second retractor muscle. However, numerous archaeogastropods, including the Haliotidae, Scissurellidae, and some Neritacea, as well as some mesogastropods, have a pair of columellar muscles (Knight, 1952, p. 12; Fretter and Graham, 1962, p. 140). All of these taxa have asymmetrically coiled shells, and the posttorsional right muscle is always larger than the left muscle. Symmetrical paired columellar muscle scars on the internal molds of a number of bellerophontaceans have been described (table 15).

In the bilaterally symmetrical patellacean gastropods (limpets), the shell muscles form a horseshoe-shaped ring around the inner shell margin, the open anterior end marking the position of the mantle cavity. The continuous horseshoe-shaped muscle is the product of a pair of lateral muscles, one on either side of the torted visceral mass, that increase in size and gradually extend their insertions in a backward direction during ontogeny until they coalesce (Fretter and Graham, 1962, p. 140; Bandel, 1982, p. 32, 33). All of these patelliform gastropods are thought to be descended from asymmetrically coiled ancestors which are presumed to have had two asymmetrical shell muscles. Therefore, the bilateral symmetry of the shell muscles in patelliform gastropods is an adaptation to the secondary symmetry of their shells.

Just as in the Monoplacophora, the arrangement of muscle scars around the inner periphery of the shell opening in patelliform gastropods indicates a clamping mechanism for protection, while a circumumbilical muscle position demonstrates the ability to retract the body into the shell. Linsley (1978a, b) and Peel (1980) have suggested that the location of muscle scars half a whorl back from the aperture in sinuitid monoplacophorans, as well as their fusion into fewer attachment sites, were adaptations favorable to development of torsion. Peel (1980) proposed that these sinuitid muscles may represent a morphological grade similar to possible gastropod ancestors in terms of retraction.

Peel (1980) and Harper and Rollins (1982) stressed how muscle arrangements in bellerophontiform mollusks are controlled by the mechanical requirements of shell form



and by the functional requirements of the animal's mode of life. Both monoplacophorans and gastropods can have muscles arranged in a ring around the aperture. Further, the discreteness of these muscle scars is not significant, as the supposedly continuous horseshoe-shaped muscle scar of diotocardian limpets actually represents a series of discrete bundles of muscle fibers, which may leave discrete scars in some cases (Fretter and Graham, 1962; Harper and Rollins, 1982). Moreover, muscle scars positioned in the circumumbilical region in retractile monoplacophorans can appear quite similar to the columellar scars of gastropods (Peel, 1980).

I agree with Peel (1980) and Harper and Rollins (1982) in their conclusion that muscle scars are not a reliable criterion for assessing class-level affinities of molluscan univalves. The genera *Cyrtolites* and *Sinuities* are assigned to the Monoplacophora in this study because of their multiple sets of discrete muscle scars, and because their apertural forms can be rationalized as serving an exogastric animal. However, much more work on modern gastropod muscle patterns is needed before transfers of taxa from the Gastropoda to the Monoplacophora can be made confidently. Studies such as that of Gundrum (1981) are heading in the right direction, but tangible data remain rather scarce. Another factor that should be recognized is that muscle scars on internal molds are quite difficult to see. For instance, Runnegar (1981, p. 315), Knight (1952), and Peel (1980) have all observed different numbers and forms of muscle scars on a single specimen of *Sinuities cancellatus*.

Runnegar (1981, p. 315) described a single pair of muscle scars that cross the edges of the umbilici in a specimen of *Bucania christiana* (Koken). It should be noted that this species was described by Koken (1925) as a species of *Bucaniella*, a sinuate genus. Even Runnegar stated that the specimen was sinuate and did not possess a slit-selenizone complex, and thus it is unclear why he referred the specimen to the slit-bearing genus *Bucania*. Runnegar (1981, p. 315) agreed with Peel (1980) and Harper and Rollins (1982) that positions of muscle scars can be directly correlated with shell form, and he illustrated an evolutionary sequence for these two characteristics in monoplacophorans that matches another sequence of opposite polarity in living trochacean gastropods (Runnegar, 1981, fig. 4). On the basis of these two sequences, he concluded that all bellerophonts were probably monoplacophorans. I disagree with Runnegar's conclusion. If anything, Runnegar's figure seems to show what Peel (1980) and Harper and Rollins (1982) claimed; that is, muscle patterns in gastropods and monoplacophorans can be essentially identical, and therefore cannot be used exclusively as a reliable criterion in determining the class-level assignment of bilaterally symmetrical molluscan univalves. Muscle patterns are controlled by

the mechanical requirements of shell form and by functional aspects related to the animal's mode of life.

## PHYLOGENY AND CLASSIFICATION

### THE BELLEROPHONT CONUNDRUM

The class-level assignment of Paleozoic bellerophontiform mollusks has been debated since the early 19th century (Yochelson, 1967). The current controversy over the classification of the Bellerophontacea centers on whether or not these mollusks had undergone torsion, the larval process that defines the class Gastropoda. Torsion is the process by which the larval shell and visceral mass of the veliger are rotated 180 degrees with respect to the head-foot mass. According to Crofts (1937, 1955), torsion results from the differential development and growth of the larval left and right retractor muscles. However, Bandel (1982, p. 27, 28) recently observed that torsion is caused by the differential growth of epithelial cells and is not related to muscle activities. As a result of torsion, the originally posterior mantle cavity, and its respiratory, sensory, reproductive, and renal organs, are brought into an anterior position above the head and the shell coils backward away from the head (endogastrically). Monoplacophorans, which are believed to be the group ancestral to the gastropods, do not undergo torsion, and therefore their mantle cavity remains posteriorly positioned and the shell coils forward over the head (exogastrically). The debate over classification of the bellerophontaceans was rekindled in recent years by the discovery of multiple symmetrical pairs of discrete muscle scars in some bellerophontiform taxa, and by the description of diverse Lower and Middle Cambrian mollusk faunas. One group of paleontologists claims that this new evidence from the fossil record indicates that the Paleozoic bellerophontiform univalves were untorted, exogastrically oriented mollusks assignable to the class Monoplacophora (Wenz, 1940; Moore and others, 1952; Runnegar and Pojeta, 1974; Pojeta and Runnegar, 1976; Salvini-Plawen, 1980; Runnegar, 1981, 1983). However, most Paleozoic gastropod specialists consider such fossils to represent torted, endogastrically oriented archaeogastropods (Knight, 1947a, b, 1952; Knight and others, 1960; Yochelson, 1967, 1978; Berg-Madsen and Peel, 1978; Linsley, 1978a, b; Peel, 1980, 1987; Harper and Rollins, 1982). The latter viewpoint is accepted herein. Below, evidence is reviewed that suggests that the slit-bearing bellerophontaceans, and many of the morphologically similar sinuate taxa, are gastropods and are closely related to the pleurotomariaceans.

In the early 19th century, *Bellerophon* and its allies were generally considered nautiloid cephalopods (Yoch-

elson, 1967). This opinion persisted even after DeFrance (1824) demonstrated that bellerophonts lacked both a siphuncle and septa. Some other authors of that period considered bellerophonts to be heteropods, prosobranch gastropods adapted to a pelagic mode of life (Yochelson, 1967). De Konnick (1843) and Meek (1866) first linked bellerophonts to the archaeogastropods by comparing their labral emarginations to those of *Emarginula*, the modern keyhole limpet. Meek (1866) also argued that the shells of most bellerophonts seemed much too thick and heavy for the animals to have led a pelagic mode of life.

Since Meek's (1866) paper, the association of the bellerophonts with the archaeogastropods has been widely accepted, with some notable exceptions. Simroth (1906) proposed a separate class of mollusks for the bellerophonts, which he termed Amphigastropoda. This class was later also used by Thiele (1935) in his mollusk classification. Also, Naef (1911) taxonomically isolated the bellerophonts by placing them in a division that he called the Planospiralia. All of these authors considered the bellerophonts to be pelagic swimming animals, a belief that Yochelson (1967, p. 149) claimed must have influenced their views on classification. Moore and others (1952, p. 289), who also used Amphigastropoda and allied the group with the tryblidiids, did not consider them to be pelagic.

The current period of controversy was initiated by Wenz's (1938) observation that the symmetrical, paired muscle scars of the Silurian patelliform genus *Tryblidium* seemed to indicate that the animal's soft parts were symmetrical and untorted. He proposed that *Tryblidium* and its allies be transferred from the Patellacea to a new superfamily, the Tryblidiacea. Wenz (1940) then also found multiple pairs of muscle scars on an internal mold of the Devonian species *Cyrtionella mitella* (Hall), an incompletely coiled isostrophic form. On the basis of this evidence, Wenz (1940) concluded that all Paleozoic bellerophontiform taxa represent primitive untorted mollusks. He placed all such taxa in the subclass Amphigastropoda, and all anisostrophic gastropods in the subclass Prosobranchia.

Knight (1947a, 1952) strongly contested Wenz's (1940) conclusion that the bellerophonts had not undergone torsion. In rebuttal, Knight (1947a) described single pairs of gastropodlike columellar muscle scars in two species of *Bellerophon* and in *Sinuities cancellatus*. However, additional muscle scar pairs have recently been recognized in Knight's specimen of *S. cancellatus*, thus apparently demonstrating its monoplacophoran affinities (Peel, 1980; Runnegar, 1981). Knight (1952, fig. 10) also reconstructed the soft anatomy of a bellerophontacean on the basis of the pleurotomariacean gastropod design. He claimed that the median labral slit in these two groups was a homologous structure and therefore indicated that

bellerophontaceans had undergone torsion. He envisioned the bellerophontacean animal to have an anterior dibranchiate mantle cavity. As known from pleurotomariaceans having this arrangement, oxygenated water enters the mantle cavity anteriorly and passes over the gills, and then the deoxygenated water and waste products are expelled through the dorsal labral emargination (Yonge, 1947). This reconstruction is accepted herein. Knight (1952, p. 52) argued that three common morphological characteristics demonstrated a close relationship between the bellerophontaceans and the pleurotomariaceans: (1) a deep, hollow, usually closely coiled shell, (2) a sinus or a slit (and selenizone), and (3) a single pair of columellar retractor muscles. As is discussed below, it now seems likely that monoplacophorans could also have a coiled shell and a labral sinus.

Horny (1963c) reported multiple pairs of discrete muscle scars in the Upper Ordovician isostrophic species *Cyrtolites ornatus*, and Rollins and Batten (1968) also described such scars in the Middle Devonian sinuitid *Sinuitiesopsis acutilira* (table 15). *S. acutilira* bears a deep labral sinus, and some Middle Ordovician species of *Cyrtolites* bear a shallow labral sinus. Recently, monoplacophoranlike muscle scars have also been reported in the sinuitids *Sinuities* and *Sylvestrosphaera* (Peel, 1980; Runnegar, 1981). So far, all isostrophic species reported to have multiple pairs of monoplacophoranlike muscle scars have been cyrtolitids and sinuitids, except for a single specimen of questionable taxonomic affinity cited by Runnegar (1981) as *?Bucania christiana* (table 15). Bellerophont genera reported to have a single pair of gastropodlike columellar muscle scars include *Bellerophon*, *Pharkidonotus*, *Tremanotus*, *Salpingostoma*, *Sinuitiesina*, and *Megalomphala* (table 15).

The reliability of muscle scars as a primary taxobase on which to base class-level assignments of bellerophontiform fossils may be questionable. First, the muscle scar patterns of most extinct or extant gastropods have not been assessed, and therefore the range of variability of this feature is unknown. Second, muscle scars are rarely preserved, and when they are, their recognition and interpretation is open to differences of opinion. A case in point is the specimen of *Sinuities cancellatus* on which Knight (1947a) saw a single pair of columellar scars, but on which Runnegar (1981) recognized a second pair, and Peel (1980) recognized yet a third pair (see Runnegar, 1981, p. 315). In another case, Runnegar and Jell (1976, p. 127) recognized monoplacophoranlike muscle insertions on illustrations of species of *Sinuitiesina* and *Tremanotus* by Horny (1963a, pl. 8, fig. 9, and pl. 19, figs. 3-5, respectively), but Berg-Madsen and Peel (1978, p. 123) criticized these observations. The latter authors claimed that in the specimen of *Sinuitiesina*, the proposed scar might be no more than a spurious mark. Regarding the

specimen of *Tremanotus*, Berg-Madsen and Peel (1978, p. 123) claimed that Runnegar and Jell's (1976) supposed muscle scars were actually umbilical nodes, which are common in tremanotids. Moreover, gastropodlike columellar scars have also been reported in other species of *Sinuitina* and *Tremanotus* by Rollins and others (1971) and Peel (1972), respectively.

Recently, evidence from comparative and functional morphological observations has been cited to suggest further hazards in total reliance on muscle scars as class discriminators in bellerophontiform fossils (Linsley, 1978b, p. 437, 438; Peel, 1980, p. 95, 96; Harper and Rollins, 1982, p. 228–230). Many authors have concluded that the number and position of muscle scars are related primarily to shell form and mode of life, and that therefore the muscle scars in some monoplacophorans and gastropods could appear identical. For example, tryblidiid and some cyrtoneid monoplacophorans have numerous pairs of muscle scars or a muscle band arranged around the aperture opening. Similarly, patellacean gastropods have a horseshoe-shaped muscle scar around their aperture openings. It should be noted that although the muscle band of most patellacean gastropods is continuous, it actually consists of separate bundles of muscle fibers, a condition that is in some cases reflected in the muscle scars (Fretter and Graham, 1962; Harper and Rollins, 1982). All of these arrangements suggest a clinging animal that could not retract into its shell for protection, but rather clamped the shell opening down onto firm substrates. Starobogatov (1970) has argued that the Archinacellacea, which herein are assigned to the Monoplacophora, were actually limpet-form gastropods, because their continuous muscle band would leave no room for a head if exogastrically oriented. It appears, therefore, that a ring of muscles, whether a continuous band or consisting of multiple discrete pairs, may be either functional or phylogenetic in origin. Detailed analyses of muscle scars are needed, but even then, as in Archinacellacea, interpretations are open to question.

Isostrophic taxa that are capable of retracting into the shell for protection typically have muscle insertions set deep into the shell. Bellerophontaceans and some coiled monoplacophorans, such as *Sinuities* and *Sylvestrosphaera*, have deeply inset circumumbilical muscle scars (Peel, 1980, p. 95, 96). Although *Sinuities* also has one or more dorsal pairs of muscle scars, *Sylvestrosphaera* apparently has no dorsal scars (Peel, 1980). The fusion of muscle scars into more localized lateral positions improved the ability to retract into the shell, and it is probable that some coiled monoplacophorans having only a single pair of circumumbilical muscles are present in the fossil record. In such a case, it would be virtually impossible to distinguish isostrophic gastropods from

monoplacophorans on the basis of muscle scars only (Peel, 1980, p. 96).

Linsley (1978a, b), Peel (1980), and Harper and Rollins (1982) have suggested that morphological features other than muscle scars, such as the form of the aperture opening, may be more reliable taxobases for class-level assignments of bellerophontiform taxa. As discussed in the section "Functional Morphology," an endogastric versus exogastric orientation for bellerophontiform shells should be discernible from the functional analysis of shell morphologies. For example, Peel (1974) has demonstrated that the trilobate isostrophic shell is an adaptive strategy by which an endogastric gastropod separates incoming and outgoing mantle cavity currents. Linsley (1978b, p. 440) has shown that the deep slit of the narrow tropidodiscid shell (pl. 44, figs. 3, 6) effectively provides a posterior exhalant area in a gastropod presumed to be endogastric. The same effect would be had in broader shell forms having deep slits, such as *Undulabucania* (pl. 23, figs. 5, 10) and the *Bucania sulcatina* group (pl. 12, figs. 1–9) (see "Functional Morphology"). Harper and Rollins (1982, p. 228) concluded that massive secondary parietal deposits may be the most reliable criterion for recognizing gastropods among Paleozoic isostrophic shells. I agree with the importance of this characteristic (see "Functional Morphology"). The massive parietal deposits on bellerophontaceans such as *Sphenosphaera clausus* would clearly serve as a stabilizing structure in an endogastric gastropod, but they would seem to be a hindrance to an exogastric monoplacophoran. The large parietal platforms of the specialized Ordovician bellerophontaceans *Carinaropsis* and *Pterotheca* are analogous in position, and presumably in function, to the parietal platform of the modern gastropod *Crepidula*. The presence of a slit that generates a selenizone is strong evidence of a close affinity between the bellerophontaceans and pleurotomariacean gastropods.

Functional morphological interpretations have also been used to support an exogastric orientation for some bellerophontiform taxa (see "Functional Morphology"). For example, Starobogatov (1970) interpreted the lateral angles of the typically diamond shaped aperture of *Cyrtolites* as inhalant ducts to a posterior mantle cavity. Subsequently, Linsley (1978b, p. 437) suggested that such diamond-shaped apertures could serve to distinguish untorted monoplacophorans in bellerophontiform genera where muscle scars were unknown. Starobogatov (1970, p. 295) also noted narrow umbilical grooves on *Sinuities* which he interpreted as inhalant channels to a posterior mantle cavity. Peel (1975c) has since noted similar umbilical grooves in two species of *Pharetrolites*, and Berg-Madsen and Peel (1978, p. 120, 121) have ob-

served such channels in the minute Middle Cambrian *Protowenella*.

The other body of evidence used to suggest that all Paleozoic bellerophontiform taxa were monoplacophorans are the recently described diverse Early and Middle Cambrian mollusk faunas, such as those from the Early Cambrian Tommotian Stage of the Siberian Platform (Rozanov and others, 1969; Runnegar and Pojeta, 1974; Matthews and Missarzhevsky, 1975; Pojeta and Runnegar, 1976; Runnegar and Jell, 1976; Runnegar, 1981, 1983). All of these Early and Middle Cambrian mollusks are minute in size, and many are preserved as phosphatized internal molds (Runnegar, 1983). The univalved mollusks occur as both isostrophic and anisostrophic forms. The higher taxonomic assignment of many of these minute fossils, such as the low-spined pelliellaceans, is a matter of some debate (Knight, 1952; Yochelson, 1967, 1975, 1978; Berg-Madsen and Peel, 1978; Runnegar, 1983). Rozanov and others (1969) regarded all the Tommotian molluscan univalves as gastropods, but Runnegar and Pojeta (1974) have interpreted them all as monoplacophorans and have used them as groundwork for a new viewpoint on molluscan phylogeny. Runnegar and Pojeta (1974, p. 313, 314) have proposed that the pelliellaceans were anisostrophic monoplacophorans ancestral to the pleurotomariacean gastropods through an intermediate primitive gastropod form such as the Cambrian genus *Aldanella*. They preferred Ghiselin's (1966) theory concerning the origin of torsion, which states that torsion is a necessary consequence of helical coiling. They suggested that the larval shell of the anisostrophic pelliellacean was awkward to balance upon settling from the plankton, so the animal adopted a functional torsion in order to move the shell into a more manageable position. Subsequently, torsion was selected for because of its advantages to the larval animal. Runnegar (1983) has elaborated on pelliellaceans and the adult animals' ability to cope with some degree of functional torsion.

Knight (1952) had previously proposed that torsion in isostrophic monoplacophorans gave rise to the bellerophontacean gastropods, which in turn gave rise to the anisostrophic pleurotomariacean gastropods. In support of this model, Morton (1958) suggested that torsion was of obvious benefit to the adult animal, as well as to the larva, by moving the mantle cavity into an anterior position, where the gills and pallial sense organs were put in a more advantageous place from which to sample the environment into which the animal was moving. In further support of this model, Batten, Rollins, and Gould (1967) concluded that an exogastric isostrophic shell would be as difficult to balance as an exogastric anisostrophic shell for both the larval and adult monoplacophoran, and therefore it would be beneficial to both mor-

photypes to move the coil around 180 degrees to rest on the foot. Linsley (1978a, b) and Peel (1980) have attempted to demonstrate that there was a trend in isostrophically coiled monoplacophorans to fuse and localize muscle insertions into lateral areas deep in the shell, which resulted in a morphological grade favorable to the development of torsion. They claimed that the development of an isostrophically coiled monoplacophoran shell was accompanied by the development of a narrow neck between the visceral and head-foot masses, which would have facilitated the torsional rotation of the visceral mass and shell.

In Knight's (1952) model, it is assumed that there are both monoplacophorans and gastropods among the Paleozoic bellerophontiform taxa. However, in Runnegar and Pojeta's (1974) model, no torted isostrophic intermediate form is required in the evolution of the Pleurotomariacea from the Monoplacophora. Because of this viewpoint, and the fact that some bellerophontiform taxa have been found to have multiple pairs of discrete muscle scars, Runnegar and Pojeta (1974) have concluded that all bellerophontiform taxa were untorted monoplacophorans. Peel (1987) has pointed out that there is no evidence that torsion was a unique event, as both the above models assume. Rather, the Gastropoda may represent a grade of evolution, and torsion may have occurred in both ways, and even several times in different lineages. Rollins and Batten (1968, p. 134) have suggested that the bellerophontaceans themselves may be polyphyletic, evolving from monoplacophoran ancestors as many as three different times during the early to middle Paleozoic.

Regardless of how torsion originated, for reasons of comparative and functional morphology the Bellerophontacea are herein considered to be archaeogastropods related to the pleurotomariaceans. If this viewpoint is accepted, then there are three main phylogenetic models to consider (fig. 17). First, (fig. 17B), as Knight (1952) proposed, the Bellerophontacea may be evolutionary intermediates between the isostrophic monoplacophorans and the pleurotomariacean gastropods. Second, (fig. 17C), the bellerophontaceans may represent one or more independent lineages of gastropods that evolved from isostrophic monoplacophorans but did not give rise to any descendant groups. Such a scenario could accept multiple origins of torsion. It would also deny the homology between the slit-selenizone complexes of the bellerophontaceans and pleurotomariaceans, unless a common ancestral slit-bearing monoplacophoran group existed. A third possible phylogenetic model has not been adequately considered, in my opinion (fig. 17D). The bellerophontaceans may be secondarily symmetrical and descended from the pleurotomariaceans. Yochelson (1967, p. 154; 1978, p. 177; 1984, p. 262) has repeatedly

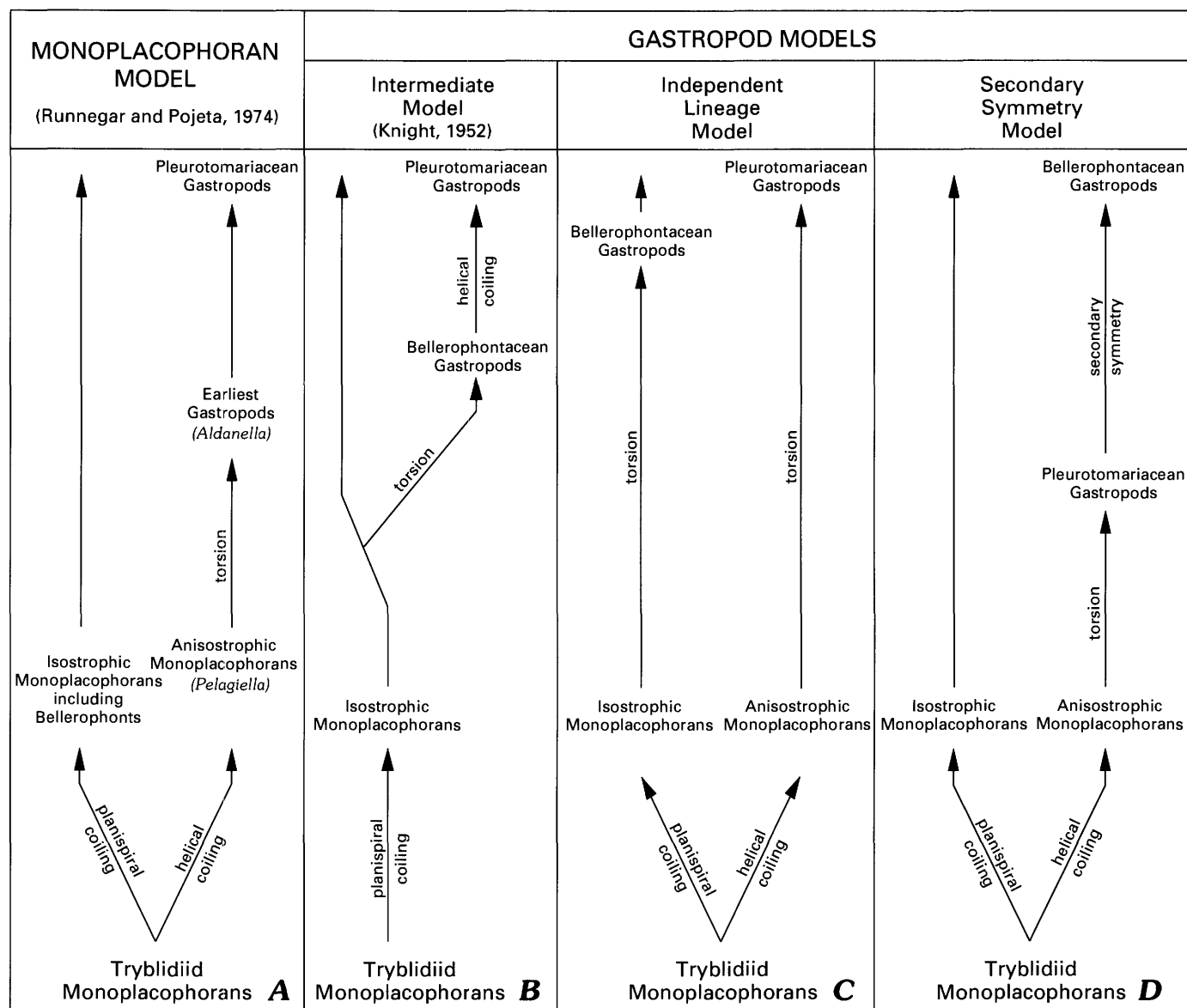


FIGURE 17.—Four primary models suggesting possible phylogenetic relationships between monoplacophorans, bellerophontaceans, and pleurotomariaceans. **A**, Considers bellerophontaceans to be isostrophic monoplacophorans and suggests that pleurotomariacean gastropods descended from anisostrophic monoplacophorans. **B-D**, Consider bellerophontaceans to be gastropods. The intermediate model (**B**) suggests that bellerophontaceans are phylogenetically interme-

mediate between isostrophic monoplacophorans and pleurotomariacean gastropods. The independent lineage model (**C**) suggests that bellerophontaceans and pleurotomariaceans developed independently from different monoplacophoran ancestors. The secondary symmetry model (**D**) suggests that pleurotomariaceans developed from anisostrophic monoplacophorans, and that bellerophontaceans are secondary symmetrical pleurotomariaceans.

expressed this opinion but has never documented it. Such a model has ample precedent. Secondary symmetry is known in at least nine stocks of Tertiary and modern archaeogastropods (Eales, 1950, p. 191; Vermeij, 1975, p. 419).

The derivation of the bellerophontaceans from the pleurotomariaceans can be supported both by comparative morphology and by the biostratigraphic development of the two groups. Well-documented pleurotomar-

iaceans are known from rocks as old as Late Cambrian and rapidly diversified into three families: the Sinuopeidae, Eotomariidae, and Raphistomatidae (Knight and others, 1960). Slit-bearing bellerophontaceans also first appeared during the Late Cambrian, but are currently known from only the single tropidodiscid genus *Chalarostrepsis* Knight. A number of sinuate bellerophontiform genera also appeared during the Late Cambrian, but many of these taxa are still poorly understood, and

the group probably contains both monoplacophorans and gastropods. Bellerophontacean diversity appears to have remained low through the Early Ordovician, with only *Eobucania* Kobayashi known from that time. It was not until the late Middle Ordovician (Blackriveran-Shermanian) that the bellerophontaceans radiated into a diversity of forms.

Many of the early pleurotomariaceans (Late Cambrian-Early Ordovician) had very low spired shells and wide-open umbilici. Of particular interest is the raphistomatid subfamily Ophiletinae (see Knight and others, 1960, p. 1200, fig. 113), which contains such genera as *Dirachopea* Ulrich and Bridge and *Calaurops* Whitfield. These genera are characterized by very low spires (low rate of whorl translation), large, open umbilici, lanceolate whorl shapes, slits with selenizones, and disjunct coiling in adulthood. Such forms could have been ancestral to the Late Cambrian tropidodiscid bellerophontacean *Chalarostrepsis*, which differs from this description only in its planispiral coil. The Late Cambrian sinuate genus *Strepsodiscus* Knight, which was placed in the Cyrtolitidae by Knight and others (1960, p. 1174), also matches this description fairly well, and it is even slightly anisotrophically coiled. *Schizopea* Butts represents a Ophiletinae morphotype that has a broader whorl shape and a greater rate of whorl expansion, and it could similarly represent an ancestor of a bellerophontacean such as *Eobucania*. The low-spired, widely umbilicate shells of the Ophiletinae probably were awkward to carry. Secondary symmetry would have allowed the shell to be more easily carried in a vertical position on the foot.

Salvini-Plawen (1980, p. 254) pointed out that the apparent absence of a helically coiled protoconch in bellerophontaceans speaks against a secondary symmetrical origin for the group. Salvini-Plawen may be correct in this observation, but it should be noted that bellerophontacean protoconchs have never really been investigated. Moreover, Bandel (1982, p. 32, 33) has asserted that some patellaceans and other related archaeogastropod limpets do not have a trochospiral shell stage in early ontogeny. He has observed that the bilateral symmetry of the adult secondary shell may be carried into the early development of the embryonic (primary) shell, so that the trochospiral twist of the larval shell may disappear completely. Also, it is of interest to note that Lemche (1957, p. 414) reported a dextrally coiled helical protoconch on the modern monoplacophoran *Neopilina galathea*, although other modern monoplacophorans have been reported to have only bulbous protoconchs (Pojeta and Runnegar, 1976, p. 30).

The secondary symmetry model for the origin of bellerophontacean gastropods deserves further investigation. More detailed comparison of early pleurotomariacean and bellerophontacean morphologies is needed

before the model can become a viable alternative. One possibly attractive aspect of the model is that it allows acceptance of Runnegar and Pojeta's (1974) theory of the evolution of the Gastropoda, but also accepts Knight's (1952) premise that the bellerophontaceans were archaeogastropods. The apparent absence of an anisostrophic protoconch in bellerophontaceans (Salvini-Plawen, 1980) does not necessarily exclude the hypothesis from further consideration.

In summary, there is good evidence from functional morphological analyses and muscle scar patterns to indicate that there are both monoplacophorans and gastropods among the Paleozoic bellerophontiform taxa. So far, only sinuate bellerophontiform taxa have been proven to be monoplacophorans. The slit-bearing bellerophontaceans, and many similar sinuate forms, are thought to be archaeogastropods and closely related to the pleurotomariaceans. The diverse minute molluscan faunas of the Early and Middle Cambrian are not typical bellerophontaceans, and conclusions derived from such forms cannot be automatically applied to all planispiral molluscan univalves. Many conclusions drawn from those minute faunas are based on an unproven theory on the origin of torsion and on highly interpretive functional morphology. On the other hand, the comparative and functional morphologic evidence supporting the assignment of most bellerophontaceans to the Gastropoda is much more tangible and relies on direct comparison with living animals. Clearly, a great deal more detailed morphological analysis is needed to clarify the phylogenetic role of bellerophontaceans. At least four possible phylogenetic models bear close scrutiny (fig. 17). Continued concentrated and cooperative research should eventually result in the resolution of the problem, or at least a consensus.

#### CLASSIFICATION AND PHYLOGENY OF THE MONOPLACOPHORA

Knight (1952) proposed the Monoplacophora as an order of the gastropod subclass Isopleura. However, he credited the concept of the taxon to Wenz (1938, 1940). Wenz recognized that the presence of multiple pairs of discrete muscle scars in Paleozoic symmetrical molluscan univalves, such as *Tryblidium* and *Cyrtoneilla*, suggested that they had not undergone the larval process of torsion. Wenz (1940) concluded that all symmetrical molluscan univalves were untorted, and he assigned them to Simroth's (1906) subclass Amphigastropoda. Knight (1952, p. 5) disagreed with this conclusion and restricted the Monoplacophora to three families—the Tryblidiidae, Hypseloconidae, and Archinacellidae. A few years later, Lemche (1957) described the living monoplacophoran *Neopilina galathea* and elevated the Monoplacophora to class level. Knight and Yochelson

(1958, p. 37–39) recognized this new class and modified Knight's (1952) classification accordingly. Also at that time, Knight and Yochelson (1958, p. 38) developed the modern concept of the class Gastropoda as mollusks that undergo larval torsion, the process by which the visceral mass and shell are rotated counterclockwise 180 degrees with respect to the head-foot mass. Knight and Yochelson (1958, p. 38–40) included three orders within the Monoplacophora—the Tryblidioidea, Archinacelloidea, and ?Cambridioidea. The Tryblidioidea was considered the “heart of the class” and included those symmetrical forms having discrete paired muscle scars assigned to the superfamilies Tryblidiacea and Cyrtoneallacea. The Archinacelloidea was considered an artificial grouping of forms that did not fit conveniently in the Tryblidioidea, but some of which were known to have completely or nearly completely fused muscle scar bands. The single superfamily Archinacellacea included the families Archinacellidae and Hypseloconidae. The order Cambridioidea accounted for questionable monoplacophorans and included elongate, slightly asymmetrical shells in which the muscle scars were unknown. Knight and Yochelson (1960, p. I77–I83) continued to follow this classification in their “Treatise on Invertebrate Paleontology.”

Horny (1965b, p. 10) outlined a revised higher classification of the Monoplacophora in which he presented two new subclasses—the Tergomya and Cyclomya. The Tergomya included limpetlike genera having several pairs of discrete muscle scars arranged in a ring, with the anterior apex of the shell located outside that ring. The Cyclomya included limpetlike, cone-shaped, and planispiral genera having discrete paired or fused muscle scars arranged in a ring, with the apex of the shell located inside that ring. The Tergomya included the order Tryblidiida, and the Cyclomya included the orders Archinacellida and Cyrtoneallida. Horny (1963c) had erected the order Cyrtoneallida for incompletely or completely coiled forms whose muscle scars are reduced in number and, in many cases, specialized. In the Cyrtoneallida, Horny (1965b, p. 10) included the family Cyrtolitidae with the subfamilies Cyrtolitinae, Cyrtoneallinae, and Cyrtoneallopsinae.

Starobogatov (1970) proposed another revision of the classification of the Monoplacophora based on his functional analyses of shell features and muscle scars. First, he excluded the family Palaeacmeidae (including *Scenella*) and the Cambridioidea from the class because, he claimed, the scars reported from genera of both groups were not really muscle scars. However, subsequent to Starobogatov, Runnegar and Pojeta (1974, fig. 2) convincingly reconstructed the musculature of *Scenella* using the modern monoplacophoran *Neopilina* as a model. Starobogatov (1970) also removed the Archinacellida from the Monoplacophora and suggested that

they were a specialized order of the Gastropoda. He argued that the circular muscle of *Archinacella* approached so near the apical end of the shell that there was no room left for the animal's head, and he reinterpreted the pair of discrete muscle scars at the contra-apical end of the muscle ring in *Archinacelliopsis* as radular muscle scars. Starobogatov (1970) recognized three monoplacophoran orders—the Tryblidiida, Cyrtoneallida, and the new order Sinuitopsida. He redefined the Cyrtoneallida as those planispiral shells having few whorls and two or three pairs of shell muscles inserted on the periphery of the final whorl, and he concluded that such forms retained multiple pairs of gills. Only the family Cyrtoneallidae was included in this order. He proposed the order Sinuitopsida for planispiral forms having several whorls and only one pair of shell muscles. He concluded that other muscle scars described in *Cyrtolites* by Horny (1963c) and in *Sinuitopsis* by Rollins and Batten (1968) were muscle scars of the radula and genitalia. He interpreted apertural features of these genera as indicating narrow inhalant channels to a posterior mantle cavity, and concluded that these forms must have had only a single pair of enlarged posterior gills. In the Sinuitopsida, he placed the families Cyrtolitidae, Bucanellidae, and Cyclocyrtoneallidae. In the order Tryblidiida, he included the superfamilies Tryblidioidea, Neopilinoidea, and Kirengelloidea.

Bjaly (1973, p. 326) added the order Multifariida to the class Monoplacophora, and based the order on the single species *Multifariites lenaensis* Bjaly from the Lower Ordovician of the Siberian Platform. The Multifariida was said to be similar to the Sinuitopsida in its number of whorls, but was distinguishable by its four pairs of identical muscle scars. The new order was considered unique in its duplication of the muscles during the growth of the shell.

Rosov (1975) elevated the superfamily Kirengelloidea to the order Kirengellida and included three families—the Kirengellidae (including *Scenella* and *Moyerokania*), the Romaniellidae (including *Romaniella* and *Hypseloconus*), and the Archaeophialidae (including *Archaeophiala*). He defined the order as having conical shells, with the apex generally anterocentrally located but varying from anterior to central to postcentral, and sometimes having a tendency to coil, but for no more than one-third of a whorl (fig. 18A). Muscle scars in the order vary from six to eight pairs arranged around the apex. Rosov (1975) suggested that the Kirengellida were the most primitive monoplacophoran group known and that they gave rise to the Archinacellida (fig. 18B) and Tryblidiida (fig. 18C) through forward displacement of the apex and simultaneous flattening of the shell, and to the Cyrtoneallida by further coiling of the shell (fig. 18D). He claimed that



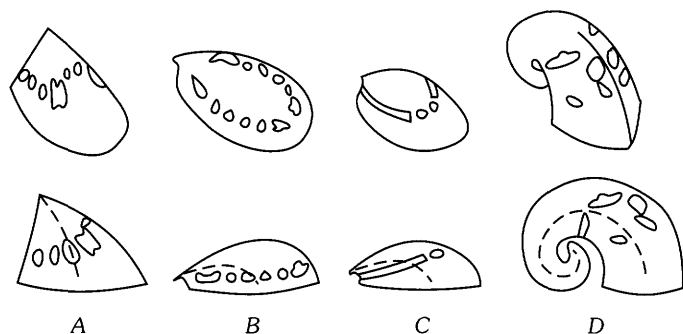


FIGURE 18.—Four general morphotypes of monoplacophorans representing four superfamilies. A, Kirengellacean: Simple conical shell with discrete to fused muscle scars. B, Tryblidiacean: Low limpet-form shell with discrete muscle scars. C, Archinacellacean: Low to high limpet-form shell with fused muscle scars. D, Crytonellacean: Coiled shell with multiple discrete muscle scars. According to Rosov (1975), the kirengellaceans gave rise to the tryblidiaceans and archinacellaceans through forward displacement of the shell apex and simultaneous flattening of the shell, and to the crytonellaceans through progressive coiling of the conical shell.

evolution toward fusion of the muscle scars occurred in all four orders.

Runnegar and Jell (1976) proposed a new classification of the Monoplacophora based on a theory of molluscan evolution proposed by Runnegar and Pojeta (1974) and Pojeta and Runnegar (1976). Their concept of the Monoplacophora closely approximated that of Wenz (1940), in which all Paleozoic symmetrical univalves were considered to be untorted. Unlike other modern classifiers of the Monoplacophora, Runnegar and Jell (1976) emphasized shell morphology in their ordinal diagnoses and did not mention muscle scar patterns. They recognized three orders—the Tryblidiida, Cyrtoneilliida, and Bellerophonitida. They defined the Tryblidiida as limpet-shaped forms having an anteriorly placed protoconch; the Cyrtoneilliida as orthoconic, cyrtconic, laterally compressed, and evolute planispiral forms lacking a well-formed apertural sinus or slit; and the Bellerophonitida as involute to evolute planispiral forms having an apertural sinus or slit. They included in the order Bellerophonitida the families Bellerophonitidae, Sinuitidae (=Sinuitopsida Starobogatov, 1970), and Multifariidae (=Multifariida Bjaly, 1973).

The classification of Runnegar and Jell (1976) cannot be accepted here, primarily because I consider the taxa in their family Bellerophonitidae to be archaeogastropods rather than monoplacophorans. Also, Runnegar and Jell's (1976) concept of the Cyrtoneilliida does not seem acceptable. Their diagnosis of that order departs greatly from the original meaning of the taxon given by Horny (1963c, 1965a, b). Moreover, Runnegar and Jell (1976, p. 116) stated that Horny's (1965a) subclass Cyclomya is an alternative taxon to Cyrtoneilliida, but was not appropri-

ately named. However, Horny (1965a, b) cited the Cyrtoneilliida as one of two orders in the subclass Cyclomya, and therefore the two taxa should not be considered alternative to one another. Finally, Runnegar and Jell's (1976) use of the presence or absence of a labral emargination as an ordinal taxobasis is placed in doubt here by the demonstration that Middle Ordovician species of *Cyrtolites* bear a labral sinus (pl. 5, figs. 7, 10, 13), whereas similar Upper Ordovician species of *Cyrtolites* lack a labral sinus (pl. 6, figs. 7, 10, 17).

As previously discussed, Berg-Madsen and Peel (1978), Linsley (1977, 1978b), and Peel (1980) have argued against the claim that all bellerophonitiform mollusks are monoplacophorans. On the basis of analyses of functional morphology, those authors concluded that both gastropods and monoplacophorans are present in that group. That opinion is shared here. On the other hand, Harper and Rollins (1982) concluded that muscle scar patterns reflect life habits and shell form rather than phylogenetic origins, and proposed that all cyrtoneillid monoplacophorans and bellerophonitaceans were gastropods. They accepted only the Tryblidiida as true monoplacophorans.

The higher classification of the class Monoplacophora adopted here is shown in table 16. This classification is considered conservative and tentative, but workable. The classification is based on my experience with mainly Ordovician taxa and on a survey of the literature. At present I consider the Monoplacophora to consist of two orders—the Tryblidiida and the Cyrtoneilliida.

The order Tryblidiida sensu Starobogatov (1970) is accepted here with some important modifications. The Archinacellacea is retained within the Monoplacophora as a superfamily of the Tryblidiida. Certainly Starobogatov's (1970) argument for returning the Archinacellacea to the Gastropoda warrants further investigation, but at present, the bulk of the evidence more strongly suggests that the group evolved from the Kirengellacea, as proposed by Rosov (1975), and should remain within the Monoplacophora. Also, the superfamily Kirengellacea Starobogatov, 1970, is recognized here in the sense of Rosov's (1975) order Kirengellida, consisting of the three families, the Kirengellidae, Romaniellidae, and Archaeophialidae. Rosov's (1975) order Kirengellida is quite similar in concept and composition to the family Scenellidae Wenz, 1938, sensu Runnegar and Jell (1976, p. 117). Noting the similarities in muscle scar patterns in the Cambrian *Scenella*, the Silurian *Tryblidium* and *Pilina*, and the modern *Neopilina*, Runnegar and Jell (1976, p. 119) suggested that these taxa represent a conservative lineage of monoplacophorans that survived from the Cambrian to the present. I agree with Runnegar and Jell (1976), and with the views of Rosov (1975), and support the proposal that



TABLE 16.—*Classification of the class Monoplacophora to family level*


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Class Monoplacophora Wenz in Knight, 1952
Order Tryblidiida Lemche, 1957
Superfamily Tryblidiacea Pilsbry in Eastman, 1899
Family Tryblidiidae Pilsbry in Eastman, 1899
Family Proplinidae Knight and Yochelson, 1958
Family Bipulvinidae Starobogatov, 1970
Family Drahomiridae Knight and Yochelson, 1958
Family Neopilinidae Knight and Yochelson, 1958
Superfamily Kirengellacea Starobogatov, 1970
Family Kirengellidae Starobogatov, 1970
Family Romaniellidae Rosov, 1975
Family Archaeophialidae Knight and Yochelson, 1958
Family Hypseloconidae Knight, 1956
Superfamily Archinacellacea Knight, 1956
Family Archinacellidae Knight, 1956
Order Cyrtoneillida Horny, 1963c
Superfamily Cyrtoneillacea Knight and Yochelson, 1958
Family Cyrtolitidae Miller, 1889
Family Cyrtoneillidae Knight and Yochelson, 1958
Family Cyclocyrtoneillidae Horny, 1962
Family Sinuitidae Dall in Eastman, 1913
Family Multifariidae Bjaly, 1973
Order Uncertain
Superfamily Helcionellacea Wenz, 1930
Family Helcionellidae Wenz, 1930 (sensu Runnegar and Jell, 1976)
Family Yochelcionellidae Runnegar and Jell, 1976
Superfamily Uncertain
Family Palaeacmaeidae Grabau and Shimer, 1909

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the simple conical kirengellaceans seem to be the most morphologically primitive group of monoplacophorans. I also agree that they probably gave rise to the tryblidiaceans and archinacellaceans through forward displacement of the apex and simultaneous flattening of the shell, and to the cyrtoneillaceans through progressive coiling of the lengthening conical tube.

The order Cyrtoneillida here includes both the orders Cyrtoneillida and Sinuitopsida sensu Starobogatov (1970). As pointed out by Peel (1980, p. 92), the order Sinuitopsida was inappropriately defined in terms of interpreted muscle functions and numbers of supposed gills. Furthermore, Rollins (1969) has shown that the muscle scar patterns of *Cyrtoneilla* and *Sinuitopsis* are more alike than previously thought, and Peel (1980) has demonstrated that the musculature of sinuitids can vary considerably.

Herein, the superfamily Helcionellacea and some other problematical taxa are assigned to the Monoplacophora, but their affinities within that group remain unclear.

#### SUPRAGENERIC CLASSIFICATION AND PHYLOGENY OF THE BELLEROPHONTACEAN GASTROPODA

In the discussion of the conundrum of the class-level assignment of the Bellerophontacea, I concluded that the

group belongs to the class Gastropoda and is closely related to the pleurotomariacean Archaeogastropoda. In this section, the suprageneric classification of the Bellerophontacea is reviewed, and a classification is proposed that satisfies both morphological similarities and inferred phylogenetic relationships. The families and subfamilies of the Bellerophontacea are discussed individually and in more detail in the "Systematic Paleontology" section.

The monograph by Ulrich and Scofield (1897) on the Ordovician gastropods from the Cincinnati arch and upper Mississippi Valley regions of North America laid the groundwork for subsequent classifications of the Bellerophontacea. They recognized five bellerophontacean families—the Cyrtolitidae, Protowarthiidae (=Sinuitidae), Bucaniidae, Bellerophontidae, and Carinaropsidae. Both the Cyrtolitidae Miller, 1889, and the Sinuitidae Dall, 1913, now are considered families of the class Monoplacophora. The Bucaniidae Ulrich and Scofield (1897) was established to account for planispiral genera that are involute and relatively loosely coiled, with a wide-open umbilicus, a slit and selenizone, collabral and revolving ornament that always cross at or nearly at right angles, and, commonly, expanded apertures. Ulrich and Scofield (1897, p. 849–852) included in the Bucaniidae the genera *Bucania*, *Tetranota*, *Kokenia* (= *Kokenospira*), *Megalomphala*, *Salpingostoma*, *Trematodus*, *Conradella* (= *Phragmolites*), and *Oxydiscus* (= *Tropidodiscus*). Ulrich and Scofield (1897, p. 852–857) considered the family Bellerophontidae to contain planispiral shells that are involute, rapidly expanding, and relatively tightly coiled, with a small or closed umbilicus, a slit and selenizone, and, generally, only collabral ornament. When revolving ornament was present in a bellerophontid, it was said to always parallel the longitudinal axis of the shell whorl, and not to curve to maintain right angles with curving collabral ornament, as it does in the Bucaniidae. Within the Bellerophontidae, Ulrich and Scofield placed the genera *Bellerophon*, *Bucanopsis*, *Patellostium*, *Euphemites*, *Warthia*, *Mogulia*, and *Stachella*. Although the concept of this family has remained essentially unchanged to the present, the generic composition has changed greatly. *Euphemites*, *Warthia*, and *Stachella* have been found to lack a true slit and selenizone and were transferred to sinuate families, *Mogulia* has been placed in synonymy with *B. (Bellerophon)* by Knight and others, (1960, p. 1182), and *Patellostium* is considered problematical and may be a heterogeneous taxon. More recently, a number of new genera have been added to the Bellerophontidae (see Knight and others, 1960, and Horny, 1963a). The family Carinaropsidae Ulrich and Scofield, 1897, was established for planispiral shells having greatly expanded apertures and a small or completely reduced coil, with a slit and a well-developed inner apertural platform. Ulrich and

Scofield (1897, p. 857, 858) included the genera *Carinaropsis* and *Pterotheca* in this family.

Koken (1925) recognized the single family Bellerophontidae, but he divided it into four subfamilies—the Bellerophontinae, Cyrtolitinae, Bucaniinae, and the new Salpingostomatinae, which housed the single genus *Salpingostoma*.

Wenz (1938, p. 93–112) recognized the same five families as Ulrich and Scofield (1897), but added the families Pterothecidae and ?Procarinariidae. *Procarinaria* is now considered a pelecypod (Horny, 1963a, p. 69). Wenz (1938) retained *Salpingostoma* in the family Bucaniidae.

In "Treatise on Invertebrate Paleontology," Knight and others (1960, p. I171–I184) constructed a familial classification for the Bellerophontacea based primarily on the character of the labral emargination. This classification was the first to arrange bellerophontacean suprageneric taxa in such way as to suggest phylogenetic relationships within the group. The Cyrtolitidae were defined by a shallow, commonly angular, labral sinus, with no slit. The Sinuitidae were defined by an open, U-shaped labral sinus, with no slit. Three subfamilies were recognized within the Sinuitidae—the Sinuitinae, Bucanellinae, and Euphemitinae. It was said that in some advanced Euphemitinae, the sinus could become a broad slit. All of the slit-bearing bellerophontaceans were placed in the family Bellerophontidae and were divided among the subfamilies Tropidodiscinae, Bucaniinae (tribes Bucaniides and Salpingostomatides), Carinaropsinae, Pterothecinae, Bellerophontinae, and Knightitinae. The Tropidodiscinae Knight, 1956, were separated from the Bucaniinae because of the former's narrow coil, broad umbilicus, deep slit, and posterior labral train (Knight and others, 1960, p. I179). The Knightitinae Knight, 1956, was distinguished from the Bellerophontinae by the former's strong spiral ornament. It should be noted that Knight and others (1960, p. I172) included the superfamily Helcionellacea Wenz, 1938, in the suborder Bellerophontina. The class-level assignment of the Helcionellacea has also been a matter of debate in recent years (Knight, 1952; Knight and others, 1960; Yochelson, 1967; Pojeta and Runnegar, 1976; Runnegar and Jell, 1976). The Helcionellacea is assigned to the Monoplacophora herein, but its relationships within that class are considered unresolved.

Horny (1963a, p. 69) proposed a number of amendments to the classification of Knight and others (1960). First, because of the discovery of multiple pairs of discrete muscle scars in *Cyrtolites ornatus*, he transferred the family Cyrtolitidae to the class Monoplacophora. He (1963a, p. 69) elevated the Euphemitinae to the family Euphemitidae because of the unique development of the apertural region and anal emargination, and the

peculiar development of inductural deposits over much of the shell. He also reestablished the family Pterothecidae because the existence of a true selenizone in the group has not been confirmed, and because of the lack of shell coiling and the presence of a large parietal platform. He reestablished the family Salpingostomatidae, including *Salpingostoma*, *Tremanotus*, and *Boiotremus*, all of which have either a deep slit or a series of open tremata across the dorsum of an expanded aperture. He (1963a, p. 69) erected the new subfamily Grandostomatinae of the family Sinuitidae for sinuate taxa having greatly laterally expanded apertures. He also erected the new subfamily Temnodiscinae of the family Sinuitidae for taxa in which the sinus became a parallel-sided notch similar to a true slit. Finally, he (1963a, p. 69) erected the new subfamily Cymbulariinae of the family Bellerophontidae for taxa having the slit diverging into a V-shaped sinus rather than meeting the anterior margin of the shell aperture at nearly right angles.

Boucot and Yochelson (1966, p. A7) cited evidence confirming the presence of a true slit in the trilobate genus *Plectonotus*, which previously had been assigned to the sinuate subfamily Bucanellinae of the Sinuitidae by Knight and others (1960). Because of this new evidence, they transferred *Plectonotus* to the family Bellerophontidae and proposed the subfamily Plectonotinae for bellerophontids having a trilobate cross section.

Peel (1972, p. 419) demonstrated that *Tremanotus* was sinuate and that its series of open tremata was the result of successive closings of a deep sinus. Therefore, he separated the genera *Tremanotus* and *Boiotremus* into the new subfamily Tremanotinae of the family Sinuitidae, and returned *Salpingostoma* to the subfamily Bucaniinae of the Bellerophontidae, thereby eliminating the family Salpingostomatidae.

Golikov and Starobogatov (1975) preferred to recognize most suprageneric taxa within the Bellerophontacea as distinct families. They listed the Sinuitidae, Grandostomatidae, Temnodiscidae, Tropidodiscidae, Bucaniidae, Salpingostomatidae, Carinaropsidae, Pterothecidae, Bellerophontidae, Cymbulariidae, Knightitidae, and Euphemitidae.

Because of the discovery of monoplacophoranlike muscle scars in *Sinuities* and the morphologically similar *Sinuitiesopsis* and *Sylvestrosphaera*, the family Sinuitidae has recently been transferred to the Monoplacophora. *Strangulites* Horny, 1962, almost certainly belongs in this family also. Other genera included in the Sinuitidae by Knight and others (1960) have little in common with the true sinuitids except for a rounded sinuate aperture and have been variously assigned to the Monoplacophora or Gastropoda.

As previously discussed, Runnegar and Jell (1976, p. 121) assigned the superfamily Bellerophontacea to the

TABLE 17.—*Suprageneric classification of the Bellerophontacea with diagnoses of family-level taxa*


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Class Gastropoda
Subclass Prosobranchia
Order Archaeogastropoda
Suborder Bellerophontina
Superfamily Bellerophontacea
Family Bucanellidae—Shell sinuate, phaneromphalous, broad dorsally; transverse and radial ornament.
Family Grandostomatidae—Shell explanate, phaneromphalous, sinuate; transverse and radial ornament.
Family Tremanotidae—Shell gradually expanding, phaneromphalous, having bell-shaped aperture, sinuate, having tremata developed.
Family Euphemitidae—Shell somewhat inflated, anomphalous; inductural deposits over most or all of shell; sinus narrow to slit-like.
Family Tropicodiscidae—Shell laterally compressed, phaneromphalous; slit deep.
Family Bucaniidae—Shell gradually expanded, widely phaneromphalous; whorls depressed to evenly rounded; apertural margins tending to flare; usually collabral and radial lines; slit short to deep.
Subfamily Bucaniinae—Slit short to deep, open at apertural margin; dorsum rounded.
Subfamily Salpingostomatinae—Slit deep, closed at apertural margin in adult.
Subfamily Plectonotinae—Whorls trilobate in cross section; slit short.
Subfamily Undulabucaniinae—Slit deep; ornament of closely spaced, regularly wavy, fine collabral threads only.
Family Bellerophontidae—Shell rounded, with narrow to closed umbilicus; apertural margins tend to flare; parietal lip generally reflexed; slit short.
Subfamily Bellerophontinae—Shell convolute or nearly so; whorls rounded to globose; no median ridge on whorl floor; growth lines only.
Subfamily Bucanopsinae—Shell anomphalous or nearly so; median ridge on whorl floor; selenizone slightly elevated in many cases.
Family Carinaropsidae—Shell greatly expanded; aperture explanate, having coil nearly or completely reduced; posteromedian platform developed within aperture.
Subfamily Carinaropsinae—Shell with small coil, then rapidly and broadly expanded; slit or short notch generating a selenizone.
Subfamily Pterothecinae—Coil completely reduced; apex marginal and low.
Subfamily Pedasiolinae—Coil completely reduced; apex submarginal and elevated.

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Monoplacophora. They placed all sinuate bellerophontiform taxa in the Sinuitidae and all slit-bearing taxa in the Bellerophontidae. They did not give any subfamily groupings. As previously stated, I disagree with their classification.

The suprageneric classification of the Bellerophontacea adopted herein is shown in table 17. It is based mainly on my experience with Ordovician taxa, and conclusions regarding the placement of post-Ordovician taxa are based primarily on the current literature. The classification attempts to show phylogenetic relation within the Bellerophontacea by the grouping of related subfamilies within more broadly based and traditional families.

The sinuate families Bucanellidae Koken, 1925, Grandostomatidae Horny, 1963a, and Tremanotidae Peel, 1972, are tentatively recognized here. However, the relations among these sinuate families, and between them and the slit-bearing families, are unresolved. Herein, taxa from these sinuate families are present in the fauna under consideration. The class-level assignment of many sinuate bellerophontiform genera is not yet resolved. Some genera are still too poorly known to classify with confidence; however, others have morphological features indicative of gastropod affinities (Peel, 1974, p. 232–234). *Sinuitina* (of the Bucanellidae herein) has been shown to have gastropodlike columellar muscle

scars (Rollins and others, 1971). *Ptomatis* and related genera of the Grandostomatinae are quite different morphologically from the sinuitids, and *Ptomatis* has been functionally interpreted to be a gastropod (Rollins, 1966). The euphemitids are considered herein to be gastropods, primarily because of their extensive inductural deposits. Herein, the tremanotids, which Peel (1972) showed to be sinuate, are considered to be gastropods because their series of open tremata appear to be homeomorphic with the long, open slit of the salpingostomatids. Much work needs to be done on these groups in order to determine whether sinuate forms and morphologically similar slit-bearing forms are phylogenetically related or are homeomorphic. It should be noted that Bandel (1982, p. 37) concluded from his studies of the development of modern fissurellids and scissurellids that the presence or absence of a slit is of questionable value in assessing systematic assignments.

All of the slit-bearing families, and many of their subfamilies are represented in the fauna under consideration. Four slit-bearing families (nine subfamilies) are recognized herein—the Tropicodiscidae, Bucaniidae, Bellerophontidae, and Carinaropsidae (fig. 19). Each of these families represents a morphological grade of development. The Tropicodiscidae is the most primitive slit-bearing family, and its genera are characterized by narrow, loosely coiled, widely phaneromphalous shells

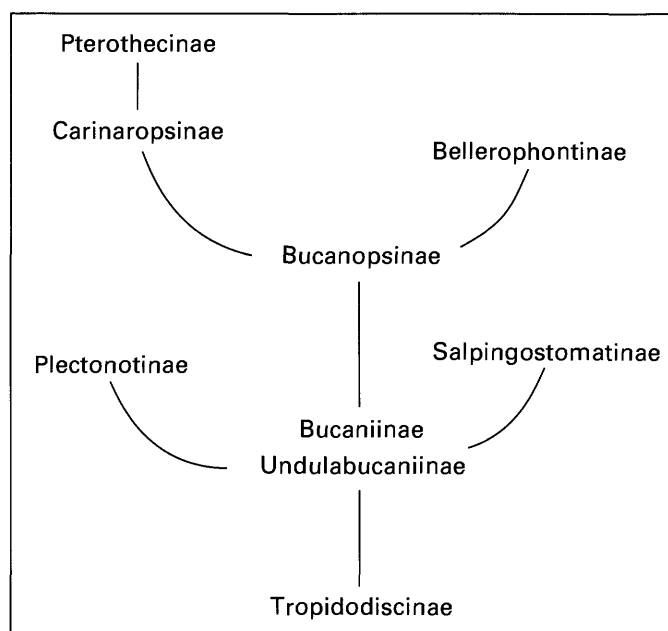


FIGURE 19.—Phylogenetic relationships of bellerophontacean slit-bearing subfamilies present in Eastern North America during the Late Cambrian-Middle Ordovician.

having slits as deep as one-half whorl back from the apertural margin. The Bucaniidae developed from tropidodiscid ancestors. Primitive members of the subfamilies Bucaniinae (such as the *Bucania sulcatina* group of Ulrich and Scofield, 1897) and Undulabucaniinae are also widely phaneromphalous and have deep slits like the tropidodiscids, but their whorls are wider and more depressed. The Salpingostomatinae, with their deep, closed-off slit, probably developed from primitive Bucaniinae. Juvenile specimens of *Salpingostoma*, prior to the adult expansion of the aperture, closely resemble members of the *Bucania sulcatina* group.

In more advanced Bucaniinae (such as species of the *Bucania lindsleyi* group of Ulrich and Scofield, 1897), the shell becomes more tightly coiled, reducing the size of the umbilicus, the whorls become more rapidly expanding and more rounded, and the slit becomes shorter. A similar trend can be seen in the genus *Tetranota* of the Plectonotinae.

In the family Bellerophontidae, the shells have become still more tightly coiled, so that the umbilicus is closed, or nearly so, and the whorls are generally quite rapidly expanded and rounded, resulting in a more compact shell. The subfamily Bucanopsinae is probably the most primitive in the family. Within that subfamily is seen the incipient building of a parietal platform in the genus *Sphenosphaera*, which is thought to be ancestral to the Carinaropsidae. In the Carinaropsidae, the rate of whorl expansion has increased to the point where the coil is nearly or completely reduced in the adult, and a large

parietal platform has developed to support the visceral mass within the shell. This development reached its peak in the genus *Pterotheca*.

The morphological trends summarized in the above paragraphs are treated in more detail in the section on "Functional Morphology." This morphological progression can also be traced upward stratigraphically from the Upper Cambrian through the Middle Ordovician. The tropidodiscid *Chalarostrepsis* appeared during the Late Cambrian, followed by the somewhat transitional genus *Eobucania* during the Early Ordovician. The primitive bucaniids of the *Bucania sulcatina* group appeared during the early Middle Ordovician (Chazy-Blackriveran). The more advanced Bucaniinae, the Salpingostomatinae, and the Plectonotinae appeared near the beginning of the late Middle Ordovician (Blackriveran-Rocklandian). The Bucanopsinae, as well as the Carinaropsidae, appeared during the latest Middle Ordovician (Rocklandian-Shermanian).

The broad epicontinental seas of the Middle Ordovician transgression apparently provided an ideal environment for the radiation of the bellerophontaceans, as well as many other invertebrate groups. The Middle Ordovician radiation of the bellerophontaceans probably had internal and external driving forces. The beginning of continental convergence during that time may have played a part by creating depositional topography over the cratonic sea floor (such as the proto-Lexington and proto-Nashville domes—see section on stratigraphy), which provided heterogeneous, and even somewhat isolated, environmental settings. As mentioned in the section on paleoecology, there was also a radiation of calcareous algal groups during the early Middle Ordovician, which would have offered a greater variety of food sources, and thus niches, to the predominantly algal feeding archaeogastropods. The contemporaneous diversification of other invertebrate groups during the Middle Ordovician also would have encouraged bellerophontacean radiation as entire new communities evolved. Finally, the trend toward more rapid whorl expansion and tighter coiling in the bellerophontaceans produced more mobile shell forms, which must have enabled the group to occupy new, particularly higher energy, environments and additional niches.

## SYSTEMATIC PALEONTOLOGY

In the following taxonomic descriptions of species, the type species of a genus is described first, where possible, and all other species descriptions are arranged in ascending stratigraphic order.

The following abbreviations for museum depositories are used:

- AMNH American Museum of Natural History, New York, N.Y.  
 CMNH Cincinnati Museum of Natural History, Cincinnati, Ohio  
 GSC Geological Survey of Canada, Ottawa, Ontario, Canada  
 MU Miami University Geology Museum, Oxford, Ohio  
 UC Field Museum of Natural History, Chicago, Ill.  
 UCGM University of Cincinnati Geology Museum, Cincinnati, Ohio  
 USNM U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C.

The U.S. Geological Survey collections cited in the text have a four-digit number and the -CO (Cambrian-Ordovician) suffix (for example, 6134-CO). The collecting localities for these and other collections are listed in the "Locality Register" (appendix).

**Phylum MOLLUSCA Cuvier, 1797**

**Subphylum CYRTOSOMA Runnegar and Pojeta, 1974**

**Class MONOPLACOPHORA Wenz in Knight, 1952**

*Diagnosis.*—Mollusks having a single, bilaterally symmetrical, cap-shaped, orthoconic, cyrtoconic, or planispiral shell, the apex generally being anteriorly situated, with symmetrical muscle scars arranged in discrete pairs or in partly to completely fused ring around aperture.

*Stratigraphic range.*—Lowest Cambrian (Tommotian)-Holocene.

*Discussion.*—The diagnosis given above is conchological. The Monoplacophora can be further defined in zoological terms, on the basis of limited information provided by the few known living species, as untorted mollusks having an anterior mouth, a posteromedian anus, a lateral to posterior mantle cavity, pseudometamerically arranged organ systems, a radula, and a gastropodlike foot.

**Order TRYBLIDIIDA Lemche, 1957**

*Diagnosis.*—Shells cap shaped to cone shaped; apex may be central, but generally is anteriorly situated, being subcentral, submarginal, marginal, or supramarginal, and in many cases incurved to varying degrees; muscle scars arranged nearly or completely around inner margin of shell, either in discrete pairs or in partly to completely fused ring.

*Stratigraphic range.*—Lower Cambrian-Holocene.

*Discussion.*—This order was defined by Lemche (1957), who described it primarily in zoological terms on the basis of the then newly discovered Holocene monoplacophoran *Neopilina*. His definition is difficult to apply to a study of fossils, and in reality is probably too limited even for the group of genera Lemche recognized as members. The diagnosis given above is paleontological in

its applications, and is most similar to that of Starobogatov (1970), but with significant differences in the composition of the order. Herein, the superfamily Archina-cellacea is included in this order; the order Archina-cellida is rejected. The superfamily Kirengellacea also is included in the Tryblidiida, but it has the same composition as Rosov's (1975) order Kirengellida. The superfamily Tryblidiacea is included nearly as conceived by Starobogatov (1970), except for the transfer of the family Archaeophialidae to the superfamily Kirengellacea. For further discussion of these actions, see the section on "Phylogeny and Classification" and table 16.

**Superfamily TRYBLIDIACEA Pilsbry, 1899**

*Diagnosis.*—Shell cap shaped, apex marginal or supra-marginal; muscle scars in discrete pairs.

*Stratigraphic range.*—Lower Cambrian-Holocene.

**Family TRYBLIDIIDAE Pilsbry, 1899**

*Diagnosis.*—Shell more or less cap shaped, being broadly rounded posteriorly, narrowing rapidly near anterior end; convexity low; apex marginal or slightly supramarginal; comarginal growth lines distinct, in some cases lamellose, in many cases accompanied by radial lines; muscle scars in five to eight discrete pairs, commonly more complex anteriorly.

*Stratigraphic range.*—The family contains species from the Upper Cambrian (*Propilina* Kobayashi, 1933) to the Holocene (*Neopilina* Lemche, 1957), but members are most common in Middle Ordovician to Middle Silurian strata.

*Discussion.*—The original concept of the family Tryblidiidae by Pilsbry (1899) was as follows: "Limpets with muscle scars broken into numerous separate impressions." This definition would now more closely fit the order Tryblidiida. As muscle scars were found in more genera, a considerable diversity was discovered and the concept of the family was restricted to fit the Ordovician-Silurian genus *Tryblidium* and closely related forms.

**Subfamily TRYBLIDIINAE Pilsbry, 1899**

*Diagnosis.*—Same as for family.

**Genus HELCIONOPSIS Ulrich and Scofield, 1897**

*Diagnosis.*—Shell having slightly supramarginal apex and distinct, widely spaced growth lines crossed by prominent radiating threads.

*Description.*—Shell cap shaped, moderate in size, convexity low; apertural outline subovate; posterior broadly rounded, narrowing anteriorly to small beak area; apex protruding slightly beyond anterior apertural margin; comarginal growth lines distinct, widely and irregularly spaced; radial threads prominent, bifurcating posteriorly; muscle scars unknown.

*Type species.*—*Helcionopsis fissicostata* Ulrich and Scofield, 1897, by original designation; *lapsus calami* for *Helcionopsis striata* Ulrich and Scofield, 1897 (Knight, 1941, p. 142).

*Distribution.*—Middle Cambrian (Ordian stage of Australia)-Middle Silurian (Wenlockian) of Gotland (Sweden). In North America the genus is known only from the Ordovician (Shermanian?-Richmondian).

*Discussion.*—Runnegar and Jell (1976) reported *Helcionopsis* sp. from the Middle Cambrian of Australia on the basis of small internal molds having the shell form and radial markings characteristic of the genus. Their identification appears to be correct. Easton (1943) described *Helcionopsis? reticulatus* from the Upper Mississippian Pitkin Formation of Arkansas, but this occurrence requires reexamination.

When Ulrich and Scofield (1897, p. 826, 827) named the genus *Helcionopsis*, they included three species: *H. striata* Ulrich and Scofield, *H. subcarinata* Ulrich and Scofield, and *H. radiata* (Lindstrom). *H. striata*, from the Maysvillian and Richmondian strata of the Cincinnati province, is a well-known, distinctive species. *H. subcarinata* is known from only a few internal molds from the Prosser Formation (Ulrich, 1911) (Shermanian-Edenian) of Minnesota. Its placement in this genus is questionable. From Ulrich and Scofield's (1897, pl. 61, fig. 28) figure of this species, it appears to have the shell outline of an archinacellid, and its radial ornament is very poorly defined. The third species, *H. radiata*, was described by Lindstrom (1884, p. 58) as *?Tryblidium radiatum* from the Silurian "crystalline limestone of Wialmsudd near Farosund," and it appears to be a valid member of the genus.

The muscle scars of this genus are unknown, and its higher systematic position is difficult to determine. Knight and Yochelson (1960) placed a question mark before the genus name and associated it with *Pilina* because of similarities in shell forms and the common possession of radial ornament. These two genera are closely related, but *Helcionopsis* is distinct in its possession of heavy radiating threads, rather than the faint radiating grooves exhibited by *Pilina*.

#### *Helcionopsis striata* Ulrich and Scofield, 1897

Plate 2, figures 1-6

*Helcionopsis striata* Ulrich and Scofield, 1897, p. 827, pl. 61, figs. 29, 30; Knight, 1941, p. 142, 143, pl. 3, fig. 5; Knight and Yochelson, 1960, p. 179, figs. 46, 7.

*Tryblidium striatum* (Ulrich and Scofield), Shimer and Shrock, 1944, p. 437, pl. 174, fig. 3.

*Diagnosis.*—Shell elongate, subovate, broadly rounded posteriorly, with narrow anterior beak area; apex slightly supramarginal, pointing horizontally to slightly downcurved in later growth.

TABLE 18.—Measurements (in millimeters) of *Helcionopsis striata*

USNM No.	Shell length	Shell width	Shell height	Aperture length	Apex height
45827	23.25	17.40	6.1	22.90	1.5
263785	14.20	11.85	5.2	13.70	3.5
47494	14.00	11.15	4.3	13.55	2.0

*Description.*—Shell elongate, subovate in outline, broadly rounded posteriorly, narrowing rapidly to small beak area at anterior end; lateral apertural margin horizontal; dorsally low and broadly convex, becoming more gently convex on posterior slope; anterior slope tightly concave; apex extending slightly beyond anterior apertural margin, pointing essentially horizontally in immature specimens, becoming increasingly downcurved in mature growth stages; protoconch small smooth cone; shell thin, with surface marked by widely, mostly irregularly spaced comarginal growth lines of varying prominence; radial threads slightly rounded, bifurcate posteriorly, with secondary ribs intercalated in maturity; radiating costellae varying in spacing over length of shell (four per millimeter near beak, three per millimeter 5 or 6 mm from apex, and two per millimeter 20 mm from apex).

*Measurements.*—Measurements of *H. striata* are listed in table 18. Table 19 lists measurements of the distances between growth lines of the holotype (USNM 45827), and figure 20 graphically displays the apparent growth rate of the specimen.

*Material.*—No new specimens were found in the USGS silicified collections from the Cincinnati arch region. Only three specimens were located in the U.S. National Museum of Natural History and examined. The holotype, USNM 45827, is an external mold in the base of a bryozoan colony (pl. 2, figs. 1-3 are latex molds made from the holotype), as is specimen USNM 47494 (pl. 2, figs. 4, 5; fig. 5 is a latex mold). The third specimen, USNM 263785, retains the shell and protoconch (pl. 2, fig. 6).

*Distribution.*—The holotype, USNM 45827, is from Richmondian-age strata in Marion County, Ky.; no further stratigraphic or locality data are given with the

TABLE 19.—Measurements (in millimeters) of distances between growth lines of the holotype of *Helcionopsis striata* (USNM 45827)

[Row A gives the numbers assigned to each growth line, moving from anterior to posterior. Row B designates the relative strength of each growth line (s = strong, m = medium, and w = weak). Row C gives the measurements from one growth line to the next, the first measurement being taken from the apex to the first distinct growth line]

A	1	2	3	4	5	6	7	8	9	10	11	12
B	s	w	m	w	w	s	s	s	m	w	s	m
C	3.4	1.7	2.8	0.5	1.0	1.0	1.9	6.0	1.0	1.4	1.3	1.0

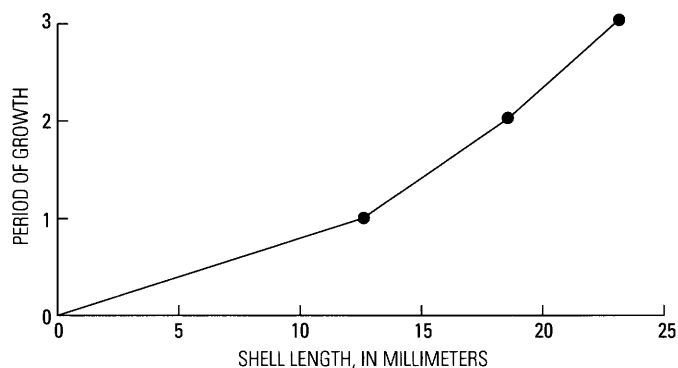


FIGURE 20.—Apparent growth rate of the holotype (USNM 45827) of *Helcionopsis striata*. The strongest growth lines were measured from the apex to the posterior shell margin on the assumption that these lines marked annual growth increments. Three periods of growth are recognized, and an apparent decrease in growth rate with age is evident.

specimen. Specimen USNM 263785, Maysvillian or Richmondian in age, is from the Arnheim Formation at Clifton, Tenn. Specimen USNM 47494 is from the Maysvillian-age Bellevue Tongue of the Grant Lake Limestone at Cincinnati, Ohio. Therefore, the species is known only from the middle and upper Upper Ordovician (Maysvillian-Richmondian) of the Cincinnati arch province (table 4).

**Comparison.**—*H. striata* is the only species of monoplacophoran in the Cincinnati arch province to have prominent radial ribs that cross growth increments (pl. 2, figs. 1–6). *Vallatothera unguiformis* (Ulrich, 1897) (Kirkfieldian-Shermanian) (pl. 1, figs. 12–31) and *V. manitoulini* Foerste, 1914a (Richmondian) (pl. 1, figs. 8–11), have regular, closely spaced, sublamellose growth lines and fine radiating threads that are restricted to individual growth increments.

**Discussion.**—The two specimens preserved as external molds in the bases of calcitic bryozoan colonies (pl. 2, figs. 1–3, 4, 5) strongly suggest that the shell of *H. striata* was aragonitic in composition, having been preferentially dissolved away. The specimen from Tennessee (pl. 2, fig. 6) is the only known specimen of the species preserving the shell. The shell is somewhat worn, but it is clear that it was very thin and probably quite delicate. This in part accounts for the rareness of *H. striata*.

The protoconch preserved in the Tennessee specimen (pl. 2, fig. 6) is very small, apparently smooth, and symmetrically cone shaped. It is nothing like the supposed protoconch of *Neopilina galathea* described by Lemche and Wingstrand (1959), which was said to be coiled. All other monoplacophorans have had noncoiled, bulbous protoconchs. In any case, the pointed, cone-shaped protoconch of *H. striata* is neither coiled nor bulbous.

The bifurcation and intercalation of the radial ribbing in this species is strikingly reminiscent of brachiopod costallae patterns (pl. 2, fig. 1). If other species of *Helcionopsis* are found, these patterns might prove useful for specific differentiation.

The unusual cone-shaped protoconch, the bifurcation and intercalation of radial ribs, and the absence of data on musculature cause me some uncertainty in the higher systematic assignment of this taxon.

Of considerable interest is the periodicity of the comarginal growth lines in the holotype of *H. striata* (pl. 2, figs. 1–3). Table 19 lists the distances between these lines and the relative strength of the lines. The pattern shown by the growth lines in figure 20 could be interpreted as representing seasonal or annual growth increments. The first possible growth period (lines 1–7) shows a general decrease in the width of the growth increments. It should be noted that there were two very faint lines between lines 2 and 3 which were about 1.0 mm from each other and from stronger adjacent lines. The second period (lines 7–8) shows more continuous growth over a relatively large distance and only very faint cessation of growth. The third period is again more punctuated (lines 9–12), similar to the first. These period boundaries were identified subjectively, but they appear to form a pattern. When the length of each growth period is plotted, the general decrease in growth rate is obvious (fig. 20).

The holotype and its encrusting bryozoan occur in a matrix of fairly coarse biosparite containing fragments of brachiopods, bryozoans, and trilobites. Because this specimen's shell markings are well preserved, and considering the rather high energy conditions indicated by the matrix, it seems the animal might have been encrusted while it was alive. The encrusting bryozoan is not very thick, so the animal probably could have supported it easily. As is the case with *Cyrtolites* (*Cyrtolites*) *ornatus*, such encrustation may have furnished camouflage and protection from predation. In contrast, the second encrusted specimen (pl. 2, figs. 4, 5) probably was encrusted after the animal died. The bryozoan is well preserved, but the external mold of the shell in its base is somewhat worn. Furthermore, the bryozoan colony is quite large relative to the monoplacophoran shell, and most likely would have been too massive for the animal to have supported it in life.

The Tennessee specimen (pl. 2, fig. 6) also occurs in a rather coarse, fragmental biosparite matrix, but it must have been buried quickly in order for the thin shell to have been preserved. It is difficult to determine whether the slight breakage and wear of the shell occurred before burial or by weathering on the outcrop. The latter seems more likely, because the shell retains the protoconch, which would have been readily broken off during transport.



Evidence suggests that *H. striata* lived in normal marine waters of moderate to high energy, but well offshore in a bryozoan-brachiopod community.

**Family PROPLINIDAE Knight and Yochelson, 1958**

*Diagnosis.*—Shell elongate, more or less cap shaped, wider posteriorly, quite narrow anteriorly, moderately to strongly convex; apex distinctly extending past anterior shell margin; six pairs of elongate muscle scars situated normal to margin of aperture, posterior pair particularly elongate and continuing well into interior of shell.

*Stratigraphic range.*—Upper Cambrian-Upper Ordovician.

*Discussion.*—Knight and Yochelson (1958, 1960) recognized this grouping as a subfamily of the family Tryblidiidae, including in it *Proplina* Kobayashi, 1933, and ?*Vallatotheca* Foerste, 1914a.

Starobogatov (1970) used the grouping at the family level and added three genera: *Kotysium* Horny, 1961; *Litavina* Horny, 1963a; and ?*Pilinopsis* Horny, 1961. Horny (1961) had originally placed both *Kotysium* and *Pilinopsis* in the subfamily Trybliniinae. *Kotysium* resembles *Proplina* in its shell form, but Horny claimed that its five known pairs of muscle scars are quite different from the muscle scars of *Proplina*. *Pilinopsis* resembles *Pilina* in its shell form, but its muscle scars are unknown. The genus *Pilinopsis* is based on *Helcionopsis eminens* Perner, and bears closely spaced comarginal growth lines, with short radiating lines restricted to the spaces between these growth lines (Perner, 1903, fig. 10c), resulting in an ornament pattern very similar to that of the genus *Vallatotheca*. The shell form of *Pilinopsis* (according to Perner, 1903, figs. 10a, b) is very similar to that of *Helcionopsis*, or even to that of some archinacellids. Clearly, the assignment of these genera to higher taxonomic groupings is difficult because of the differing levels of knowledge of their rather simple morphologies.

*Vallatotheca*, the only genus of the family studied here, is a distinctive taxon that is included in the Proplinidae because of its general shell form and its distinctly supramarginal apex, both of which resemble *Proplina*. Unfortunately, nothing is known about the muscle scars of *Vallatotheca*.

**Genus VALLATOTHECA Foerste, 1914a**

*Diagnosis.*—Shell distinctly convex; apex curved downward; growth lines closely and regularly spaced, sublamellose, with fine radial threads restricted to growth increments between sublamellose growth lines.

*Description.*—Shell distinctly convex dorsally, broadly rounded in posterior two-thirds, anterior third narrowing rapidly to blunt beak area; apex blunt, down-

curved, becoming more so with growth, and extending far beyond apertural margin; apertural outline elongate-oval; lateral apertural margin horizontal; growth lines closely and regularly spaced, sublamellose; radial threads fine, closely spaced, restricted to growth increments between sublamellose growth lines; shell moderately thick.

*Type species.*—*V. manitoulini* Foerste, 1914a, by original designation, reported from the "Cape Smyth or Waynesville Member of the Richmond, at Clay Cliffs on the eastern side of Cape Smyth, three miles north of Wekmemikongsing, on the eastern shore of Manitoulin Island" (Ontario, Canada) (Foerste, 1914a, p. 482).

*Distribution.*—The genus is known with certainty from the Lexington Limestone (upper Middle Ordovician) of central Kentucky, and from the Richmondian (upper Upper Ordovician) strata of southwestern Ohio and of Manitoulin Island, Ontario, Canada. Runnegar and Jell (1976) assigned some Middle Cambrian specimens from Australia to the genus, but for reasons given below, this assignment is not accepted. Talent (1959) has described specimens from the Lower Devonian of Australia that appear to represent a valid species of *Vallatotheca*. Therefore, the genus is currently known from the late Middle Ordovician to the Early Devonian.

*Comparison.*—The shell form of *Vallatotheca* is similar to that of *Proplina* Kobayashi, 1933, but its sublamellose growth lines with their enclosed fine radial threads distinguish it from *Proplina*.

*Vallatotheca* is similar to *Helcionopsis*, as both have radial ornament. However, the close, regular spacing of the growth lines, the fine character of the radial threads, and particularly their restriction to individual growth increments, and the general shell form of *Vallatotheca* easily distinguish it from *Helcionopsis*.

*Discussion.*—Foerste (1914a) originally placed two species in the genus—*V. manitoulini* Foerste, 1914a, and *V. unguiformis* (Ulrich, 1897). The latter species was described from the Middle Ordovician Lexington Limestone of central Kentucky as *Stenotheca unguiformis*. The former species was described as the type species of the genus (Foerste, 1914a, p. 482, pl. 4, figs. 4a, b): "Genotype differing from the congeneric *Stenotheca unguiformis* Ulrich, in its much larger size, and the greater curvature of the beak. The concentric markings are not due to transverse folds, but are successive lamellose outgrowths of the shell, striated only on their apical sides."

Miller (1897) believed *S. unguiformis* should be included in the genus *Tryblidium* Lindstrom. Shimer and Shrock (1944, p. 437) placed the species in the genus *Proplina*, and assigned *V. manitoulini* to the genus *Tryblidium*. The present investigation revealed no justification for separating the two species originally placed

in *Vallatotherca* by Foerste (1914a). On the contrary, the new silicified material from the Ordovician of Kentucky shows that the two species are morphologically closer than originally believed. Knight and Yochelson (1958, 1960) were influenced by the lack of confidence shown by these previous authors in the validity of the genus *Vallatotherca* when they placed a question mark before the genus name.

Runnegar and Jell (1976, p. 131, 132, figs. 9A, 1–5) referred four small specimens from the Middle Cambrian of Australia to *Vallatotherca* sp., but this assignment seems unwarranted because the Australian Cambrian specimens have very coarse comarginal and radial shell markings. Runnegar and Jell referred to the coarse comarginal rings as “plicae,” and it is clear from their fine photographs that this is the appropriate terminology. Furthermore, their figure 9A, 2, clearly shows that the radial ribs cross over and between the plicae. In contrast, the American Ordovician species have fine radial threads that are restricted to individual concentric lamellae. Therefore, it appears that the Australian Cambrian specimens are only superficially similar to *Vallatotherca*, differing significantly in the basic mode of growth of the shell. Runnegar and Jell’s specimens bear much closer resemblance to some species of the comarginally plicate genera *Latouchella* and *Helcionella*, which are also illustrated in their figure 9. However, the occurrence of radial ribbing on their specimens may give a clue to the ancestry of Ordovician genera that also exhibit radial ornament, including *Vallatotherca*, *Helcionopsis*, *Cyrtolites*, and others. Radial ornament seems to be more common in the Monoplacophora and Bellerophonitida than is generally recognized. Most of these genera show a basic difference in their types of radial ornament. The types of comarginal and radial ornament in *Vallatotherca* and *Cyrtolites* (*Cyrtolites*) may indicate a common origin for the genera.

***Vallatotherca manitoulini* Foerste, 1914a**

Plate 1, figures 8–11

*Vallatotherca manitoulini* Foerste, 1914a, p. 482, pl. 4, figs. 4a, b.  
*Tryblidium manitoulini* (Foerste), Shimer and Shrock, 1944, p. 437,  
pl. 174, fig. 2.

**Diagnosis.**—Shell relatively broad (shell length/width ratio 1.30), somewhat inflated.

**Description.**—Shell broadly teardrop shaped in outline, quite broad posteriorly, narrowing in anterior third to blunt beak; shell length/width ratio 1.30; dorsally and posteriorly broad and somewhat inflated; apex bluntly pointed, markedly downcurved to near level of aperture, extending well beyond anterior apertural margin; growth lines closely and regularly spaced, sublamellose; radial threads fine, closely spaced, restricted to individual growth increments.

**Measurements.**—The specimens examined were not sufficiently exposed to allow reliable measurements. Foerste’s (1914a, pl. 4, figs. 4a, b) figure of the holotype was measured, and the shell length/width ratio was 1.30.

**Material.**—Only two specimens of this species were available for examination, MU 244T (pl. 1, figs. 8, 9) and MU 245T (pl. 1, figs. 10, 11), both calcitic replacements. The holotype, No. 8448 in the collections of the Geological Survey of Canada, Ottawa, was not examined, but both Foerste (1914a, pl. 4, figs. 4a, b) and Knight (1941, pl. 3, figs. 4a, b) adequately illustrated this specimen.

**Distribution.**—Foerste (1914a, p. 482) described the species from “the Cape Smyth or Waynesville Member of the Richmond, at Clay Cliffs on the eastern side of Cape Smyth, three miles north of Wekmemikongsing, on the eastern shore of Manitoulin Island,” Ontario, Canada. The two specimens examined here came from correlative strata in southwestern Ohio. Specimen MU 244T came from the Elkhorn biofacies of the Drakes Formation (Richmondian), just south of Morning Sun, Ohio. MU 245T came from the Whitewater Formation (Richmondian) near Camden, Ohio.

**Comparison.**—Foerste (1914a, p. 482) stated that *V. manitoulini* differs from *V. unguiformis* “...in its much larger size and the greater curvature of the beak.” The new silicified material from Kentucky shows that *V. unguiformis* attains a larger size than previously known (up to 22 mm in shell length), and that the beak increases in its downward curvature in later adult growth so that it nearly reaches the apertural plane (pl. 1, figs. 27, 28). Nevertheless, the two species can be separated on the basis of their convexity, *V. manitoulini* being more inflated, and their relative shell length/width ratios. *V. manitoulini* has a ratio of 1.30, and *V. unguiformis* has a ratio of 1.40, showing that the former species is somewhat wider.

**Discussion.**—The new specimens of *V. manitoulini* described herein are the first reported since the original description of the species from Manitoulin Island (Foerste, 1914a). It is likely that the species is more widespread than currently recognized, and its rarity may in part be due to poor preservation of small aragonitic shells. Also, as is later speculated about *Cyrtolites* (*Cyrtolites*) *ornatus*, bryozoan encrustation may have played a part in camouflaging the shells from detection by Ordovician predators, as well as Holocene collectors. *V. manitoulini* and *C. (C.) ornatus* have very similar shell sculpturing, which in both cases may have been preferred by settling bryozoan larvae (see discussion of *C. (C.) ornatus*). Lending some support to this speculation is specimen MU 245T of *V. manitoulini* (pl. 1, figs. 10, 11), which was revealed only after an encrusting bryozoan was partly removed.

TABLE 20.—*Measurements (in millimeters) of Vallatotheca unguiformis*

USNM No.	Shell length	Shell width	Shell height	Aperture length	Beak height	No. of growth lines in 1 mm
45990	12.65	9.05	4.85	10.9	0.5	3
265930	13.45	9.40	5.50	11.1	0.9	—
265931	7.50	6.30	3.50	6.9	—	5
265932	7.10	6.15	3.20	—	—	—
265933	9.55	6.85	3.35	—	—	—
387030	6.60	5.05	3.10	—	—	—
387030	5.80	4.55	2.20	—	—	—
265934	9.80	7.55	3.80	9.2	—	2
265935	10.30	7.30	3.50	—	—	—
265936	21.60	13.50	7.85	18.4	—	2
387031	9.20	6.60	4.30	—	—	2
387031	—	9.20	5.45	—	—	—
387032	22.50	15.00	10.00	—	—	—

**Vallatotheca unguiformis (Ulrich, 1897)**

Plate 1, figures 12–31

*Stenotheca unguiformis* Ulrich in Ulrich and Scofield, 1897, p. 843, pl. 61, figs. 42–44.

*Tryblidium unguiforme* (Ulrich), Miller, 1897, p. 771.

*Vallatotheca unguiformis* (Ulrich), Foerste, 1914a, p. 482.

*Proplina unguiformis* (Ulrich), Shimer and Shrock, 1944, p. 397, pl. 174, figs. 7, 8.

**Diagnosis.**—Shell narrowly teardrop shaped in dorsal outline (shell length/width ratio 1.40), moderately convex.

**Description.**—Shell narrowly teardrop shaped in dorsal outline, broadly rounded posteriorly, tapering rapidly in anterior third to blunt beak; shell length/width ratio 1.40; apex bluntly pointed, extending well beyond anterior apertural margin, curving downward, the curvature increasing in later growth so that apex may reach to plane of apertural margin; dorsal shell surface broadly and gently convex, increasing in convexity over beak area; growth lines closely and regularly spaced, sublamellose; radiating threads fine, closely spaced, restricted to individual growth increments.

**Measurements.**—Measurements of *V. unguiformis* are listed in table 20 and shown graphically in figure 21.

**Material.**—The type suite consists of three silicified syntypes cataloged under the number USNM 45990. The specimen shown herein on plate 1, figures 12–15, is designated the lectotype and retains the original USNM number. The other two syntypes, shown on plate 1, figures 21, 22 and 23, 24, are designated paralectotypes and assigned the numbers USNM 265930 and 265931, respectively.

Fifteen specimens of this species were found in the new silicified collections from samples 5015-CO, 6915-CO, 6916-CO, and 7784-CO. Specimens USNM 265932 (pl. 1, figs. 18–20), USNM 265933 (pl. 1, figs. 30, 31), and USNM 387030 are from sample 5015-CO. Specimens USNM 265934–265936 (pl. 1, figs. 16, 17, 29, and 25–28,

respectively) and USNM 387031 are from sample 6915-CO. Collections 5015-CO, 6915-CO, and 6916-CO are from the Salvisa Bed, Perryville Limestone Member, Lexington Limestone, Perryville quadrangle, Kentucky. Collection 7784-CO is from the Curdsville Limestone Member, Lexington Limestone, Little Hickman quadrangle, Kentucky.

**Distribution.**—The museum label with the type suite (USNM 45990, 265930, 265931) reads “Upper Trenton” at “Harrodsburg Junction, Cincinnati and Southern Railroad, Kentucky.” Ulrich (*in* Ulrich and Scofield, 1897) listed the locality for the types as “Upper beds of the Trenton Group, between Burgin and Danville, Kentucky.” The geologic map of the Danville quadrangle, Boyle and Mercer Counties, Ky. (USGS GQ-985; Cressman, 1972), shows that the tracks of the Southern Railroad between Burgin and Danville pass mainly through exposures of the Curdsville Limestone and Grier Limestone Members of the Lexington Limestone, but they also cut across exposures of the Perryville Limestone Member of the same formation just south of Burgin and just north of Danville.

In the USGS silicified collections, one questionable specimen of the species was found in sample 7784-CO from the Curdsville Limestone Member (Kirkfieldian), Lexington Limestone. All other specimens were found in samples 5015-CO, 6915-CO, and 6916-CO, all from the Salvisa Bed of the Perryville Limestone Member (Shermanian) of the Lexington Limestone near Perryville, Ky.

**Comparison.**—*V. manitoulini* is distinguished by its wider, more convex shell form.

**Discussion.**—*V. unguiformis* is known with certainty only from the Salvisa Bed of the Perryville Limestone Member of the Lexington Limestone in central Kentucky. The Salvisa Bed is a calcilutite containing ostracodes, gastropods, and other shelly megafossils, and has been interpreted to represent shallow, quiet marine

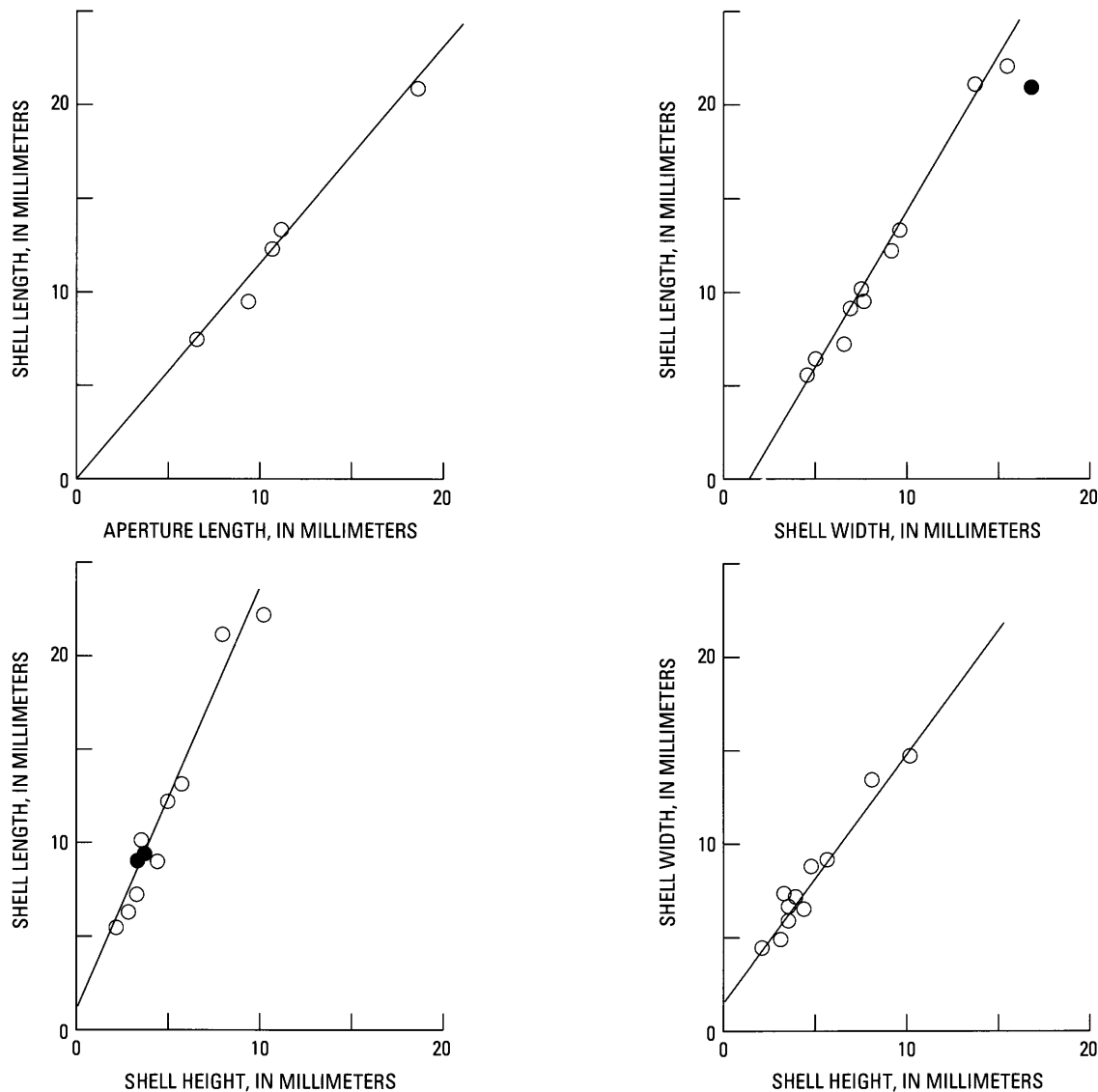


FIGURE 21.—Bivariate plots of measurements made on specimens of *Vallatotherca unguiformis*. The solid dots in the graphs of shell length to shell height and shell width represent *Vallatotherca manitoulini*, which is slightly wider than *V. unguiformis*.

conditions of greater than normal salinity, such as tidal lagoons (Cressman, 1973). It therefore appears that *V. unguiformis* occupied nearshore to onshore depositional environments. It is inferred that the species was an algal grazer.

#### Superfamily KIRENGELLACEA Starobogatov, 1970

**Diagnosis.**—Shell conical, some with tendency to coil for one-fourth to one-third whorl; apex high, in most cases located in a slightly anterocentral to marginal position, but may be central or even posterocentral in position; muscle scars in six to eight discrete pairs located about halfway between shell margin and apex.

**Stratigraphic range.**—Lower Cambrian-Lower Devonian.

**Discussion.**—Starobogatov (1970) proposed this superfamily for the single genus *Kirengella* Rosov, 1968. Rosov (1975) erected the order Kirengellida, including three families—Kirengellidae Starobogatov, 1970 (genera *Scenella* Billings, 1872; *Kirengella* Rosov, 1968; *Moyerokania* Rosov, 1970), Romaniellidae Rosov (*Romaniella* Doguzhaeva, 1972; *Hypseloconus* Berkey, 1898; *Nyuella* Rosov, 1975), and Archaeophialidae Knight and Yochelson, 1958 (*Archaeophiala* Koken in Perner, 1903). Concerning this new order Rosov (1975) stated,

We have combined the oldest monoplacophorans into a new order with a stratigraphic range extending from the Lower Cambrian to the Middle Ordovician inclusive. They are apparently the most primitive members of the class, ones that gave rise to other branches: to the orders Tryblidiida Lemche, 1957, Archinacellida Knight and Yochelson, 1958, and Cyrtoneidida Horny, 1963c. Evolution proceeded in the direction of further curling of the shell (order Cyrtoneidida) or farther forward displacement of the apex with simultaneous flattening of the shell (orders Tryblidiida and Archinacellida); the muscle scars evolved toward fusion of adjacent pairs of scars, which is to be seen to some degree in members of all four orders. [See fig. 18 herein.]

Rosov's (1975) concept of the Kirengellida is considered useful, but is used herein as a superfamily, the Kirengellacea, of the order Tryblidiida.

#### Family ARCHAEOPIHALIDAE Knight and Yochelson, 1958

**Diagnosis.**—Shell broadly conical, with subcircular to oval aperture outline; apex high, slightly anterocentral to nearly marginal; muscle scars in six to eight discrete pairs, the anterior pairs being more complex.

**Stratigraphic range.**—Middle Ordovician-Lower Devonian.

**Discussion.**—Knight and Yochelson (1958, 1960) included three genera in this group—*Archaeophiala* Perner, 1903, *Micropileus* Wilson, 1951, and *Calloconus* Perner, 1903—but used the taxon as a subfamily (Archaeophialinae) of the family Tryblidiidae. Starobogatov (1970) elevated the taxon to the family level in the superfamily Tryblidiacea. Then Rosov (1975) transferred the family to his new order Kirengellida. The muscle scars of *Micropileus* and *Calloconus* are unknown, but because of similarities in shell form the genera are generally classified with *Archaeophiala*, whose muscle scars are well known. Starobogatov (1970) included a fourth genus, *Platypilina* Horny, 1961, whose type species is *Scenella? tardissima* Perner, 1903. This species, as figured by Perner (1903, figs. 23a-c, and 1907, pl. 117, figs. 1-3) has radial ornament crossed by growth lines on a shell having a slightly curled anterocentral apex. *Platypilina tardissima* seems to be close to *Macroscenella* Wilson, 1951, which was proposed to include many of the Ordovician species assigned to *Scenella* by Ulrich and Scofield, 1897. The subcentral apex and closely similar shell sculpturing suggest a close relationship between *Platypilina* and *Macroscenella*. They seem better accommodated in the superfamily Kirengellacea, and provisionally in the family Archaeophialidae or, because of their *Scenella*-like markings, possibly in the family Kirengellidae.

Rosov (1975) included the genera *Romaniella* Doguzhaeva, 1972, *Nyuella* Rosov, 1975, and *Hypseloconus* Berkey, 1898, in the then newly proposed family Romaniellidae. Rosov pointed out that the similar shell forms and ranges of *Romaniella* and *Hypseloconus* indicate that they are synonyms. This group of genera is characterized in part by the fusion of some pairs of

muscle scars. *Hypseloconus* was once placed in the Archinacellacea by Knight and Yochelson (1958, 1960) because it was thought to have fused scars. Stinchcomb (1980, p. 45-47) described discrete, paired muscle scars in specimens of *Hypseloconus*, as well as one or more continuous rings that have previously been interpreted as muscle bands. The classification of *Hypseloconus* in the superfamily Kirengellacea seems valid; however, its familial affinities remain uncertain. The species *Nyuella bjalvi* Rosov, 1975, has a shell form that is quite comparable to that of some archinacellids. For example, compare the species (Rosov, 1975, figs. 2a-d) with *Archinacella arca* n. sp. (herein, pl. 3, figs. 7-10); dorsally there is a resemblance, but *N. bjalvi* has a convex lateral apertural margin, whereas *A. arca* has a distinctly concave apertural margin. It seems that the Romaniellidae may be the ancestors of the archinacellids, through flattening of the shell and fusion of the shell muscles, as suggested by Rosov (1975).

#### Genus MICROPILEUS Wilson, 1951

**Diagnosis.**—Shell having blunt, elevated, submarginal apex; shell slopes smooth to slightly wrinkled, with no distinct ornament; apertural outline subcircular to subovate.

**Description.**—Shell high, cap shaped; apertural outline subcircular to subovate; apex blunt, elevated, located slightly within, or nearly over, anterior shell margin; anterior shell slope slightly concave (particularly in immature shells), flat, or slightly convex; posterior slope broadly convex; comarginal striae and (or) weak undulations; muscle scars unknown.

**Type species.**—*M. obesus* Wilson, 1951, by original designation; reported from the Lowville-Leray beds (Blackriveran) of eastern Canada.

**Distribution.**—Wilson (1951) described two species from the Lowville-Leray beds (Blackriveran) of the Ottawa-St. Lawrence Lowland, Canada. The new species described below was found in the Curdsville Limestone Member of the Lexington Limestone (Kirkfieldian). On the basis of the figures and description given by Hussey (1926, p. 171, pl. 6, fig. 1), *Archinacella simmonsii* Hussey from the Stonington beds (Richmondian) of Michigan is herein transferred to *Micropileus*. Therefore, the genus is known from the upper Middle Ordovician (Blackriveran) to the upper Upper Ordovician (Richmondian).

**Discussion.**—Wilson (1951) proposed two new genera, *Micropileus* and *Macroscenella*, for Ordovician cap-shaped shells originally assigned to the genus *Scenella*, which is currently considered to be restricted to the Cambrian Period. *Macroscenella* differs from *Micropileus* in its more subcentral apex, the presence of a supposed labral emargination, and a reticulate type of

TABLE 21.—Measurements (in millimeters) of *Micropileus variabilis*

USNM No.	Shell length	Shell width	Shell height
265926	12.70	11.4	7.25
265927	—	12.4	10.65
265928	13.50	11.6	7.60
265929	12.45	10.6	8.25

shell ornament formed by comarginal growth lines and radial striae (rather than only comarginal growth lines and (or) undulations as in *Micropileus*). Wilson assigned a number of Middle Ordovician species placed in *Scenella* by Ulrich and Scofield (1897) and others to *Macroscenella*, but did not assign any previously described species to *Micropileus*, although she believed many Ordovician species that had been assigned to *Scenella* would eventually be transferred to *Micropileus* when better known. Herein, the following North American species are placed in *Micropileus*: *M. obesus* Wilson, *M. ottawaensis* Wilson, *M. simmonsii* (Hussey), and *M. variabilis* n. sp.

Although Wilson (1951) was uncertain where to place *Micropileus* in the hierarchy, it now seems best to recognize it as a genus closely related to the European Ordovician genus *Archaeophiala* based on the similar shell form. *Macroscenella* seems more closely related to *Scenella* than to *Micropileus*, as indicated by its more central apex and reticulate ornament.

#### *Micropileus variabilis* new species

Plate 1, figures 1–7

**Diagnosis.**—Shell having submarginal apex and slightly concave to nearly flat anterior slope; apertural outline subcircular; shell exterior in some specimens having irregular comarginal undulations.

**Description.**—Shell medium sized (up to 13.5 mm long), high cap shaped; apertural outline subcircular to broadly subovate, length about 1.15 times width, and about 1.60 times shell height; apex position somewhat variable, but in all specimens submarginal and generally located about halfway between center of shell and anterior shell margin; apex bluntly pointed, elevated; anterior slope steep, slightly concave to flat; posterior slope more gently sloped and broadly convex; shell essentially smooth, but commonly with one or more comarginal undulations; fine radial striae faintly visible near aperture of some specimens; shell fairly thin.

**Measurements.**—Measurements of *M. variabilis* n. sp. are listed in table 21.

**Material.**—This species is known from about 15 silicified specimens from USGS sample 7784-CO and from 1 silicified specimen from USGS sample 7817-CO. The

latter specimen (pl. 1, figs. 1–4) is herein designated the holotype (USNM 265926). Three paratypes from USGS 7784-CO are figured: USNM 265927 (pl. 1, fig. 7), USNM 265928 (pl. 1, fig. 5), and USNM 265929 (pl. 1, fig. 6). The other paratypes, most of them fragments, are combined under the number USNM 265956.

**Distribution.**—*M. variabilis* is known only from the lower 6 ft of the Curdsville Limestone Member of the Lexington Limestone (Kirkfieldian). It was found at USGS localities 7784-CO and 7817-CO in the Little Hickman quadrangle, Jessamine County, Ky. The holotype (USNM 265926) is from 6 in above the Curdsville-Tyrone contact at a roadcut along Kentucky Route 39, 0.3 mi (miles) southeast of Black Bridge, which crosses Hickman Creek (USGS 7817-CO). The paratypes are from the basal 2 ft of the Curdsville Limestone Member, at an exposure 0.3 mi southeast of a bridge crossing the Kentucky River on U.S. Route 27 (7784-CO).

**Comparison.**—*M. variabilis* n. sp. differs from the type species *M. obesus* Wilson in its slightly smaller size and centrally located apex.

**Discussion.**—Two specimens of *M. variabilis*, USNM 265926 (pl. 1, figs. 1–4) and USNM 265927 (pl. 1, fig. 7), show a comarginal undulation in the shell about halfway between the apertural margin and the apex. These bandlike comarginal undulations are suggestive of a muscle scar in their appearance and location. It is possible that at maturity, the muscles caused an undulation in these thin-shelled animals. Considering that the basal Lexington Limestone is transgressive in nature, the animal may have occupied a higher energy environment in which strength of attachment to the substrate was of paramount importance. *M. variabilis* may have led a limpetlike existence, clinging to protruding irregularities of the lithified surface of the Tyrone Limestone, which was being transgressed during Curdsville deposition. The nature of this disconformable contact was described by Cressman (1973, p. 12, 13).

#### Superfamily ARCHINACELLACEA Knight, 1956

**Diagnosis.**—Shell cap shaped, height variable, generally widest anteriorly; apex located distinctly anteriorly, submarginal, marginal, or supramarginal; muscle scars fused completely into ringlike band, or incompletely into horseshoe-shaped scar that is open posteriorly; accessory scars in some cases located along band itself or in opening of horseshoe-shaped scar.

**Stratigraphic range.**—Chazy (middle Middle Ordovician)-Richmondian (upper Upper Ordovician). It should be noted that Knight and Yochelson (1960) listed the range for the superfamily as Upper Cambrian to Lower Silurian, but with the transfer of *Hypseloconus* to the Kirengellacea (Rosov, 1975), all Upper Cambrian and Lower Ordovician taxa were removed from the super-

family. I know of no Silurian archinacellaceans. Horny (1965a, p. 63) listed the superfamily as Upper Cambrian to ?Lower Silurian, but noted that the group is probably not known above the uppermost Ordovician. He did, however, suggest that the Silurian genus *Archaeopruga* may be a descendant of this line.

*Discussion.*—Knight and Yochelson (1958) defined the superfamily Archinacellacea as containing the families Archinacellidae Knight, 1956, and ?Hypseloconidae Knight, 1956, and placed it in the monotypic order Archinacelloidea. This classification was continued in "Treatise on Invertebrate Paleontology" (Knight and Yochelson, 1960). In 1958, these authors noted that this order was an unsatisfactory and artificial grouping of forms. They defined the Archinacelloidea as follows (1958, p. 39): "Shell shape variable, but always bilaterally symmetrical and with distinct apex, presumed to be anterior; muscle scars, where known, forming an incomplete to complete ring."

Horny (1965a) corrected the ordinal name to Archinacellida and defined it as follows: "Shell never coiled, scars often fused to form a complete ring; apex anterior or central." He did not elaborate on subordinal classification.

Knight (1952, p. 52) included molluscan univalves having a continuous muscle scar, such as *Archinacella* Ulrich and Scofield, 1897, with those having discrete paired scars in the Monoplacophora. He pointed out that in both types the scars have elements that close or nearly close the circlet anteriorly. He proposed that these forms, like the Polyplacophora, did not have an anterior pallial cavity and had not undergone torsion. He suggested that the scars narrowed anteriorly because the muscles attached in that area were extensions from the pedal muscles at each side arching over the head.

However, Starobogatov (1970) has argued in favor of the return of the Archinacellida to the class Gastropoda, based on interpretation of the muscle scar patterns in *Archinacella*, *Archinacelliopsis*, *Archinacellina*, and *Archaeopruga*. It should be noted that *Archinacellina* and *Archinacelliopsis* are not present as such in "Treatise on Invertebrate Paleontology" (Knight and Yochelson, 1960). *Archinacellina* was erected by Horny (1961) for those species originally assigned to *Archinacella* that have two pairs of nearly isolated, triangular scars posterolaterally on the inner side of the ring-shaped principal scar. *Archinacelliopsis* was erected by Horny (1963c) for those archinacellids having an open contra-apical end on the main muscle band, with a pair of discrete scars located in the gap; this genus is represented in Knight and Yochelson (1960, fig. 50.4) by *Archinacella patelliformis*. Starobogatov (1970) argued that the circular muscle of *Archinacella* approaches slightly too close to the shell margin at the apical end, leaving no room for the

head. Conversely, at the contra-apical end the circular muscle is sufficiently removed, and is even open in *Archinacelliopsis*. Starobogatov interpreted the pair of discrete scars in the gap at the contra-apical end of *Archinacelliopsis* as radular muscle scars similar to those of the cap-shaped Monoplacophora and Docoglossa. He believed that the looplike thickenings of the circular muscle located along the sides of the apex of both genera indicate the original point of insertion of the shell muscles. He compared the position of the pair of muscle scars on the Silurian patellid gastropod *Archaeopruga* (Horny, 1963b), which converge at the apical end and separate at the contra-apical end, with the position of the circular muscle in *Archinacella*, *Archinacelliopsis*, and *Archinacellina*. On the basis of this comparison, Starobogatov concluded that the contra-apical end, rather than the apical end, was anterior in the archinacellids and therefore that the Archinacellida should be an order within the Gastropoda.

Starobogatov's arguments (1970) are impressive, but his conclusions require more documentation. Other authors (Horny, 1965a, b; Rosov, 1975) have shown how archinacellid scars fit well into the monoplacophoran picture, and their conclusions are generally accepted. Starobogatov's interpretation concerning the placement of the discrete scars in the open contra-apical end of the muscle scar of *Archinacelliopsis* is particularly interesting. It is not understood why this monoplacophoran would preferentially segregate muscles posteriorly. But then, the problem can be looked at in an opposite manner: Maybe these discrete scars indicate a more primitive condition than seen in *Archinacella*, one in which the muscle band has not yet completely fused. Rosov (1975) suggested that the evolution toward fusion of adjacent pairs of muscle scars can be seen to some degree in members of all the orders of the Monoplacophora, the trend reaching completion in the Archinacellida. Also, Starobogatov's (1970) argument that there is not sufficient space for the head of the animal beneath the beak of *Archinacella* does not seem conclusive. The head region of *Neopilina* seems quite small. For the present, the Archinacellida should continue to be classified as monoplacophorans.

Rosov (1975) recognized the order Archinacellida but rejected placement of the family Hypseloconidae in that order, and instead included the genus *Hypseloconus* Berkeley, 1898, in the Romaniellidae of the order Kirengellida.

Runnegar and Jell (1976) placed the family Hypseloconidae in their order Cyrtoneurida and superfamily Helcionellacea, noting the group's possible ancestry to the Cephalopoda, as proposed by Yochelson, Flower, and Webers (1973). Furthermore, Runnegar and Jell rejected the order Archinacellida; they did not consider



the fusion of muscle scars a significant higher level taxobase, and placed the archinacellids in the family Tryblidiidae. While I agree with these authors that the archinacellids should not be considered a separate order of monoplacophorans, I do not agree that they should be included with the Tryblidiidae. Rather, I support placement of the superfamily Archinacellacea in the order Tryblidiida. The Tryblidiacea should be reserved for cap-shaped shells having an anteriorly placed apex and discrete muscle scars. As demonstrated by the emplacement of a pair of discrete muscle scars in the posterior gap of a fused, horseshoe-shaped muscle scar in *Archinacelliopsis*, it appears that the Archinacellacea developed from ancestors having discrete paired scars by progressive fusion of such scars. Ancestors of the Archinacellacea might be found within the family Romaniellidae of the superfamily Kirengellacea. *Nyuella bjalvi* Rosov (1975) of that family exhibits fusion of the anterior scars of its muscle ring. Fusion of muscle scars probably progressed posteriorly, resulting in such forms as *Archinacelliopsis* and finally in the completely fused ring seen in *Archinacella*.

#### Family ARCHINACELLIDAE Knight, 1956

*Diagnosis and stratigraphic range.*—Same as for superfamily.

*Discussion.*—Knight and Yochelson (1958) recognized two genera in this family: *Archinacella* and ?*Ptychopeltis*. The latter genus is a poorly understood form from the Middle Ordovician of eastern Europe (Perner, 1903) that was placed in the Archinacellidae because its shell shape has some resemblance to *Archinacella*. The muscle scars of *Ptychopeltis* are unknown, and its placement in this family is doubted.

Three genera are currently placed in the family Archinacellidae: *Archinacella* Ulrich and Scofield, *Archinacellina* Horny, and *Archinacelliopsis* Horny. Until fairly recently, *Archinacella* included all Ordovician cap-shaped species exhibiting horseshoe-shaped or circular muscle bands, as well as species sharing the general shell characteristics of forms in which the muscle scars are known. Horny (1963c) created the genus *Archinacelliopsis* for species such as *A. patelliformis* (Hall) that exhibit an incomplete muscle ring with a pair of discrete scars situated in the open posterior end of the ring. In 1961, Horny (1961) also proposed the genus *Archinacellina* for species such as *A. modesta* (Perner, 1903) that have two pairs of nearly isolated, triangular muscle scars located on the inner posterolateral margins of a complete muscle ring. The validity of these two genera is questionable, because the muscle scars of very few species of archinacellids have been described, and therefore the variation in the scar patterns within the group is virtually unknown.

#### Genus ARCHINACELLA Ulrich and Scofield, 1897

*Diagnosis.*—Shell patelliform, ovate to subcircular, generally widest anteriorly; position of apex variable; lateral apertural margin horizontal and straight to arched; only comarginal shell ornament; muscle scar a continuous band around the interior periphery of shell.

*Description.*—Shell low to fairly high, cap shaped, ovate to subcircular in dorsal profile, in most cases widest anteriorly; apex distinct, may be situated up to one-third the shell length from anterior shell margin, directly over that margin, or slightly overhanging it, but shows little or no incurving; lateral apertural profile horizontal and straight to markedly arched; shell ornament generally weak, consisting only of regular to irregular, comarginal growth lines; muscle scars form continuous band just inside periphery of shell.

*Type species.*—*A. powersi* Ulrich and Scofield, 1897, by original designation.

*Distribution.*—Chazy (middle Middle Ordovician)-Richmondian (upper Upper Ordovician). Knight and Yochelson (1960) reported the genus as extending into the Lower Silurian but did not document any Silurian species.

*Comparison.*—*Archinacella* includes a rather heterogeneous assemblage of shell forms. The apex may be situated from well posterior to the anterior shell margin (pl. 3, figs. 11–24) to slightly past the anterior margin (pl. 3, fig. 9). The lateral apertural margin is horizontal and straight (pl. 4, fig. 7) to distinctly arched (pl. 3, fig. 9). The shell ranges from low and streamlined (pl. 2, figs. 8, 10, 11) to high and somewhat inflated (pl. 3, figs. 5, 9). The genus is in most cases identified by its ovate dorsal shell profile, its elevated, anteriorly located, non-incurved to slightly incurved apex, and the presence of only comarginal growth lines. The genus is easily distinguished from the cap-shaped genera in the present study by its lack of radial ornament, its straight or nearly straight apex, and in most cases by general shell form. *Archinacella* is separated from its relatives *Archinacellina* and *Archinacelliopsis* by the form of the muscle band; the latter two genera have discrete accessory muscles posteriorly.

*Discussion.*—Ulrich and Scofield (1897) proposed the genus *Archinacella* for species previously assigned in part to *Metoptoma* Phillips by Billings (1865), and in part to *Tryblidium* Lindstrom by Whiteaves (1884) and Whitfield (1886). In addition, Ulrich and Scofield (1897) described a number of new species. Their original generic description was as follows (1897, p. 821): "Shell patelliform, ovate to subcircular, usually widest anteriorly, forming a low cone with the apex in front of the center and often submarginal. Muscle scars forming a continuous band. Surface markings concentric only." When preserved muscle scars were lacking in specimens,

they distinguished *Archinacella* from *Tryblidium* by the characteristic wider and more rounded anterior end of *Archinacella*.

Ulrich and Scofield (1897) considered the continuous muscle band of *Archinacella* to show close affinity to the patellacean gastropods, which have a continuous horseshoe-shaped scar that opens anteriorly. In *A. powersi*, they described a discrete pair of rostral scars on the band beneath the apex, a narrow pair of scars just within the band on either side of the beak, an anterolateral pair of scars outside the band, a pair of loops extending outward from the band at about midlength, and numerous looplike irregularities along the outer band around the posterior end (Ulrich and Scofield, 1897, p. 829, pl. 61, fig. 5). However, Knight (1941, p. 44, 45, pl. 1, figs. a-g) disagreed with their interpretation of the form of the muscle ring in *A. powersi*. He stated:

These authors interpret what I regard as the sharply impressed inner margin of the principal horseshoe-shaped scar as the principal scar itself, wholly ignoring the outer margin of the scar. The evidence for what they regard as rostral scars is almost nonexistent. What they interpret as a narrow pair of scars lying close to the principal scar just within its forward ends I interpret simply as local thickening of the secondary deposits within the circle of the principal scar. It must be remembered that molluscan muscle scars are commonly produced by resorption of shell material, not by piling up of secondary deposits. Their "faint impressions of a larger anterior pair without the band" are simply slight spots of seemingly fortuitous ferruginous stain within the area of what I regard as the principal muscle scar.

Knight and Yochelson (1958, p. 43, 44) reaffirmed Knight's (1941) interpretation of an "unbroken ring-shaped muscle scar" in *A. powersi*, and noted the discovery of a specimen of *A. patelliformis* (Hall) from the Blackriveran strata of New York State that shows, instead of a continuous ring, an incomplete ring with a pair of scars at the posterior of the exposed continuous ring (Knight and Yochelson, 1958, pl. 5, fig. 4). They (1960, fig. 50, 1b and 4) later illustrated both types of archinacellid muscle scars. As previously pointed out, Horny (1963a) erected *Archinacelliopsis* for *A. patelliformis*.

Thirty-two species of *Archinacella* from North America have been proposed; all are from Ordovician strata in the eastern half of the continent. This large number of species in a genus having such a simple shell form and ornament seems unlikely. The conceptualization of the species is complicated by the high degree of intraspecific variability in the shell form of many monoplacophorans. Unfortunately, many species of *Archinacella* are known from only a few specimens, many of which are poorly preserved. Given the present state of knowledge of the species of *Archinacella*, there is no alternative to proposing new species names for distinctive morphologies. Even the new silicified collections described herein do not contain adequate numbers of specimens of *Archinacella* for variability analyses, and in general the quality

of preservation is not good. The archinacellids generally were too badly fragmented to allow reliable measurements. However, these samples are sufficient to give a better impression of intraspecific variability on a qualitative level than any other collections known, largely because it is known whether or not all of the specimens came from a single bed.

Many species of *Archinacella* are known only from internal molds, and thus are unsatisfactory for diagnosis and comparison. The preservation of *A. indianensis* (Miller) as external molds in the bases of calcitic bryozoan colonies (pl. 3, fig. 16; pl. 4, figs. 8, 9) suggests that the shell of *Archinacella* was aragonitic, and thus easily dissolved. Also, where known, the shells of *Archinacella* seem to be fairly thin (pl. 2, figs. 13, 14, pl. 3, figs. 19, 20). These facts suggest why well-preserved specimens are rare. Collections of any one species generally consist of only a few specimens; this may simply be a result of poor preservation, or it may be partly related to the population dynamics of the species. It is possible that these animals maintained small populations, or had widely spaced population distributions. Still another factor may be the apparent ecology of these animals. Their continuous muscle bands suggest that the archinacellids led a limpetlike existence, clinging to solid objects in environments or even microenvironments where rapid burial was unlikely.

Specific differences are based on five main criteria: (1) position of the apex relative to the anterior apertural margin, (2) relative convexity and height of the shell, (3) the horizontal or arched character of the lateral apertural margins, (4) the shape of the shell aperture, and (5) shell length/width ratio. In most specimens examined, the shell margins are fragmented and incomplete, so criteria 3 and 4 were often difficult to evaluate. The species of *Archinacella* recognized herein are based on small samples, and some may be synonymized when better material becomes available.

#### *Archinacella simulatrix* Ulrich and Scofield, 1897

Plate 2, figures 7-12

*Archinacella simulatrix* Ulrich and Scofield, 1897, p. 833, pl. 61, figs. 10, 11; Grabau and Shimer, 1909, p. 606, figs. 805f, i.

**Diagnosis.**—Shell small (up to 15 mm long), subovate, wider anteriorly, with narrowly rounded dorsomedian crest; aperture horizontal; apex sharp, scarcely incurved, extends to nearly over anterior shell margin.

**Description.**—Shell small for genus (up to 15 mm long), subovate, slightly wider anteriorly; convexity low; narrowly rounded dorsomedian crest runs most of length of shell, crest sharpest toward apex; lateral slopes splay outward slightly in larger specimens; apex sharply pointed in dorsal view, scarcely incurved with gently

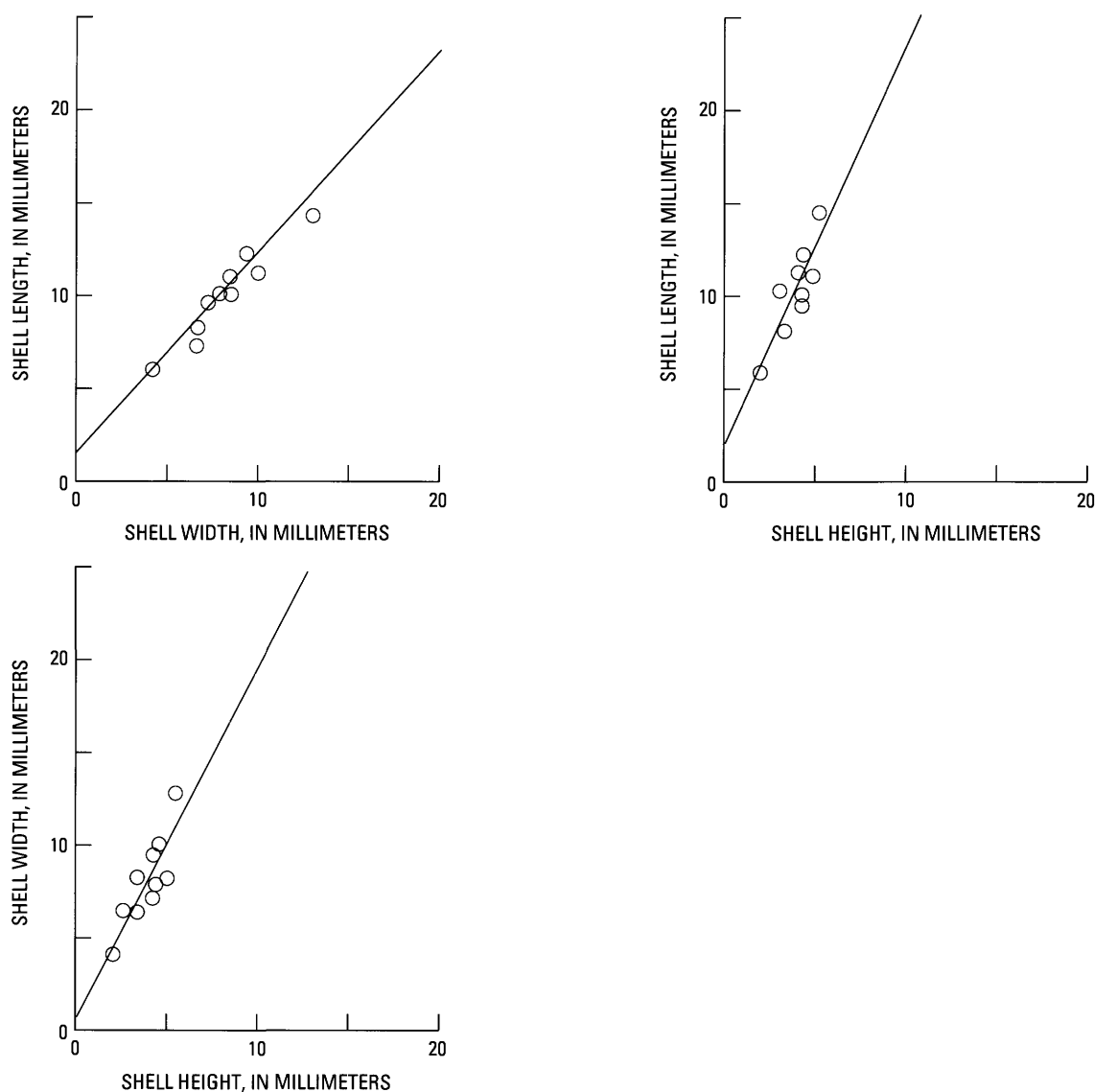
TABLE 22.—Measurements (in millimeters) of *Archinacella simulatrix*

USNM No.	Shell length	Shell width	Shell height	Apex height
45695	10.50	8.3	3.30	2.1
47471	14.88	13.0	5.50	2.8
265944	11.55	10.0	4.60	—
265945	12.60	9.6	4.60	—
387033	9.90	7.3	4.50	—
387033	8.40	6.8	3.40	—
387033	6.10	4.2	2.15	—
387034	10.15	8.5	—	—
387035	10.20	8.0	4.50	—
387035	11.20	8.3	5.00	—
387036	7.70	6.6	2.85	—

concave anterior shell slope, extends to just over to scarcely beyond anterior shell margin; comarginal growth lines faint.

*Measurements.*—Measurements of *A. simulatrix* are listed in table 22 and shown graphically in figure 22. Note that many measurements were made on incomplete specimens and therefore are open to some amount of error.

*Material.*—The holotype of *A. simulatrix* (USNM 45695) is an external mold in the base of a bryozoan colony from the Decorah Formation (Rocklandian-Kirkfieldian), St. Paul, Minn. A latex replica is shown on plate 2, figures 7, 8. The best preserved specimen

FIGURE 22.—Bivariate plots of measurements made on specimens of *Archinacella simulatrix*.

examined was USNM 47471 (pl. 2, fig. 12), which the museum label says is from the "*Modiolodon* beds of the Hermitage member" of the Lexington Limestone. These beds are now included in the upper Logana Member of the Lexington Limestone.

The new silicified collections contain mostly fragmented specimens of *A. simulatrix*. Poorly preserved specimens, here termed *A. cf. A. simulatrix*, were recognized from the Tyrone Limestone (one specimen from 6035-CO; USNM 387034), and from the Curdsville Limestone (7784-CO; USNM 387035) and Grier Limestone (4874-CO and 4959-CO; USNM 387036) Members of the Lexington Limestone. A number of fairly well preserved specimens of *A. simulatrix* were found in sample 4073-CO (USNM 387033) from the Grier Limestone Member; two of these, USNM 265944 (pl. 2, fig. 11) and USNM 265945 (pl. 2, fig. 10), are figured here.

**Distribution.**—Ulrich and Scofield (1897, p. 833) listed *A. simulatrix* from the "Black River Group, *Phylloporina* bed, St. Paul, Minnesota; Trenton Group, *Modiolodon* bed, Frankfort, Kentucky." According to Weiss (1957), the *Phylloporina*-Fucoid bed in Minnesota would now be considered the upper Decorah Formation, which is Kirkfieldian rather than Blackriveran in age. The *Modiolodon* bed of Kentucky would now be placed in the Logana Member of the Lexington Limestone, which is also Kirkfieldian in age.

The new silicified collections contain probable specimens of this species from the Tyrone Limestone (Rocklandian) and the Curdsville Limestone and Grier Limestone Members of the Lexington Limestone (Kirkfieldian-Shermanian). Specimen USNM 47471 confirms the occurrence of the species in the Logana Member of the Lexington Limestone. *A. simulatrix* may occur in the Rocklandian strata of Kentucky; it does occur in the Kirkfieldian-age rocks of Kentucky and Minnesota, and in the Shermanian rocks of Kentucky.

**Comparison.**—*A. simulatrix* is generally easily recognized by its small size, wide anterior end, and relatively sharp dorsomedian crest leading to its marginal apex.

Ulrich and Scofield (1897) stated: "This species is distinguished from *A. deleta*, *A. valida*, *A. patelliformis* in having a less regularly elliptical outline, the anterior half being wider. In this particular it is like the much larger *A. cingulata*."

**Discussion.**—This is the most common species of *Archinacella* in the upper Middle Ordovician of Kentucky. The fact that it is known in Kirkfieldian strata of Kentucky and Minnesota suggests that it is useful for midcontinent correlation.

The preservation of the holotype as an external mold in the base of a calcitic bryozoan colony suggests that the shell was aragonitic. The specimen apparently was

encrusted after the animal died. The shell was somewhat worn before encrustation, as the surface of the latex replica (pl. 2, figs. 7, 8) is somewhat irregular.

The specimens from sample 4073-CO (pl. 2, figs. 10, 11) from the Grier Limestone Member occur with the pelecypod *Cyrtodonta* sp. Specimens from the Logana Member of the Lexington Limestone (pl. 2, fig. 12) occur with the pelecypod *Modiolodon* sp. It is therefore inferred that *A. simulatrix* was commonly a member of molluscan communities.

#### *Archinacella valida* (Sardeson, 1892)

Plate 2, figures 15, 16

*Tryblidium validum* Sardeson, 1892, p. 337, pl. 6, figs. 1, 2.

*Archinacella valida* (Sardeson), Ulrich and Scofield, 1897, p. 832, pl. 61, figs. 14, 15.

**Diagnosis.**—Moderate-sized shell (16–18 mm long) with ovate outline; apertural margin horizontal; apex small, submarginal, slightly incurved.

**Description.**—Shell moderate in size, regularly ovate in outline, length/width ratio about 1.2; apertural margin horizontal; apex laterally compressed, dorsally narrowly rounded, broadening posteriorly, located just within shell margin, slightly incurved so that anterior shell slope is distinctly concave; growth lines faint but distinct, closely and fairly regularly spaced.

**Measurements.**—Measurements of USNM 47467 are as follows: length from apex to posterior margin 17.2 mm; aperture length 18.2 mm; aperture width 15.4 mm; shell height 6.0 mm; height of apex over anterior shell margin 3.3 mm. Ulrich and Scofield (1897) gave measurements of a small specimen as "length 16.5 mm; width 15.4 mm; height nearly 7 mm."

**Material.**—Only one specimen was examined (USNM 47467); it is labeled "*Archinacella patelliformis*, from the Trenton (*Ctenodonta* horizon), Mt. Parnassus, Columbia, Tennessee." This specimen is not *A. patelliformis* Hall, because it is larger and relatively broader, its dorsum is not as carinate, and its apex is submarginal. The specimen is a calcitic cast embedded in a buff biosparite matrix; most associated skeletal debris is brachiopod fragments, but there is also a small bellerophonid, possibly *Bucanopsis*.

**Distribution.**—Ulrich and Scofield (1897, p. 833) listed *A. valida* as from the "Trenton Group, *Clitambonites* bed, near Canyon Falls and Kenyon, Minnesota." According to Weiss (1957, fig. 1), the *Clitambonites* bed, which was then regarded as basal "Trenton," is now considered the Cummingsville Member of the Galena Formation (Kirkfieldian-Shermanian). Specimen USNM 47467 came from the *Ctenodonta* member of the Hermitage Formation of Tennessee (Kirkfieldian). *A. valida* is therefore known from Kirkfieldian- and Shermanian-age strata in Minnesota and Tennessee.

*Comparison.*—Ulrich and Scofield (1897, p. 832) stated: "Specifically *A. valida* is nearer *A. (Carinaropsis) patelliformis* Hall from the Trenton of New York, than any other form known to us. The lateral profile especially is nearly or quite the same in the two species. The New York species, however, is smaller, has more distinct surface markings, and is obtusely carinated on the back. It should be noted further that the apex of *A. patelliformis* is more incurved and extends past the anterior shell margin slightly." This differs from the specimen of *A. valida* figured here, in which the apex is submarginal.

In dorsal view *A. valida* is similar to *A. powersi* Ulrich and Scofield (Ulrich and Scofield, 1897, pl. 61, figs. 4, 14), but the two species can be easily distinguished in lateral view, the former being higher and having a horizontal lateral apertural margin, the latter being lower and having an arched apertural margin.

*Discussion.*—The single well-preserved specimen (USNM 47467) studied here agrees with every essential aspect of *A. valida* described by Ulrich and Scofield (1897). The only notable difference is that the specimen from Tennessee is not as inflated as the specimens they described from Minnesota.

#### *Archinacella cingulata* Ulrich, 1897

Plate 2, figures 22–26

*Archinacella cingulata* Ulrich in Ulrich and Scofield, 1897, p. 829, 830, pl. 61, figs. 1, 2.

*Diagnosis.*—Shell large (up to 44 mm long), with broadly convex lateral profiles; apex blunt, slightly downcurved, projecting slightly beyond apertural margin; growth lines distinct, sublamellose, with close, regular spacing.

*Description.*—Shell relatively large for genus, outline subovate, wider anteriorly, gradually narrowing posteriorly; lateral profile broadly convex, with greatest shell height about one-third shell length back from anterior shell margin; lateral apertural margin nearly horizontal, scarcely arched; apex blunt, curved downward slightly to about one-half shell height, and projecting just beyond anterior apertural margin; growth lines distinct, sublamellose fine ridges, with close regular spacing; nearly consistent 1 mm spacing of growth lines over most of shell.

*Measurements.*—Measurements of *A. cingulata* are listed in table 23.

*Material.*—The holotype of the species (USNM 45686) (pl. 2, figs. 22–24) is a worn silicified replica from the "Amygdalocystites bed" of the Curdville Limestone Member of the Lexington Limestone. The only other known specimen is in the Miami University collections (MU 249T) (pl. 2, figs. 25, 26); that specimen is a large

TABLE 23.—Measurements (in millimeters) of *Archinacella cingulata*

Museum No.	Length—Apex to posterior margin	Shell height	Aperture length	Aperture width	Apex height
USNM 45686	30.4	11.5	29.0	23.85	4.5
MU 249T	44.1	12.1	43.6	34.5	6.8

internal mold from the Clays Ferry Formation, collected near Owenton, Ky., about 2 mi east of the intersection of U.S. Route 127 and Kentucky Route 35.

*Distribution.*—Kirkfieldian (upper Middle Ordovician) to Edenian (lower Upper Ordovician) of Kentucky.

*Comparison.*—Ulrich and Scofield (1897) noted that *A. powersi* differs from *A. cingulata* in its strongly arched aperture. *A. simulatrix* resembles *A. cingulata* somewhat in general shell form, but the latter species is much larger and has much more distinct growth markings.

*Discussion.*—Ulrich and Scofield (1897) described the aperture of *A. cingulata* as horizontal, but in both specimens examined here, the lateral apertural profile is slightly arched. There also seem to be faint traces of radiating lines between the growth lines in this species, but this observation cannot be confirmed without more specimens. If so, the species should be removed from the *Archinacella* and possibly be placed in *Helcionopsis* or *Vallatotheca* because of the similarity in their regular sublamellose growth lines.

#### *Archinacella* cf. *A. depressa* Ulrich and Scofield, 1897

Plate 2, figures 13, 14

*Archinacella depressa* Ulrich and Scofield, 1897, p. 830, pl. 61, figs. 8, 9.

*Description.*—Shell medium sized for genus (16–17 mm long), outline broadly oval, convexity low; anterior slope gently concave, posterior slope gently convex; apex located distinctly within anterior shell margin; lateral apertural margin slightly arched; growth lines faint and closely spaced through most of shell, becoming strong and lamellose near outer shell margin.

*Measurements.*—Measurements of the single specimen examined are as follows: length from beak to posterior margin 15.0 mm; aperture length 16.8 mm; aperture width 15.2 mm; shell height 5.2 mm; height of apex 3.6 mm.

*Material.*—The single specimen identified as *A. cf. A. depressa* (USNM 59295) is a siliceous cast embedded in a wackestone matrix containing fragments of bryozoans and brachiopods.

*Distribution.*—Ulrich and Scofield (1897) reported *A. depressa* from the "Stones River Group, Vaunexemia bed, Minneapolis, Minnesota." According to Weiss (1957, fig. 1), this would be in the middle part of the Platteville

Formation (Rocklandian) (regarded as Blackriveran by Ross and others, 1982). The specimen described herein (USNM 59295) is from the Cannon facies of the Bigby-Cannon Limestone (Kirkfieldian-Shermanian) at Hartsville, Trousdale County, Tenn.

*Comparison.*—Ulrich and Scofield (1897) emphasized the similarity between *A. depressa* and *A. perovalis* (Whitfield) from the Platteville Formation of the Minnesota-Wisconsin area, saying that the only difference of any consequence between the two species is the greater width of *A. depressa*.

*A. subrotunda* Ulrich and Scofield from the Decorah Formation (Rocklandian-Kirkfieldian) of Minnesota is also somewhat similar to *A. depressa*, but the former is higher and more convex, based on Ulrich and Scofield's (1897, pl. 61, figs. 26, 27) illustration. Wilson (1951, p. 18, pl. 1, figs. 9, 10) described *A. subrotunda* from the Cobourg beds (Edenian) of Ontario, Canada, but her figures look more like *A. depressa*, having a shell of low convexity.

*Discussion.*—The specimen from the Cannon facies of Tennessee compares favorably with the description of *A. depressa* given by Ulrich and Scofield (1897). Points on which it agrees are its broad ovate outline, its low convexity, its submarginal apex, and its slightly arched lateral apertural margin. Measurements for the species reported by Ulrich and Scofield (1897, p. 830) give a length/width ratio of 1.13. The Tennessee specimen has a length/width ratio of 1.10, showing close agreement. The species is known from Blackriveran-age strata in Minnesota and Kirkfieldian-Shermanian-age strata in the Cincinnati arch province, and perhaps from the Edenian of Ontario.

#### *Archinacella alta* new species

Plate 3, figures 4-6

*Diagnosis.*—Shell medium sized, high, inflated; outline ovate; lateral apertural margin horizontal; apex blunt, slightly downcurved, situated above shell margin.

*Description.*—Shell medium sized for genus (about 15 mm long), high, somewhat inflated, with highly convex dorsal and posterior slopes; highest point on shell about one-third shell length back from anterior margin; anterior slope distinctly concave; shell outline regularly oval; beak area narrowly rounded medially in dorsal view, becoming gradually broader toward posterior; apex blunt, slightly downcurved about three-eighths the shell height, situated above anterior shell margin; lateral apertural margin horizontal to very slightly arched; growth lines barely discernible.

*Measurements.*—Measurements of the holotype are as follows: shell length at aperture or apex 14.75 mm; aperture width 13.2 mm; shell height 8.1 mm; height of

apex 4.9 mm (length/width ratio 1.12; length/height ratio 1.82; width/height 1.63).

*Material.*—The holotype (MU 248T) is the only known specimen. It appears to be a highly recrystallized calcitic cast, and was collected from the Clays Ferry Formation in northern Kentucky. The locality given for the specimen, No. OC3, could not be traced. The Miami University museum label states that the late Prof. Shideler suggested the specific name of "alta" for the new species, referring to its high shell, and that name is used here. The specimen is partly embedded in a limestone matrix.

*Distribution.*—The new species is known only from the Edenian part of the Clays Ferry Formation of Kentucky.

*Comparison.*—*A. alta* bears some resemblance to *A. laevis* Foerste (1924, p. 202, pl. 30, figs. 3a-d) from the Richmondian of Snake Island, Ontario, but the former has a much higher shell. It also resembles *A. subrotunda* Ulrich and Scofield (1897, p. 834, pl. 61, figs. 6, 7) in having a marginal apex and a horizontal apertural margin. However, when the proportionate measurements are compared, the difference is striking. For example, the shell length/shell height ratios for *A. alta*, *A. subrotunda*, and *A. laevis* are 1.8, 2.5, and 3.1, respectively (measurements for latter two species taken from illustrations of the holotypes).

#### *Archinacella? davisii* new species

Plate 3, figures 1-3

*Diagnosis.*—Shell very large, with broad subovate outline; beak long and fairly narrow, with apex slightly downcurved and apparently extending well beyond anterior shell margin; lateral apertural margin straight.

*Description.*—Shell very large for genus (70 mm long), outline broadly subovate; dorsolateral profile broadly convex; lateral apertural profile apparently horizontal; beak area long and narrow, ending in pointed apex which is slightly downcurved and apparently extends well past anterior apertural margin; anterior slope distinctly concave; shell thickness and markings unknown.

*Measurements.*—The holotype and only known specimen measures as follows: length from apex to posterior margin 70 mm; aperture length 63 mm; aperture width 54 mm; shell height 23 mm. The specimen is poorly preserved (pl. 3, figs. 1-3), and these measurements are only approximations.

*Material.*—The holotype (CMNH P2) is the only known specimen of the new species. The specimen is a large internal mold in rather fissile gray shale, and the specimen boundaries are difficult to pinpoint. The lines that appear to be possible comarginal growth lines are actually shale laminae (pl. 3, figs. 1-3).

*Distribution.*—The holotype was found in the Cincinnati Museum of Natural History Collections with only

locality data. It came from the Gallatin, Ky., area. The character of the matrix and the stratigraphy of the type area strongly suggest that the specimen came from the Kope Formation (Edenian).

*Derivation of species name.*—The species is named for Richard Davis of the Cincinnati Museum of Natural History, through whose courtesy the specimen was made available for study.

*Comparison.*—Because of the poor preservation of the holotype, its generic placement is open to question. The only other possible generic assignment is *Carinaropsis*, which also has a long, extended beak area (the coil could be missing from the internal mold). However, the dorsal beak of *A. ? davisi* shows no evidence of a carina, it is quite rounded, and there is no evidence of an anteromedian slit or a trailing slitband; also, the apertural outline appears too regularly ovate for *Carinaropsis*. If the generic assignment is correct, this is the largest known species of *Archinacella*.

***Archinacella* cf. *A. pulaskiensis* Foerste, 1914b**

Plate 2, figures 17, 18

*Carinaropsis patelliformis* Hall (in part), 1847, p. 306, pl. 83, figs. 7a, b.

*Carinaropsis patelliformis* Hall, Miller, 1874, p. 314; (in part) 1889, p. 400.

*Archinacella pulaskiensis* Foerste, 1914b, p. 309, pl. 3, figs. 3a-d; 1924, p. 203, pl. 31, figs. 3a, b; pl. 29, fig. 1.

*Description.*—Shell fairly small for genus (about 8 mm long), subovate, broader anteriorly than posteriorly; convexity low; lateral apertural margin horizontal; beak area sharply angular dorsomedially, rapidly becoming broadly convex posteromedially; apex sharply pointed, slightly incurved, situated over anterior apertural margin; comarginal growth lines fairly distinct.

*Measurements.*—The measurements of the single specimen available are as follows: shell length 8.4 mm; shell width 6.4 mm; shell height 2.2 mm; widest point on shell (from apex) 3.5 mm.

*Material.*—The only specimen available was UCGM 19640 from Maysvillian strata. This specimen is small and has poorly preserved margins. The type specimens were not examined directly. However, I did examine previous authors' illustrations of the species, including Foerste's (1914b) figures of the types.

*Distribution.*—The single specimen UCGM 19640 is labeled as coming from the "Maysville," but no further stratigraphic or locality data are given. The specimen most likely is from the Cincinnati, Ohio, area. Miller (1874, p. 314) reported finding *Carinaropsis patelliformis* (Hall) (the Cincinnati specimens placed in this species by Hall, 1847, are now considered to be *A. pulaskiensis*) from "the quarries back of Cincinnati." These hill quarries were in the Fairview Formation (Maysvillian) (Pojeta, 1984, p. E79).

*Comparison.*—This species is similar to *A. simulatrix*, but it lacks the angularity of the beak posteriorly. Without more and better material, no further comparisons are possible, but the possibility of synonymy between the two species names should be kept in mind.

Hall (1847, p. 183) remarked as follows about *C. patelliformis*: "There are one or two other species in the Hudson River Group [as the Upper Ordovician was then called], and a single more elevated one in the Trenton limestone, which has not been satisfactorily determined." Miller (1874, p. 314; 1889, p. 400) identified the same species in Maysvillian-age strata at Cincinnati, Ohio. In their discussion of *Archinacella deleta*, Ulrich and Scofield (1897, p. 831) stated:

This is the first of a group of species that seems to be related to *A. (Carinaropsis) patelliformis* Hall. One or the other of these forms occurs in, or in the equivalent of, every one of the principal beds between the base of the Black River Group and the top of the Cincinnati formation. None of the western or northwestern species however seem to be strictly identical with the New York types of *patelliformis*, all of them having a nearly smooth surface, while Hall's species according to his figures and description has the surface marked by regular concentric, sublamelliform striae.

They then compared *A. patelliformis* to *A. deleta* Sarde-son, *A. valida*, *A. semicarinata* Ulrich and Scofield, and *A. simulatrix*.

Foerste (1914b, p. 309) described *A. pulaskiensis* from the late Maysvillian-age Pulaski Formation of New York and Quebec, starting his description as follows: "The form figured by Hall from the Lorraine at Pulaski, New York, as *Archinacella patelliformis*, differs in outline from his Trenton types.... This shell [*A. pulaskiensis*] is broader and more convex along the middle and the outline, therefore, rather broadly ovate than ovate oblong. Otherwise the shells are closely similar." Foerste (1924, p. 203) also cited this species from the *Cryptolithus* zone of New York and Quebec, which he correlated with the "Southgate member of the Eden" in the Cincinnati area.

The species in the Maysvillian strata of the Cincinnati area reported by Miller (1874, 1889) is here placed in *A. pulaskiensis* Foerste because the two agree in their small size, low convexity, and sharply pointed marginal apex. The exact apertural outline of the shell of the specimen studied herein is not shown, and this characteristic is stressed by Foerste in comparing it with *A. patelliformis*. A review of all species that are directly comparable to *A. patelliformis* is needed; however, sufficient collections to carry out such a study are not available.

***Archinacella rugatina* Ulrich, 1897**

Plate 2, figures 19-21

*Archinacella rugatina* Ulrich in Ulrich and Scofield, 1897, p. 835, pl. 82, figs. 5, 6.



*Diagnosis.*—Shell medium sized, nearly circular in outline, moderately high and convex in lateral profile; apex inset from shell margin; apertural margin nearly horizontal; strong sublamellose growth lines in later adult growth.

*Description.*—Shell medium sized for genus (about 20 mm long), outline nearly circular, lateral profile moderately high and convex; highest point on shell near apex; apex distinct, fairly blunt, slightly curved anteriorly, situated distinctly just within anterior shell margin; anterior slope convex near shell margin, becoming concave beneath apex; lateral apertural margin nearly horizontal, but arches slightly dorsally; growth lines strong and apparently sublamellose in later growth stages.

*Measurements.*—Measurements of the holotype are as follows: length from apex to posterior margin 19.5 mm; aperture length 20.85 mm; aperture width 20.4 mm; shell height 7.0 mm; height of apex 5.7 mm; width between later growth lines 1.5–2.0 mm.

*Material.*—The holotype of the species was examined (USNM 45693). It is an internal mold with some highly recrystallized and weathered shell material around the posterior margin. One other specimen of the species was located. It is an unnumbered specimen on display in the Miami University Geology Museum, Oxford, Ohio.

*Distribution.*—The holotype (USNM 45693) is from what was formerly called the “Arnheim Formation” and now is placed in the Bull Fork Formation (early Richmondian-upper Upper Ordovician) at Middletown, Ohio. Nickles (1902) listed the species as part of the “Lower Richmond Fauna.”

*Comparison.*—Ulrich (Ulrich and Scofield, 1897) compared *A. rugatina* as follows: “This species agrees closely with *A. richmondensis* [*A. indianensis*] Ulrich, but may be distinguished by its more distinct and slightly incurved apex, somewhat arched aperture, and stronger surface markings. The latter are coarsely lamelliform in the outer third.” Herein, *A. richmondensis* is placed in subjective synonymy with *A. indianensis* Miller. Ulrich’s comparison can be expanded. First, *A. indianensis* can have a horizontal or slightly arched aperture (pl. 3, figs. 21, 22; pl. 4, fig. 7), so this morphological feature is not a reliable basis for comparison. Better distinctions are provided by the character of the apex, it being more curved in *A. rugatina* (pl. 2, figs. 20, 21), the general form of the shell, which in *A. rugatina* is much broader in outline and more convex in lateral profile (pl. 2, figs. 19–21), and the sublamellose growth lines of *A. rugatina*.

*Discussion.*—*A. rugatina* is known only from the lower Richmondian strata of Ohio, whereas *A. indianensis* occurs in the middle and upper Richmondian strata of a much greater area. The two species are quite similar morphologically, and it is likely that *A. indianensis* was

descended from *A. rugatina*; alternatively, the two species may have had a common ancestor.

On the left posterolateral slope of the holotype of *A. rugatina* (pl. 2, figs. 19–21) there is a prominent comarginal protuberance. I have concluded that this feature is probably a product of weathering, but it may represent the position of a muscle scar.

#### *Archinacella arca* new species

Plate 3, figures 7–10

*Diagnosis.*—Shell medium sized, highly convex, nearly circular in outline; apex bluntly pointed, situated high over, and slightly past, anterior apertural margin; lateral apertural margin strongly arched.

*Description.*—Shell medium sized for genus (about 19 mm long), nearly circular in outline, quite high and strongly convex dorsally and posteriorly; lateral slopes nearly flat, anterior slope broadly concave; apex distinct, bluntly pointed, slightly curved anteriorly, situated high over, and slightly past, anterior apertural margin, which is slightly convex; posterior apertural margin broadly convex; lateral apertural margin strongly arched, increasingly so posteriorly; growth lines fairly widely spaced in immature shell, in mature shell become more closely spaced and slightly irregular, even showing mild wrinkling near base of anterior slope.

*Measurements.*—The measurements of the holotype are as follows: length from apex to posterior margin 19.5 mm; aperture length 17.85 mm; shell width 20.5 mm; shell height 9.3 mm; height of apex 7.7 mm; distance between growth lines 1.0 to 1.5 mm.

*Material.*—Only the holotype (USNM 40615) of the species is known; it apparently is a partial composite mold. No shell material seems to be present, but rather the surface of the specimen is coated by a hard, dense, dark outer layer, as is often the case with composite molds. The specimen is embedded in a matrix of gray micrite, the only other skeletal material visible being a brachiopod fragment.

*Distribution.*—The single known specimen is labeled as coming from the “Waynesville Formation (Richmond)” at Waynesville, Ohio. This unit is now part of the Bull Fork Formation (Richmondian-upper Upper Ordovician).

*Comparison.*—There can be no doubt about the distinctiveness of this species. The only similar species is *A. powersi* Ulrich and Scofield, the type species of *Archinacella*. It too has a strongly arcuate lateral apertural margin and a broad shell, and its apex is similarly positioned and formed (Ulrich and Scofield, 1897, p. 829, pl. 61, figs. 3–5). But *A. arca* is higher and more convex, and is proportionately wider, even being slightly wider than long. *A. arca* cannot be confused with other Rich-

mondian species of the study area, all of which have submarginal apices, straighter lateral apertural margins, and less convex shells.

*Discussion.*—The only species comparable to *A. arca* is *A. powersi*, which is listed by Ulrich and Scofield as coming from the "Stones River Group" at Beloit, Wis. In modern terms, this probably means the Platteville Formation, which is Rocklandian (late Middle Ordovician) in age (Weiss, 1957; Sweet and Bergstrom, 1976). Both these species have a strongly arcuate lateral aperture, which results in a broad posterior apron (pl. 3, figs. 8, 9). The arched lateral margins probably allowed better flow of oxygenated water to the pairs of lateral gills. The broad posterior apron does not seem to have provided an efficient exit for water circulating through the mantle cavity, but it must have provided protection for a broad foot.

As seen particularly well on plate 3, figures 7, 8, there seems to be a wide, smooth band over the posterodorsal slope of *A. arca* which angles slightly downward and narrows anteriorly and runs beneath the apex (pl. 3, figs. 9, 10). This band does not seem to be a positive relief feature, but it may represent a broad muscle band insertion. It appears to be identical in position to the muscle band of *A. powersi* (Ulrich and Scofield, 1897, pl. 61, fig. 5; Knight and Yochelson, 1960, fig. 50, 1b), although in *A. arca* the band is extraordinarily wide. On the other hand, it is possible that the borders of this band are simply growth lines. If it does represent a remnant of a muscle band like that in *A. powersi*, then these species might be interpreted as strong clingers, where the apron protected the large muscular foot posteriorly, and the fused muscle band furnished strong, even pulling force for adherence. Morphology suggests that *A. arca* is a descendant of *A. powersi*.

#### *Archinacella indianensis* (Miller, 1892)

Plate 3, figures 13–24; Plate 4, figures 1–14; Plate 5, figures 27, 28

*Tryblidium indianense* Miller, 1892, p. 695, pl. 14, fig. 14; Cumings, 1908, p. 977, pl. 39, fig. 11.

*Archinacella richmondensis* Ulrich in Ulrich and Scofield, 1897, p. 834, pl. 61, figs. 6, 7; Foerste, 1924, p. 201, 202, pl. 34, figs. 1a, b.

*Archinacella kagawongensis* Foerste, 1924, p. 202, pl. 35, figs. 2a–d; Hussey, 1926, p. 171, pl. 6, figs. 2, 3, 4, 9, 10.

*Diagnosis.*—Shell medium sized, with subovate outline and fairly low convexity; apex distinct, elevated, not incurved, located distinctly within shell margin; lateral apertural margin horizontal to slightly arched.

*Description.*—Shell medium sized for genus (up to about 20 mm long), subovate in outline, fairly low convexity; anterior slope gently concave and sloped anteriorly, posterior slope broadly convex to nearly flat, particularly in later growth; lateral slopes flat to slightly concave near margins; apex distinct, elevated, not

TABLE 24.—*Measurements (in millimeters) of Archinacella indianensis*

Museum No.	Length—Apex to posterior	Shell width	Shell height	Aperture length	Beak height
USNM					
45691	20.50	20.20	6.00	24.40	5.5
47468	13.40	14.10	4.40	16.30	3.6
70467	20.30	16.50	6.00	21.20	4.2
265946	—	12.20	6.15	16.20	—
265950	—	10.20	5.65	13.50	—
265951	—	12.55	6.10	16.70	—
265954	12.75	4.40	—	9.45	—
265954	12.85	—	—	—	—
265954	13.50	5.30	—	10.20	—
265954	9.50	3.70	—	8.10	—
265954	11.15	4.30	—	8.30	—
265954	10.70	3.70	—	7.70	—
265954	7.80	3.00	—	5.80	—
265954	19.00	6.80	—	16.40	—
265954	18.46	—	—	10.25	—
265854	10.95	4.25	—	8.90	—
UCGM					
10048	16.0	15.4	4.6	20.0	—
10048	—	10.7	—	13.9	—
19642	19.6	20.3	6.1	22.6	—
19642	6.6	7.0	5.0	8.2	—
MU					
247T	17.0	15.70	6.55	20.00	—
15541	17.1	14.20	6.20	18.15	—
15542	15.5	11.80	5.90	16.50	—
246T	14.3	14.20	5.30	17.00	—
15540	—	15.50	—	18.40	—
15540	11.1	11.15	5.00	12.50	—
250T	24.0	21.50	6.90	26.55	—
15545	18.2	17.60	6.20	20.45	—

incurved, located well within the shell margin at about one-sixth shell length from anterior end; lateral apertural margin generally horizontal, but slightly arched in some specimens; comarginal growth lines distinct in outer half of shell, somewhat irregular in some specimens.

*Measurements.*—Measurements of *A. indianensis* are listed in table 24. Specimens that were measured but not figured are treated as a suite and given one museum number.

*Material.*—The holotype of *A. richmondensis* (USNM 45691) (pl. 3, figs. 16–18) is an external mold in the base of a bryozoan colony, as is specimen USNM 47468 (pl. 4, figs. 8–12); the two specimens are from the Whitewater Formation at Richmond, Ind., and the Bull Fork Formation (Waynesville biofacies) at Oregonia, Ohio, respectively. Specimen USNM 70467 from Richmondian strata at Oakland, Ohio, preserves the shell and the irregular nature of the growth lines seen in some specimens (pl. 4, figs. 1, 2).

The holotype of *A. indianensis* (UC 6065) (pl. 3, figs. 13–15) is an internal mold, but it preserves the outline

and form of the shell quite well. Specimens MU 246T (pl. 3, fig. 21), MU 247T (pl. 3, figs. 23, 24), MU 250T (pl. 3, fig. 22), MU 15540–15545, and UCGM 10048, all from the Drakes Formation (Elkhorn biofacies) just south of Morning Sun, Ohio, and UCGM 19642, from the Drakes at Whitewater, Ind. (total of 15 specimens), were also examined.

New material from the USGS silicified collections consists of about 45 specimens and fragments from the Dillsboro Formation (Liberty biofacies) from the New Point quadrangle of southeastern Indiana (locality 6139-CO). Specimens USNM 265946 (pl. 3, figs. 19, 20), USNM 265949 (pl. 4, figs. 13, 14), USNM 265950 (pl. 5, figs. 27, 28), and USNM 265951 (pl. 4, figs. 3–7) of this collection are figured; all measured but unfigured specimens are placed under the number USNM 265954.

*Distribution.*—*A. indianensis* is known from Richmondian-age strata in southeastern Indiana and southwestern Ohio. It probably is present in correlative strata in central Kentucky. The subjective synonym *A. kagawongensis* extends the species' geographic range to the Upper Peninsula of Michigan and Manitoulin Island, Ontario, where it also is present in Richmondian-age rocks.

*Comparison.*—*A. indianensis* Miller has been considered as possibly conspecific with *A. richmondensis* ever since the original description of the latter species. Ulrich and Scofield (1897, p. 834) closed their discussion of *A. richmondensis* by stating, "We could come to no positive conclusion respecting Miller's *Tryblidium indianense*, but if his description is reliable it is certainly distinct." Bassler (1915) advised comparison of the two. Foerste (1924) noted only that Miller's figure of the species showed it to be shorter, relatively narrower anteriorly, and broader posteriorly than *A. richmondensis*. The holotypes of *A. indianensis* and *A. richmondensis* are very close in their shell form, having submarginal apices, gently curved posterior slopes, rather steeply concave anterior slopes, and broad, ovate apertural outlines. I regard them as conspecific, and Miller's (1892) species name has priority.

Foerste (1924) described *A. kagawongensis* with the beginning line, "Specimens similar to *Archinacella richmondensis*; one specimen being 20 mm long, 16 mm wide, and 7 mm high...." When these measurements are plotted on the graphs for *A. indianensis* in figure 23, they agree quite well with measurements of specimens of that species. Foerste (1924) went on to say that his new species from the Richmondian strata of Manitoulin Island, Ontario, differed from *A. richmondensis* by having the apex curved downward farther, by being somewhat smaller, and by having less distinct growth lines. Hussey (1926, p. 171) began his description of *A. kagawongensis* from the Richmondian strata of the

Upper Peninsula of Michigan by stating, "This is a variable species." He figured two specimens, the first (Hussey, 1926, pl. 1, figs. 3–9) appearing to be quite similar to Foerste's (1924) figured specimens; however, the second (Hussey, 1926, pl. 6, figs. 4–10) looks like a specimen of a typical *A. indianensis* from the Cincinnati arch area, and Hussey pointed out that this latter specimen was "more like the typical form."

My examination of a large number of specimens of *A. indianensis* shows clearly that their shape varies widely. Foerste's (1924) and Hussey's (1926) descriptions and figures of *A. kagawongensis* show that it clearly falls within the range of variability for *A. indianensis*. Specimens from the study area in the Miami University collections labeled *A. kagawongensis* and *A. richmondensis* are indistinguishable, and many are from the same locality at Morning Sun, Ohio. This morphological variation, as well as the exact stratigraphic correlation of the two species, argues for suppression of the name *A. kagawongensis*.

Ulrich and Scofield (1897, p. 834) compared *A. richmondensis* to the geologically older species *A. depressa* Ulrich and Scofield (see pl. 2, figs. 13, 14 herein), but stated that the latter species' "arched aperture, lesser convexity and somewhat different outline" distinguish it from the former. They further stated a belief that "*A. richmondensis* is probably more nearly related to *A. subrotunda*," but did not elaborate. *A. indianensis* shows a close morphological similarity to *A. depressa*, both having rather low shells with distinctly submarginal apices.

Specimen USNM 265955 should be noted here (pl. 3, figs. 11, 12). This single specimen from the Grier Limestone Member of the Lexington Limestone appears to be an *Archinacella*, but it is too poorly preserved to allow specific determination. It is a rather high shell with slightly convex slopes and a distinctly submarginal apex. It bears some resemblance to *A. indianensis* in its general form and the positioning of its apex, and could be related to this species.

*Discussion.*—The fact that both the holotype of *A. richmondensis* (USNM 45691) and specimen USNM 47468 are preserved as external molds in the bases of calcitic bryozoan colonies, but come from different stratigraphic levels and localities, strongly suggests that *Archinacella* had an aragonitic shell. However, a fair number of specimens of *Archinacella* (pl. 4, figs. 1, 2) are also known to have a recrystallized calcitic shell. Considerable insight into shell compositions would be gained if in future collecting, the nature of the preservation of associated mollusks were noted.

The graphs in figure 23 show high correlation values for plots dealing with shell length and width, but much lower correlation values for plots dealing with shell

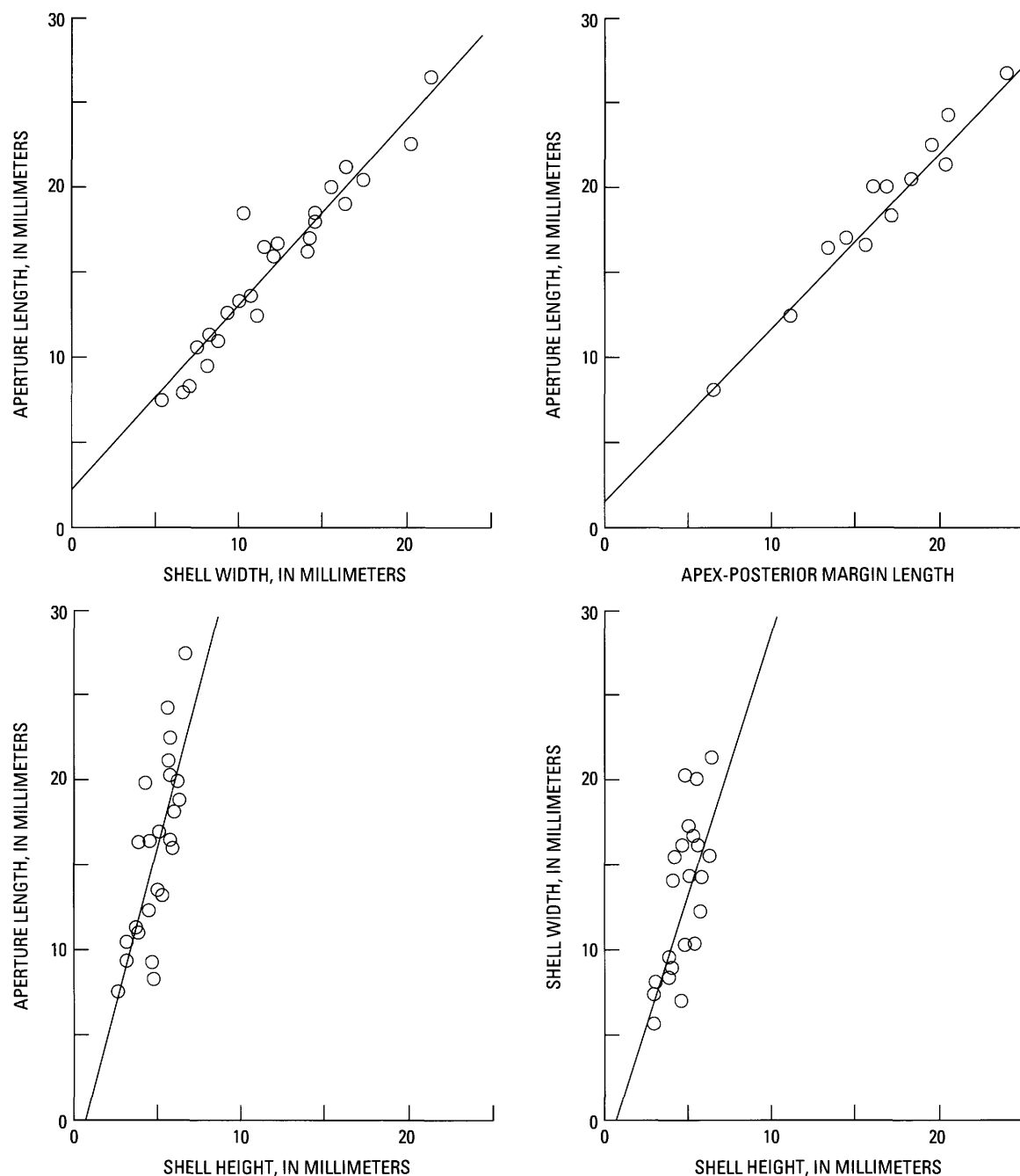


FIGURE 23.—Bivariate plots of measurements made on specimens of *Archinacella indianensis*.

height. The shell height was the most difficult measurement to make, because many specimens have fragmented margins or broken apices and many have shell margins embedded in matrix.

Ulrich and Scofield (1897) believed that the lateral apertural margin of this species is "nearly or quite horizontal." However, examination of type and new material reveals considerable variation in this characteristic. Although most specimens have essentially horizon-

tal apertural margins (pl. 3, figs. 18, 21, 24; pl. 4, fig. 7), a few have obviously arched lateral margins (pl. 3, fig. 22). If these forms are accepted as conspecific, as confluent variation suggests, then the use of shape of the lateral apertural margin (as often employed by Ulrich and Scofield) as a specific taxobasis is questionable. If the members of *Archinacella* were clinging animals, as their limpetlike form and fused ringlike muscle scar suggest, then the shape of their lateral apertural margins may

reflect ontogenetic deformation by the shape of the substrate.

#### Order CYRTONELLIDA Horny, 1963c

*Diagnosis.*—Shells planispirally coiled, with symmetrical paired muscle scars that are generally discrete but show a tendency toward fusion. Aperture nonsinuate or sinus bearing, but no slits known.

*Stratigraphic range.*—Upper Cambrian-Middle Devonian; some Lower and Middle Cambrian taxa may also be cyrtoneilids.

*Discussion.*—The diagnosis for the Cyrtoneilida given above follows the concept of Horny (1963c) rather than that of Runnegar and Jell (1976). The latter authors defined the order as essentially including all monoplacophorans that lack a labral emargination. They included many genera, such as the helcionellids, hypseloconids, and yochelcionellids, whose taxonomic placement is debated, and others, such as scenellids, that I assign to the Tryblidiida. It should also be noted that they included *Cyrtolites* in their concept of the Cyrtoneilida; however, herein I show that several species of *Cyrtolites* bear a labral sinus. Runnegar and Jell's ordinal concept needs to be restructured, as its composition, and therefore its definition, are questionable.

#### Superfamily CYRTOLITACEA Miller, 1889

*Diagnosis.*—Same as for order.

#### Family CYRTOLITIDAE Miller, 1889

*Diagnosis.*—Shell evolute to involute, with open umbilicus; whorls in many cases angular or narrowly rounded dorsally and laterally; may or may not have an apertural sinus.

*Stratigraphic range.*—Lower Ordovician-Middle Devonian.

#### Genus CYRTOLITES Conrad, 1838

*Diagnosis.*—Shell rather loosely coiled, umbilicus widely open, aperture generally quadrangular, but may be rounded; aperture sinuate in many cases; growth lines raised, in many cases with intervening fine revolving threads; collabral rugae present in many cases.

*Description.*—Shell planispiral, consisting of about three whorls as adult, with wide-open umbilicus; coils contiguous, but barely touching, and disjunct in one known species. Aperture generally quadrangular to rhomboidal; may be rounded to sharply angular laterally; dorsal crest angular in most cases, but may be carinate. Whorls generally expand gradually and show only slight tendency toward flaring in gerontic stages. Aperture with dorsomedian sinus in some species, but in all cases lacks slit and selenizone. External markings always consist of distinctly raised thin growth lines, these

passing straight over the dorsal crest or swinging abaperturally to varying degrees to form a sinus; growth lines in many cases connected by short revolving threads that form a reticulate pattern; some species have collabral rugae developed at fairly regular intervals along dorsal and dorsolateral flanks of whorls. Shell thin.

Muscle scars in five discrete symmetrical pairs arranged in main and secondary rings. Main ring consists of three pairs, the first near dorsal crest, the second on lower dorsal slope, and the third on ventral slope. Secondary ring consists of two pairs of small scars on upper and lower slopes, respectively, that lie just anterior (abaperturally) to main ring.

*Type species.*—*C. ornatus* Conrad, 1838, by monotypy.

*Distribution.*—Middle Ordovician (Blackriveran)-Lower Silurian (Llandoveryan) of North America and Europe; occurs throughout Eastern North America.

*Comparison.*—*Cyrtolites* is generally easily distinguished from similarly shaped genera, such as *Cloudia* Knight (1947b), by its quadrangular whorl shape and distinctly raised growth lines, as well as by the fine revolving threads (forming a reticulate pattern) and rugae marking many species.

*Discussion.*—The genus *Cyrtolites* was described by Conrad (1838, p. 118) in the following brief statement: "Shell with general form of *Cyrtoceras*, but destitute of septa." Conrad's (1838) original illustration of *C. ornatus* is a disjunct internal mold. For many years afterward, a variety of fossil shells were assigned to this genus (Bassler, 1915, p. 365-368). Ulrich and Scofield (1897, p. 858) recognized this vague usage of the genus for symmetrically evolute shells having a carinate or angular dorsum and a broad umbilicus. They noted: "These characters pertain to several widely distinct genera, and to use them as characteristic of a single genus is to bring together a most heterogeneous assemblage of forms.... We must return to the original type *C. ornatus*, and restrict the genus to species possessing essentially the same generic peculiarities."

Reed (1921, p. 23) criticized Ulrich and Scofield's generic definition, saying that it was too broad and included species probably referable to *Temnodiscus* Koken. However, comparison of Reed's definition with that of Ulrich and Scofield shows no greater morphological restriction of the genus. It should be noted that Ulrich and Scofield stressed removal of shells having slits from the genus *Cyrtolites*. They assigned shells having deep slits to a new genus, *Cyrtolitina*, which Knight (1941) cited as an objective synonym of *Temnodiscus* Koken, 1896, as *Cyrtolites lamellifer* Lindstrom, 1884, was designated the type species for both genera.

Prior to 1965, *Cyrtolites* had generally been considered a bellerophonitid gastropod. However, Horny

(1965a) described several specimens of *C. ornatus* Conrad from the Upper Ordovician of Canada (specimens now in the British Museum of Natural History) that show five pairs of discrete symmetrical muscle scars arranged in main and secondary rings. He placed *Cyrtolites* in the class Monoplacophora.

Horny (1965a, p. 62) argued that *Cyrtolites* differs from the Bellerophonacea in the following features: (1) absence of a sinus, (2) absence of parietal inductura, and (3) presence of symmetrical multiple pairs of discrete muscle scars. The latter two differences are still valid. However, my work shows the presence of a shallow posterior apertural sinus in several species of *Cyrtolites* from the Middle and early Late Ordovician (pl. 5, figs. 7, 9, 10, 13; pl. 7, figs. 11, 14, 23, 34, 35; pl. 8, figs. 13, 17), because the growth lines turn conspicuously abaperturally over the dorsal crests of the shells. In his discussion, Horny conceded that there appeared to be some evidence of sinus development in American *Cyrtolites*, but he suggested that if any emargination were present, these species could be regarded as true bellerophonaceans (which he considered to be gastropods). I regard such a separation of forms to be contrary to the generic unity of *Cyrtolites* expressed by other morphological features. It should be noted that Horny's study was prior to Rollins and Batten's (1968) description of symmetrical pairs of discrete muscle scars in the sinuate monoplacophoran *Sinuitopsis acutilira* (Hall).

Horny (1965a) recognized the need for a revision of the North American species of *Cyrtolites*, and predicted that they would prove rather variable with regard to coiling and external ornamentation. He also expected there would emerge a continuous gradational series between *C. disjunctus* Ulrich and Scofield, 1897, and *C. ornatus* Conrad, 1838. He was correct about the variation in external ornamentation in the American species of *Cyrtolites*, which is expressed mainly in the strength of the rugae, growth lines, and revolving threads at the intraspecific level. The most striking intraspecific variation is in the cross-sectional shape of the whorls themselves. *C. retrorsus* Ulrich and Scofield can have a variety of apertural outlines in any one population, from quadrangular (pl. 5, fig. 14) to dorsally arched (pl. 5, fig. 18) to nearly circular (pl. 5, fig. 22). *C. ornatus* is also quite variable in cross-sectional shape, but not to the extent of *C. retrorsus*. There is no gradational series showing any progressive uncoiling in *C. ornatus*. Many internal molds of this species have been examined for this study, and when the inner coils are sufficiently visible, all specimens appear disjunct (pl. 6, fig. 18; pl. 7, fig. 1); shelled specimens are not disjunct, however. When *C. ornatus* is compared with *C. disjunctus* Ulrich and Scofield (pl. 6, figs. 19–22), the difference in the rate of

whorl expansion and increase in coiling radius are clearly very different in the two species. Shelled specimens of *C. disjunctus* are disjunct.

*Discussion of subgenera.*—The two subgenera of the genus *Cyrtolites* recognized in the Cincinnati arch province, *C. (Cyrtolites)* Conrad and *C. (Paracyrtolites)* n. subgen., are separated on the basis of differences in shell sculpture. *C. (Cyrtolites)* exhibits a distinct reticulate ornament pattern formed by short revolving threads between coarser raised growth lines (pl. 5, fig. 26; pl. 8, fig. 18), as well as regularly spaced collabral swellings along the slopes of the whorls, herein termed "rugae" (pl. 5, figs. 7, 12, 26; pl. 6, figs. 6, 19; pl. 8, figs. 2, 14). This subgenus contains those species most closely fitting the traditional concept of the genus, and includes the type species of the genus *C. ornatus* Conrad. *C. (Paracyrtolites)*, on the other hand, is composed of those species that lack rugae and have only faint revolving threads (pl. 7, figs. 23, 27, 30, 32, 34, 35), in contrast to the distinct threads that give the strong reticulate ornament pattern in *C. (Cyrtolites)*.

The oldest species in each of these two subgenera, *C. (C.) retrorsus* Ulrich and *C. (P.) subplanus* Ulrich in Ulrich and Scofield, 1897, both have V-shaped growth lines deflected abaperturally on the dorsal slopes, showing that each had a sinuate aperture (pl. 5, fig. 7; pl. 7, figs. 34, 35). Both of these species are found in the Kirkfieldian-Shermanian strata of Kentucky and Tennessee. The probable descendants of *C. (P.) subplanus* in the study area are *C. (P.) carinatus* Miller (pl. 7, figs. 18–25) and *C. (P.) parvus* Ulrich (pl. 7, fig. 17). Both of these species retain a sinuate aperture and are known from only the Edenian (lower Upper Ordovician) portion of the Kope Formation of northern Kentucky and southwestern Ohio. The longer lived, more diverse lineage stemming from *C. (C.) retrorsus* loses the labral sinus after Edenian time. Both *C. (C.) claysferryensis* (latest Shermanian and Edenian; pl. 8, figs. 11–20) and *C. (C.) retrorsus* (Edenian; pl. 5, figs. 6, 7, 9, 10, 13, 19, 23, 26) retain the shallow sinus. *C. (C.) minor* Ulrich (Kirkfieldian-early Maysvillian) has growth lines that pass essentially at right angles over the dorsal crest with little or no deflection (pl. 7, figs. 2, 5, 8). All subsequent species of the lineage in the Cincinnati have nondeflected growth lines passing straight over the dorsal crest, and thus had a nonsinuate aperture.

The reasons for the loss of the sinus in *C. (Cyrtolites)* in the Late Ordovician are unclear, but may be related to the changing depositional systems from the Champlainian to the Cincinnati Series in the study area. The Champlainian was much more free of clastic sedimentation than the Cincinnati Sea. Toward the end of Middle Ordovician time, fine clastic sediments began to be fed into the system in large quantities, so that the Cincin-

natian Series is characterized by alternating shale and limestone deposition. The loss of the sinus, therefore, may have been an adaptation to protect the mantle cavity from fouling by clay-sized sediment. Other general morphologic trends in the subgenus *C. (Cyrtolites)* are (1) in some species a slight increase in the width of the aperture relative to the height, (2) a slightly looser coiling and a more open umbilicus, and (3) in the post-Edenian rocks, a general increase in size.

The distinct external sculpturing of *Cyrtolites* is of some interest. Hall (1847), Meek (1873), and Ulrich and Scofield (1897) all included magnified illustrations of the reticulate sculpturing pattern seen in *C. (Cyrtolites)*. On *C. (C.) retrorsus* (pl. 5, fig. 26), each raised growth line is the termination of a sublamellate increment of growth, and each growth increment between the growth lines bears a series of slightly finer revolving threads which are raised to, or nearly to, the same height as the lines they intersect. These short revolving threads generally alternate from one increment to the next, so that they appear as bricks in a wall (pl. 5, figs. 15, 26). The strength of the connecting threads varies among species of *Cyrtolites*, but preservation usually affects their expression.

The revolving threads between the growth lines are indistinct and faint in *C. (Paracyrtolites)*, and, therefore, so is the reticulate ornamentation. *C. (P.) subplanus* Ulrich in Ulrich and Scofield has finer growth lines than any species of *C. (Cyrtolites)* (pl. 7, figs. 27, 30, 34, 35), and its weak connecting threads are revealed only by very close examination. The descendants of *C. (P.) subplanus* retain this faint type of ornamentation (pl. 7, figs. 18, 23, 24). Miller (1874) did not recognize a reticulate pattern in the original description of *C. (P.) carinatus* Miller, but Ulrich and Scofield (1897, p. 863) observed that only the best preserved material retained the delicate revolving threads, and that just short exposure to weathering could remove them entirely. The same authors claimed that *C. (P.) parvus* Ulrich in Ulrich and Scofield has a strong ornament, but the holotype (pl. 7, fig. 17) does not support this contention.

It is important to note that the ornament of *C. (P.) carinatus* appears to decrease in strength during growth, in contrast to the strengthening of ornament during the growth of *C. (C.) retrorsus*. The presence of distinct reticulate ornament in juveniles of *C. (P.) carinatus* suggests that *C. (Paracyrtolites)* had a common origin with, or possibly was descended from, *C. (Cyrtolites)*. While the weakly reticulate subgenus *C. (Paracyrtolites)* is not known from rocks younger than Edenian (lower Upper Ordovician), the strongly reticulate *C. (Cyrtolites)* persisted throughout the remainder of Cincinnati time.

*C. (C.) ornatus* Conrad is commonly found encrusted by bryozoans in the Maysvillian and Richmondian strata of the study area (pl. 6, figs. 12–16), and one specimen of *C. (C.) minor* Ulrich from the Edenian Kope Formation is known to be similarly encrusted (pl. 7, figs. 5–7). No other species of the genus are known to be encrusted. The encrusting bryozoans may have preferred the distinctly reticulate surface of these species as a base for larval settlement and colony growth. Many of these specimens appear to have been encrusted while alive. The apertural rim is generally not encrusted in otherwise completely encrusted shells, and in few cases do the bryozoans attain a thickness such that their weight might interfere with the mollusks' locomotion (pl. 6, figs. 12, 13, 15, 16). Morris and Rollins (1971, p. 162, figs. 4, 5) also assumed a symbiotic bryozoan encrustation of a specimen of *C. (C.) ornatus* from the study area, because of additional encrustation by oriented cornulitid tubes. Such a relationship would have been mutually beneficial; the monoplacophoran would acquire greater shell strength and a camouflage to assist in protection against predation, while the bryozoan would be assured an elevated attachment site. The suspension-feeding bryozoans might have further benefited from the molluscan feeding scraps and fecal products, or the microorganisms attracted thereto. McNamara (1978) reached similar conclusions from a study of gastropods encrusted by trepostome bryozoans from the Upper Ordovician of England. He pointed out that the bryozoans might have benefited from increased water flow over the colony caused by the gastropod's movement. Vermeij (1978, p. 64) suggested that "complex shell topography" might promote encrustation of modern gastropods by calcareous algae and other epizoans, and this might increase predator resistance.

*Evolution and speciation.*—Horny (1965a, p. 63, 64) proposed that the Cyrtolitidae were descended from the Archinacellacea (Upper Cambrian-Richmondian). He claimed that the muscle scars of *Cyrtolites* resemble the complete muscle ring of the archinacellids, and that the "decomposition of the continuous archinacellan band-like scar" and the addition of the anterior scars are caused by the coiling of the shell of *Cyrtolites* and its relatives. He also proposed that *Cyrtolites* was the ancestor of the Silurian genera *Yochelsonia* and *Cyclocyrtionella* and the Devonian genera *Cyrtionella* and *Neocyrtolites*. Horny believed that *Cyrtolites* and its allies were not an important stem stock for any subsequent major taxa, and hence did not give rise to any groups of Gastropoda. Rather, he believed that they represented a "highly specialized group of mollusks," though he did not say exactly how, or for what, they were specialized.

*C. (Cyrtolites)* and *C. (Paracyrtolites)* are closely related to one another because (1) they have a common



general shell form, (2) the oldest species of both groups have shallow sinuate apertures, and (3) both exhibit reticulate surface sculpturing, although this is only weakly developed in *C. (Paracyrtolites)*. *C. (C.) retrorsus fillmorensis* from the Blackriveran strata of Minnesota was named by Ulrich and Scofield (1897, p. 862) and regarded as the oldest member of that species and the genus (this name is herein placed in synonymy with *C. (C.) retrorsus* Ulrich because knowledge of the taxon sufficient to distinguish it from *C. (C.) retrorsus retrorsus* is lacking). The oldest known species of *C. (Paracyrtolites)* is *C. (P.) subplanus* Ulrich from the Kirkfieldian-Shermanian Lexington and Bigby-Cannon Limestones of Kentucky and Tennessee, respectively. *C. (C.) retrorsus* occurs in the same strata. It is likely that *C. (P.) subplanus* had a common ancestor with *C. (C.) retrorsus*. Stratigraphic ranges of species of *Cyrtolites* in the Cincinnati arch region are given in figure 24.

*C. (Paracyrtolites)* was a relatively short lived taxon and is rare relative to members of the subgenus *C. (Cyrtolites)*. *C. (P.) subplanus* (pl. 7, figs. 26-35) apparently gave rise to *C. (P.) carinatus* (pl. 7, figs. 18-25) and *C. (P.) parvus* (pl. 7, fig. 17) near the beginning of Edenian deposition. *C. (Cyrtolites)* was a relatively long lived taxon, and some species were highly successful; for example, *C. (C.) retrorsus* (pl. 7, figs. 11-16) and *C. (C.) ornatus* (pl. 6, figs. 1-18) are abundant throughout much of their stratigraphic range in the Cincinnati arch region. *C. (C.) ornatus* is particularly abundant and widespread, being known essentially everywhere in Eastern North America where Upper Ordovician carbonates are exposed. Like *C. (P.) subplanus*, *C. (C.) retrorsus* gave rise to two descendants near the Champlainian-Cincinnati boundary in the study area. *C. (C.) claysferryensis* n. sp. (pl. 8, figs. 11-20) appears in the late Shermanian- to Edenian-age Clays Ferry and Kope Formations of Kentucky and Ohio. *C. (C.) minor* (pl. 7, figs. 2-10) Ulrich and Scofield first appears in the Edenian portion of the Kope Formation of the study area, although it has been reported from the uppermost Champlainian of Minnesota (Ulrich and Scofield, 1897) and possibly from New Jersey (Weller, 1903).

Four new species of *Cyrtolites* appeared near the Champlainian-Cincinnati (Middle Ordovician-Upper Ordovician) boundary. This correlates with a marked change in sedimentological conditions throughout the region, with predominantly carbonate deposition giving way to intermittent shale and carbonate deposition. *C. (C.) claysferryensis* is similar to the more angular forms of *C. (C.) retrorsus*, the former inhabiting a somewhat more muddy environment. The other three new species—*C. (C.) minor*, *C. (P.) carinatus*, and *C. (P.) parvus*—are found in the dominantly shaly Kope environments, which are thought to reflect somewhat deeper

SERIES	STAGE	RANGE
Cincinnati	Richmondian	<i>C. (C.) hornyi</i> <i>C. (C.) ornatus</i> <i>C. (C.) disjunctus</i>
	Maysvillian	
	Edenian	<i>C. (C.) claysferryensis</i> <i>C. (C.) minor</i> <i>C. (P.) carinatus</i> <i>C. (P.) parvus</i>
Champlainian	Shermanian	<i>C. (C.) retrorsus</i> <i>C. (P.) subplanus</i>
	Kirkfieldian	
	Rocklandian	
	Blackriveran	

FIGURE 24.—Stratigraphic ranges of species of *Cyrtolites* (*Cyrtolites*) and *C. (Paracyrtolites)* in the Middle and Upper Ordovician of the Cincinnati arch region. *C. (C.) retrorsus* is known from the Blackriveran only in the Upper Mississippi Valley (Ulrich and Scofield, 1897). Dashed line indicates uncertainty of occurrence.

water. These three small species (shell lengths generally less than 15 mm) probably led rather similar modes of life. Their small sizes may have kept them from sinking into the soft bottoms of Kope environments. Peel (1978, p. 301-304) has suggested that small gastropod species from the Lower Silurian Arisaig Group were algal foliage dwellers. Such minute gastropod faunas are well known in the modern seas living on sea grasses and various algae (Warmke and Almodovar, 1963; Brasier, 1975). As in modern sea grass communities, the Ordovician algae would have provided a protective habitat, with abundant food above a possibly turbid sediment-water interface. Johnson (1961) has demonstrated a prolific calcareous algal flora in the Ordovician and Silurian; this suggests that noncalcified algae could also have been abundant (see section on paleoecology). Although the mode of

feeding of Paleozoic monoplacophorans is not known, most previous workers have assumed an algal-feeding habit similar to that of many gastropods. The common association of gastropods and monoplacophorans in fossil assemblages provides some support for this concept.

*C. (C.) minor* was the only one of these small cyrtolites to survive into Maysvillian time (Fairview Formation of southwestern Ohio). This species most likely was ancestral to *C. (C.) ornatus*, as indicated by their very similar morphologic characteristics, except for size. *C. (C.) minor* was originally described by Ulrich and Scofield (1897) as a subspecies of *C. (C.) ornatus*, the main difference being the small size of *C. (C.) minor*. The smaller species is not known from strata younger than the Fairview Formation, and it is in that unit that *C. (C.) ornatus* first appears in the study area. The Fairview Formation is distinguished from the underlying Kope Formation by a marked increase in carbonate deposition relative to shale deposition, and it may be that this species turnover correlates with changing environmental conditions.

*C. (C.) ornatus* is believed to have given rise to *C. (C.) disjunctus* in Richmondian time, as the two are quite similar, but the coiling of the latter species is disjunct. *C. (C.) disjunctus* is known only from the Richmondian strata of Minnesota, but it is treated in this study because of the possibility of confusing it with internal molds of *C. (C.) ornatus*. It may be that this rare disjunct form is not a valid species, but rather a morphological variant of *C. (C.) ornatus*.

*C. (C.) hornyi* n. sp. (pl. 8, figs. 1–10) is known only from USGS silicified sample 6139-CO from a single locality in southeastern Indiana. It is from the upper Dillsboro Formation, from strata formerly designated the Liberty Formation or *Strophomena planumbona* Bed (see Shaver and others, 1970, p. 45–58); these strata consist of interbedded shales and limestones. This species morphologically resembles *C. (C.) claysferryensis* n. sp. from the Clays Ferry Formation of Kentucky, which also consists of interbedded shale and limestone characterized at many horizons by the strophomenacean brachiopod *Rafinesquina* (see Weir and Greene, 1965, p. B11). The presence of large, flat strophomenid brachiopods such as *Strophomena* and *Rafinesquina* is generally considered to indicate level, soft-bottom conditions (Fox, 1968; Richards, 1972; Walker and Parker, 1976).

*C. (C.) retrorsus* and *C. (C.) ornatus* have much in common. They are the longest lived and most abundant of the species of *Cyrtolites* considered herein; both show a high degree of intraspecific variability, and both inhabited depositional systems that were complex facies mosaics. In both species, different morphotypes cooccur, suggesting a genetic rather than ecophenotypic origin for their variable morphologies. These species were proba-

bly ecological generalists that maintained genetic flexibility in their populations. This flexibility permitted them to adapt readily to constantly shifting sedimentologic-environmental conditions. In contrast to these two species, the other species of *Cyrtolites* in the study area, particularly the three small species from the Kope Formation, may have been ecologic specialists. Their relatively short stratigraphic ranges and small populations suggest that they were more finely tuned to certain environmental conditions and less able to adapt to environmental fluctuations.

The modes of speciation occurring in *Cyrtolites* are difficult to discern because of the nature of cratonic stratigraphic sequences, which are characterized by shifting environments and diastemic breaks in sedimentation. Speciation events seem to happen rather quickly across boundaries of marked environmental change, such as the Champlainian-Cincinnatian boundary. However, abundant species such as *C. (C.) retrorsus*, which show a high degree of intraspecific variability and cross many environmental boundaries, give an impression of phyletic gradualism. It can be discerned that *C. (C.) retrorsus* was able to maintain large populations in a variety of dominantly carbonate environments from Rocklandian to Shermanian time, apparently without any species turnover. This success may be partly the result of a regional consistency in carbonate deposition. *C. (C.) ornatus* behaved similarly during the extended period of alternating carbonate and shale deposition during Maysvillian and Richmondian times, again a period of overall regional consistency in deposition, even though of a fluctuating character. The greatest apparent proliferation of species took place when there was a rather drastic change in regional depositional conditions, that is, during the flood of clay-sized sediments in latest Shermanian and Edenian times. Therefore, speciation in the genus *Cyrtolites* seems to be linked to regional environmental conditions, and species distribution shows a correlation with the percentage of clay-shale deposition.

*Notes on British species of Cyrtolites.*—Reed (1921) described five species of *Cyrtolites* from the Ordovician and Lower Silurian of the British Isles. These species are listed below with comments.

1. *C. budleighensis* Reed—This species is known only from internal molds occurring in Ordovician pebbles found in Triassic conglomerates. Reed cited resemblance of this species to *C. subplanus* and *C. retrorsus*. Based on his figures of the species, it most resembles *C. ornatus* in both general shape and the development of strong rugae.
2. *C. craigensis* Reed—This species from the Stinchur Limestone (Caradocian), known only from poor internal molds, has a morphology comparable to that of *C. subplanus*.

3. *C. nodosus nodosus* (Salter)—This subspecies comes from the Bala Series (Caradocian-Ashgillian) of Wales. It is characterized by growth lines that are deflected abaperturally over the dorsal crest of the shell, a distinct reticulate ornament, and rugae that are distinct and slightly rounded and extend about three-fourths of the way up the width of the dorsal whorl slope. *C. nodosus* seems to be nearly identical to the North American species *C. retrorsus* and is probably a synonym of that species.
4. *C. nodosus llandoverya* Reed—This supposed "variety" of *C. nodosus* was found in Lower Llandoveryan rocks. It differs from the type subspecies in having sharper rugae that extend all the way up the dorsal whorl slope to the dorsal carina, and in having straight growth lines that are not deflected abaperturally. Reed believed that both the longer rugae and the nondeflected growth lines suggest a relationship to *C. ornatus*.
5. *C. thraivensis* Reed—This species, collected from the Drummuck Group (Ashgillian), Scotland, is very similar in general form and style of ornamentation to *C. ornatus*, which Reed called an allied species.

Although it is beyond the scope of this study to evaluate the British species of *Cyrtolites*, some insight into their taxonomy may be gained from comparison with American species. Only three of the British species names can be used confidently (species 3–5 above); these three are adequately preserved and their stratigraphic location is given. The oldest of the three is *C. nodosus nodosus* (Caradocian-Ashgillian), which is very similar to the North American species *C. retrorsus* (Kirkfieldian-Shermanian) in the development of its rugae and the abapertural curvature of its growth lines. The other two species, *C. nodosus llandoverya* (Lower Llandoveryan) and *C. thraivensis* (Ashgillian), compare quite favorably with the American species *C. ornatus* in the lengthening of their rugae and the straightening of their growth lines dorsally. Although stratigraphic correlation between the two faunas is rather broad, the same morphologic trends toward the accentuation of rugae and the loss of an apertural sinus are seen during late Middle and Late Ordovician times in North America and Great Britain. In fact, the British and American species names are probably synonyms. The two associations seem to have been given different specific names because of their present-day wide geographic separation. In any case, there can be little doubt about their derivation from a common ancestral stock, and their similar paths of evolution strongly suggest some genetic exchange between the two faunas.

#### Subgenus CYRTOLITES (CYRTOLITES) Conrad, 1838

*Diagnosis*.—Shell having rugae developed on dorsal slopes of whorls and distinct, short revolving threads between raised growth lines to form strong reticulate external shell sculpture. Apertural sinus and abaperturally deflected growth lines present in stratigraphically older species; younger species nonsinuate, with growth lines passing straight over dorsal crest of shell.

*Type species*.—*C. (C.) ornatus* Conrad, 1838, by monotypy.

*Distribution*.—Blackriveran (Middle Ordovician)-Richmondian (Latest Ordovician) of Eastern North American; Caradocian (Middle Ordovician)-Lower Llandoveryan (Lower Silurian) of Great Britain.

*North American species*.—*C. (C.) retrorsus* Ulrich and Scofield, *C. (C.) claysferryensis* n. sp., *C. (C.) minor* Ulrich, *C. (C.) ornatus* Conrad, *C. (C.) hornyi* n. sp., *C. (C.) disjunctus* Ulrich and Scofield.

*British species*.—*C. (C.) nodosus nodosus* (Salter), *C. (C.) nodosus llandoverya* Reed, *C. (C.) thraivensis* Reed. The other two British species assigned to *Cyrtolites* by Reed (1921) are known only from internal molds and cannot be assigned to a subgenus.

#### *Cyrtolites (Cyrtolites) ornatus* Conrad, 1838

Plate 6, figures 1–18; Plate 7, figure 1

*Cyrtolites ornatus* Conrad, 1838, p. 118; Conrad, 1839, p. 63; Conrad, 1841, p. 37; Hall, 1847, p. 308, pl. 84, figs. 1a–g; Rogers, 1858, p. 820, fig. 619; Billings, 1863, p. 217, fig. 226; Meek, 1873, p. 148, pl. 13, figs. 3a–b; Miller, 1874, p. 308; Lesley, 1889, p. 182, figs. ; Miller, 1889, p. 402, fig. 669; Ulrich and Scofield, 1897, p. 860, pl. 62, figs. 27–29; Cumings, 1908, p. 962, pl. 40, figs. 8–8a; Grabau and Shimer, 1909, p. 609, figs. 815a–b; Foerste, 1924, p. 203–204, pl. 34, fig. 3; Knight, 1941, p. 94, pl. 5, figs. 5a–d; Shimer and Shrock, 1944, p. 439, pl. 175, figs. 24, 25; Knight and others, 1960, p. 1175, fig. 90, 4; Caster, Dalve, and Pope, 1955 (1961), p. 41, pl. 5, fig. 11.

*Porcelia ornata* Sharpe, Emmons, 1860, p. 102, fig. 7. (Also see possible synonyms in discussion of British species.)

*Diagnosis*.—Shell large, with subquadrangular aperture, angular dorsally and narrowly rounded at umbilical shoulders; rugae well developed, generally rounded; growth lines not deflected abaperturally, pass straight over dorsal crest.

*Description*.—Shell relatively large (up to 33 mm long); umbilici large and open; whorls loosely coiled. Aperture subquadrangular, dorsum sharply angular to distinctly carinate, dorsal slopes convex, umbilical shoulders narrowly rounded to angular, ventral slopes flat to slightly concave. Rugae well developed, broadly rounded in many specimens but narrow ridges in others; rugae extend from umbilical shoulders to dorsal crest; rugae weakly developed on upper ventral slopes of some larger specimens. Growth lines not deflected abaperturally,

TABLE 25.—Measurements (in millimeters) of *Cyrtolites* (*Cyrtolites*) *ornatus*

Museum No.	Shell length	Aperture length	Aperture width	Maximum umbilical diameter	Width at base of aperture	Wave length of rugae
USNM						
45786	27.6	14.5	16.7	15.3	4.9	2-3
265906	30.4	18.5	16.8	16.2	6.2	3-4
265907	26.9	15.4	17.1	12.9	5.7	2-3
265908	32.9	19.0	—	15.7	—	2.7-4.5
UCGM						
3097	21.8	13.9	15.8	—	—	—
19671	24.1	13.9	15.8	—	—	—
SF						
2008	29.0	15.8	15.8	—	—	—

pass straight over dorsal crest of shell; reticulate ornament formed by somewhat weaker revolving threads.

*Measurements.*—Reliable measurements could be made on only a few specimens; these are listed in table 25 and shown graphically in figure 25. The poor quality of the measurements is reflected in the value of the plot. Measurements for USNM 45786, 265906, and 265907 are fairly reliable, but USNM 265908 is a large internal mold. UCGM 3097 and 19671 and SF 2008 are totally encrusted by bryozoans, so only partial measurement was possible.

*Material.*—No new specimens of this species were found in the USGS silicified collections. Collections at the U.S. National Museum, the University of Cincinnati, Miami University, and the Cincinnati Museum of Natural History were examined. All these collections were dominated by specimens from the Cincinnati arch region, and all were predominantly internal molds, composite molds, and bryozoan-encrusted specimens. SF 2008 is from the private collection of Steve Felton of Cincinnati, Ohio, and is not figured herein.

Knight (1941, p. 94) designated the specimen illustrated by Hall (1862, pl. 11, fig. 19) the lectotype of the species, but its whereabouts is unknown. Knight suggested that a collection of specimens in the Academy of Natural Sciences of Philadelphia (No. 13307) might be Conrad's original syntypes. The only previously figured specimen examined by me is a hypotype (USNM 45786) that was figured by Ulrich and Scofield (1897, pl. 62, fig. 27). A photograph of that specimen appears here for the first time (pl. 6, figs. 1-3). A collection of specimens bearing the same USNM number as this hypotype, but found in a separate box and drawer, was also examined, and three specimens from that collection are also figured here (pl. 6, figs. 6-8, 9-11; pl. 7, fig. 1; these hypotypes are here assigned numbers USNM 265906, 265907, and 265908, respectively). All of these specimens (originally with suite number USNM 45786) are labeled as coming from the "Corryville member of the McMillan Formation (Maysvillian) at Cincinnati, Ohio" (equivalent to Grant Lake Limestone or a tongue of the Bull Fork Formation).

*Distribution.*—Maysvillian (middle Upper Ordovician) and Richmondian (upper Upper Ordovician) of Eastern North America. The species is present in all formations of the middle to upper Upper Ordovician in the Cincinnati arch area, and according to the comments of other authors, it is common in many places throughout its geographic range.

*Comparison.*—The Maysvillian-age *C. (C.) minor* is similar in shell form and ornament (pl. 7, figs. 2-10) to *C. (C.) ornatus*, but is much smaller. The only other Richmondian-age species currently recognized in North America are *C. (C.) hornyi* n. sp. and *C. (C.) disjunctus*. *C. (C.) hornyi* (pl. 8, figs. 1-10) is more angular in its form and has flatter whorl slopes than *C. (C.) ornatus*. *C. (C.) disjunctus* (pl. 6, figs. 19-22) is disjunctly coiled, being distinguished from disjunct internal molds of *C. (C.) ornatus* by the rate of whorl expansion and the rate of increase in the radius of coiling.

*Discussion.*—*C. (C.) ornatus* Conrad, 1838, is the type species of the genus *Cyrtolites*, and the species in which Horny (1963c) discovered symmetrical discrete pairs of muscle scars, which led to the transfer of the genus to the class Monoplacophora. The species is distinguished from other species by its relatively large size (pl. 6, figs. 6-8), its usually broadly rounded rugae that extend from the umbilical shoulders to the dorsal crest of the shell (pl. 6, figs. 1, 6, 17), and its straight growth lines (pl. 6, figs. 7, 10), which cross the dorsum at right angles to the dorsal crest.

Horny (1965a) believed study eventually would reveal a continuous morphological gradational series of forms between *C. (C.) ornatus* and *C. (C.) disjunctus*. This idea is not supported by this study, although rarely a gerontic specimen of *C. (C.) ornatus* is found that appears to have a slight tendency to uncoil near the end of the body whorl.

*C. (C.) ornatus* exhibits a large amount of intraspecific variability in the shape of its whorls and the expression of its rugae. Figured here is a representative collection of forms; the specimens shown on plate 6, figures 1-3, 6-8,

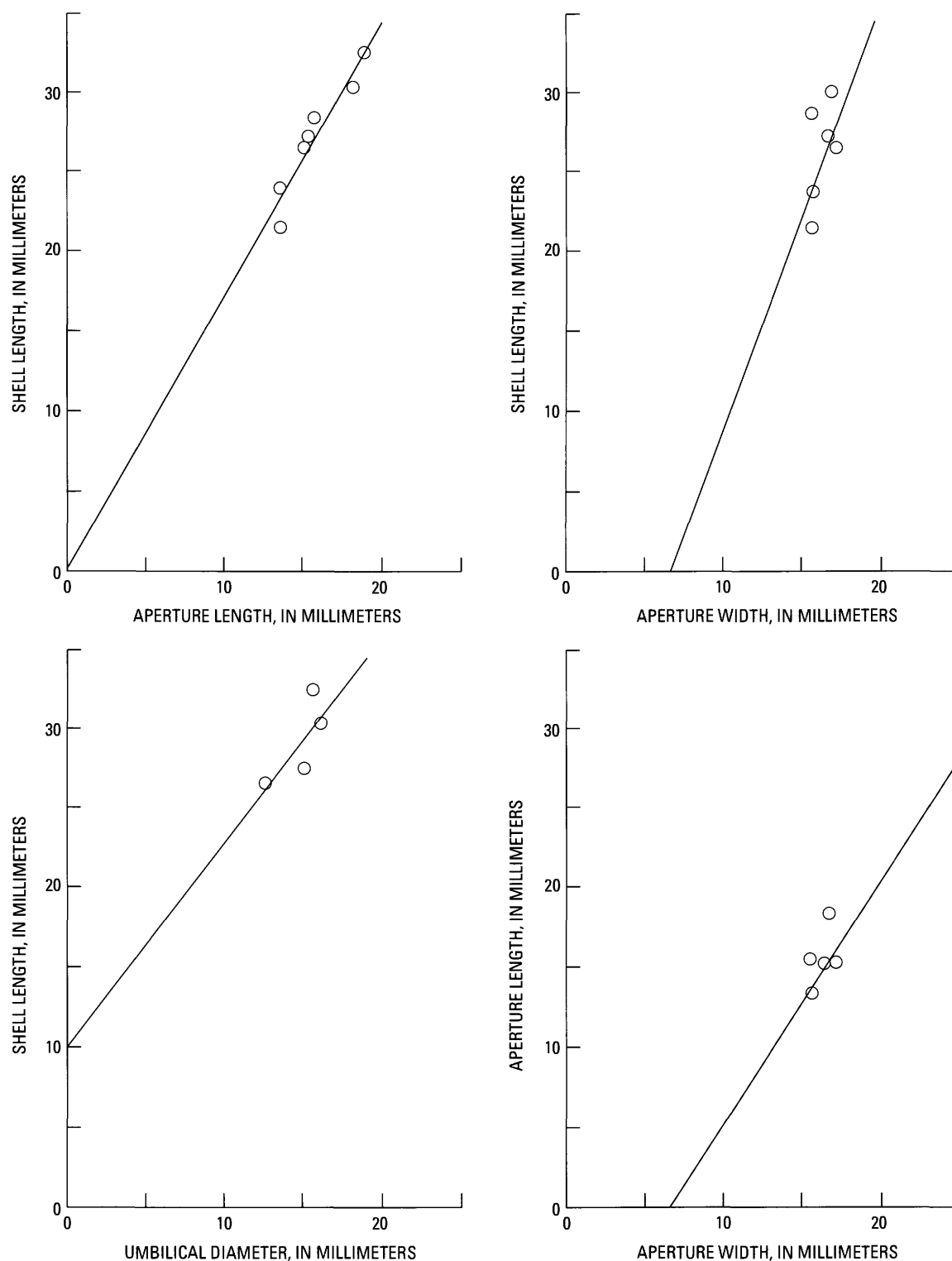


FIGURE 25. —Bivariate plots of measurements made on specimens of *Cyrtolites (Cyrtolites) ornatus*.

and 9–11, as well as the disjunct internal mold shown on plate 7, figure 1, are from one collection from Maysvillian strata at Cincinnati, Ohio. Contributing significantly to the difficulty of clearly defining the species is the variety

of preservational states in which it is commonly found. Most common are internal molds (pl. 7, fig. 1), which can be quite variable in appearance. Composite molds, in which the external mold is impressed upon the internal

mold as a result of early dissolution of the shell material while the enclosing sediment was still in a plastic state (pl. 6, figs. 6–8, 9–11), are not uncommon. Many of these composite molds, and even some internal molds, have a thin, hard, resistant coating over their surfaces. This coating may be the remains of the organic content of the shell, or could be the remnants of a micritized layer, as discussed by Bathurst (1966). Molds are commonly compressed and distorted, so their preserved morphology can vary greatly. Some calcitic casts are known (pl. 6, fig. 17); most specimens whose shells are preserved intact are encrusted by bryozoans (pl. 6, figs. 12–14, 15, 16, showing Maysvillian and Richmondian specimens, respectively).

The New York specimens of the species that I examined (Conrad originally based the species on New York material) (pl. 6, figs. 4, 5) generally are somewhat smaller, narrower, and more carinate dorsally than specimens of *C. (C.) ornatus* from the Cincinnati arch region. Comprehensive examination of material from the different areas of Eastern North America where the species has been recognized could result in the subdivision of this well-known species into subspecies, or even into discrete species. However, there is a great deal of variation in the Cincinnati arch material, and it is best interpreted as intraspecific variation.

***Cyrtolites (Cyrtolites) retrorsus* Ulrich, 1897**

Plate 5, figures 1–26; Plate 7, figures 11–16

*Cyrtolites retrorsus* Ulrich in Ulrich and Scofield, 1897, p. 861, pl. 62, figs. 32–37; Bassler, 1932, pl. 20, figs. 6, 7; Shimer and Shrock, 1944, p. 439, pl. 175, figs. 24, 25.

*Cyrtolites retrorsus fillmorensis* Ulrich and Scofield, 1897, p. 862, pl. 62, figs. 38, 39.

**Diagnosis.**—Shell moderate in size (up to 23 mm long), relatively tightly coiled; aperture varying from quadrangular to rounded; rugae as narrow, sharply rounded ridges extending from umbilical shoulders to near dorsal crest; curved growth lines and revolving threads of near equal strength form distinct reticulate ornament pattern; median labral sinus broad and shallow.

**Description.**—Shell moderate in size for genus, broad in dorsal view, relatively tightly coiled, with fairly wide umbilicus. Aperture generally quadrangular to subquadrangular, but can be quite rounded; average length/width ratio 0.85–0.90; dorsum carinate in juveniles, becoming angular to sharply rounded in adults; dorsal whorl slopes broadly convex, except near dorsal carina, where they may become concave briefly; umbilical shoulders angular to sharply rounded in juveniles, becoming sharply to broadly rounded in adults; ventral slopes generally flat to slightly concave, but can be slightly convex in inflated forms. Rugae well developed as low, narrow, rather sharply rounded, regularly spaced ridges

which extend from umbilical shoulders to near dorsal crest, generally weakening dorsally, and in some cases extending slightly onto the uppermost ventral slope; rugae generally lacking in juveniles. Distinct reticulate shell sculpture formed by coarse transverse raised growth lines that swing gently abaperturally across dorsal crest, and short revolving connecting threads of nearly equal strength that alternate from one growth increment to next. Labral sinus broad and shallow. Shell fairly thin; rugae can be very weakly expressed on shell interior.

**Measurements.**—Measurements, first of the type samples and then arranged by stratigraphic unit, are given in table 26. Figures 26 and 27 show graphs and measurements for specimens from the Logana and Grier Limestone Members of the Lexington Limestone, respectively.

**Material.**—The Logana Member (fig. 26) yielded the most and best preserved specimens of *C. (C.) retrorsus* in the USGS silicified collections. A total of 87 Logana specimens from four samples were measured for at least one parameter, depending on the quality and completeness of the preservation (USGS collections 5092-CO, 6419-CO, 7791-CO, and D-1196). Other Logana samples containing this species were USGS collections 4865-CO, 5073-CO, 5086-CO, and 5091-CO.

Nine samples from the Grier Limestone Member (fig. 27) contained this species: USGS collections 4073-CO, 4852-CO, 4876-CO, 4879-CO, 4883-CO, and 5067-CO, which contained measurable specimens, and 4874-CO, 4880-CO, and 4929-CO, which contained only poor material.

It should be noted that correlation coefficients for sets of measurements graphed in figures 26 and 27 are high (greater than 0.90) and that the ratios and slopes of graphs for the two different stratigraphic collections are in close agreement with one another.

**Types from Tennessee samples.**—The only Tennessee specimens of this species examined were four of Ulrich and Scofield's (1897) syntypes (USNM 45789), which are large silicified casts ranging from well preserved to rather worn and are labeled "Trenton, near Nashville, Tennessee." One of these specimens is here designated the lectotype of the species and retains the museum number USNM 45789 (pl. 5, figs. 5–7). The other three specimens from the Tennessee syntype suite are designated paralectotypes and have been assigned museum numbers USNM 265901 (pl. 5, figs. 8–10), USNM 265902 (pl. 5, figs. 11, 12), and USNM 265937 (not figured).

**Types from Kentucky samples.**—Ulrich and Scofield's (1897) syntypic suite included seven silicified casts and one internal mold labeled "Trenton (Flanagan), about 1 mile south of Burgin, Kentucky." The stratigraphic unit "Flanagan" is no longer used, as it was found to include

TABLE 26.—*Measurements (in millimeters) of Cyrtolites (Cyrtolites) retrorsus*

USNM No.	Shell length	Aperture length	Aperture width	Umbilical diameter	Ventral width	Wave length of rugae	No. of growth lines per mm
Type samples							
45789	23.20	13.1	18.40	10.15	4.4	3.0	6
265902	20.50	14.7	17.00	9.80	4.3	2.5	—
265901	22.45	14.3	19.60	9.20	3.7	2.0	5
265899	16.05	10.5	10.70	7.30	3.1	—	5-6
265900	21.00	11.8	14.25	11.30	3.3	—	5
265938	12.95	8.4	8.05	6.80	2.3	2.0	—
45790	12.20	6.8	7.85	6.20	2.0	—	—
Lexington Limestone							
Curdsville Limestone Member							
387024	13.1	—	—	8.8	2.7	2.0	7
387024	14.2	—	—	—	2.2	—	—
265939	14.7	9.70	11.3	8.4	2.7	—	—
265939	—	—	—	—	—	2.0	4
265940	17.7	11.95	15.7	—	3.5	—	5
Logana Member							
265942	17.1	14.4	14.90	10.00	5.2	1.50	4
265942	—	7.1	7.00	—	—	1.50	3-4
265942	—	12.7	14.35	—	—	2.00	2-3
265942	—	—	—	—	—	2.00	3
265942	—	—	—	—	—	1.75	3-4
265942	9.2	6.0	6.90	5.00	1.0	—	4
265942	11.0	—	—	6.05	—	—	—
265942	—	8.9	10.10	—	—	—	3
265942	—	12.0	12.90	—	—	—	4
265942	11.9	8.3	—	5.50	—	—	5
265942	8.8	5.5	7.00	5.00	—	1.50	—
265942	—	—	—	—	—	2.00	4
265942	11.0	6.5	8.80	4.50	—	2.00	3-4
265942	—	5.2	6.20	—	—	—	4
265942	12.4	7.5	7.00	6.50	2.0	—	5
265943	15.4	11.0	11.30	8.10	3.1	1-1.50	4
265943	14.6	10.9	11.95	8.05	3.1	1-2.0	4-5
265943	—	—	13.10	8.10	3.0	1-1.5	5
265943	13.9	9.4	—	7.90	2.8	—	4-5
265943	11.6	9.0	10.50	8.30	2.5	—	4-5
265943	9.0	6.0	8.55	5.55	—	—	4
265943	—	—	—	10.00	—	2.0	4-5
265943	—	—	—	7.60	—	—	4
265943	11.1	—	—	6.60	—	—	3-4
265943	7.9	5.0	5.00	4.70	—	—	4
265943	20.1	12.8	12.80	9.35	3.7	1.5-2.3	5
265943	17.2	10.4	12.50	—	—	2.0	5
265943	18.4	12.4	13.70	9.10	3.6	—	5
265942	20.6	13.1	14.60	10.50	3.8	2.0	5-6
265943	—	11.3	12.60	—	—	—	4
265943	—	14.5	16.35	—	—	1.5-2.0	4
265943	—	11.5	15.20	—	—	2.0	3-4
265943	18.4	12.5	14.00	9.40	—	2.0	5
265943	16.8	11.4	12.75	8.95	3.4	—	—
265943	—	14.1	16.90	—	—	—	5
265943	—	12.9	15.70	—	—	1-2	5-6
265943	18.4	—	—	10.10	—	1.5-2.0	—
265943	18.0	12.4	14.20	9.40	—	2.0	5
265943	16.7	12.1	13.10	9.20	2.5	2.0	4-5
265943	—	12.1	12.70	—	—	—	—
265943	15.7	10.2	11.90	9.00	2.7	1.5-2.0	4-5
265943	17.9	11.9	14.20	8.80	—	—	—
265943	16.8	11.9	11.95	—	—	—	4-5
265943	—	—	11.70	7.70	3.2	—	—
265943	—	10.7	12.50	—	—	—	—
265943	19.5	12.7	13.60	9.30	3.9	—	5



TABLE 26.—*Measurements (in millimeters) of Cyrtolites (Cyrtolites) retrorsus*—Continued

USNM No.	Shell length	Aperture length	Aperture width	Umbilical diameter	Ventral width	Wave length of rugae	No. of growth lines per mm
265943	18.0	11.6	12.40	9.00	3.4	—	5
265943	16.9	11.6	13.50	9.40	2.5	—	3
265943	16.0	11.0	12.20	7.70	2.9	—	4-5
265943	12.1	8.2	8.40	7.30	1.8	—	5
265943	13.6	8.4	9.65	6.60	2.4	2.0	4-5
265943	—	—	12.90	8.90	3.0	—	—
265943	17.7	11.2	11.75	8.80	3.8	—	5
265943	13.1	8.1	8.90	6.50	2.4	1.5	5
265943	10.4	6.5	7.40	6.20	—	—	5
265943	—	10.2	12.10	8.20	—	—	4
265943	—	—	11.30	7.90	2.5	—	—
265943	16.1	10.5	12.30	—	—	—	4
265943	—	—	10.40	8.80	2.7	—	—
265943	—	—	7.40	5.50	2.0	—	3-4
265943	—	8.0	9.25	—	—	—	4-5
265943	15.0	10.7	12.45	—	—	—	5
265943	18.3	13.5	13.55	9.40	3.5	—	4
265943	15.6	10.7	11.40	—	3.2	—	6
265943	14.8	10.4	11.40	8.10	3.4	1.5-2.0	4
265943	18.5	13.2	14.00	8.80	4.5	2.0	4
265943	17.5	11.2	12.90	9.00	3.4	1.5-2.0	5
265943	19.6	13.4	13.50	—	—	—	4
265943	15.3	9.6	10.95	7.40	3.1	—	5
265943	—	10.4	11.40	—	—	—	—
265943	7.9	5.2	6.15	3.80	—	—	4
387025	17.6	10.4	12.9	9.0	—	2.0	4
387025	—	4.7	5.0	4.8	—	—	—
387025	18.2	11.2	12.8	9.2	3.5	2.0	3
387025	13.4	8.3	8.4	6.4	3.0	—	4
387025	—	10.4	11.2	—	—	—	3-4
387025	17.7	11.1	14.1	10.2	—	—	—
387025	15.0	9.5	12.4	7.9	3.0	1.5-2.0	4
265953	12.7	8.5	9.2	5.8	2.8	1-1.5	—
265953	14.8	9.5	9.8	8.0	—	1.5-2.0	4-5
265953	8.3	5.2	5.8	3.9	1.4	—	—
265953	9.3	5.4	6.9	4.0	2.6	—	—
Grier Limestone Member							
387026	12.2	7.0	8.8	7.0	3.0	—	—
387026	7.3	5.0	7.0	4.5	—	—	—
387027	7.0	4.3	4.4	4.2	—	—	5
387027	11.2	5.5	8.6	5.5	—	1.5	—
265958	9.3	4.9	7.1	5.3	2.2	—	—
265958	14.6	—	12.4	7.6	—	—	—
265958	13.1	8.5	11.2	6.1	2.6	—	—
265958	11.8	7.4	9.4	—	—	—	—
265958	—	4.7	8.0	—	—	—	—
265958	—	4.5	6.5	—	—	—	—
265958	9.7	6.1	8.2	5.1	—	—	4
265958	11.7	6.7	8.7	5.8	—	2.0	3-4
387028	4.0	2.3	2.9	2.0	1.0	—	—
387028	—	3.7	3.7	—	—	—	—
387029	7.0	4.4	5.1	3.7	—	—	—
387029	—	5.5	7.6	—	—	—	—
265973	15.8	10.6	11.9	8.5	3.1	1.5-2.0	4-5
265973	17.0	10.3	12.6	8.1	3.9	—	5
265973	16.2	11.4	12.0	8.4	3.8	1.5-2.0	4-5
265973	13.3	9.0	10.4	7.1	2.4	1.5-2.0	5-6
265973	6.0	3.5	3.6	3.8	—	—	5
265973	11.0	7.3	9.0	5.6	2.2	1.5-2.0	5
Millersburg Member							
265968	18.8	11.5	14.7	11.1	3.8	2.0	4-5
265968	9.9	5.9	7.9	5.9	2.0	—	4

TABLE 26.—Measurements (in millimeters) of *Cyrtolites (Cyrtolites) retrorsus*—Continued

USNM No.	Shell length	Aperture length	Aperture width	Umbilical diameter	Ventral width	Wave length of rugae	No. of growth lines per mm
Millersburg Member—Continued							
265968	-	-	14.0	11.0	-	-	-
265968	-	-	7.8	5.3	-	-	-
Perryville Limestone Member							
265959	6.2	4.0	4.0	3.7	1.6	-	-
265959	17.8	12.8	15.0	8.0	3.8	-	4

different units in different areas, but the USGS map of the Danville quadrangle (Cressman, 1972) shows the designated area as exposing the Curdsville, Grier, and Perryville Limestone Members of the Lexington Limestone. All of these specimens are here designated paralectotypes. The five paralectotypes not figured in this

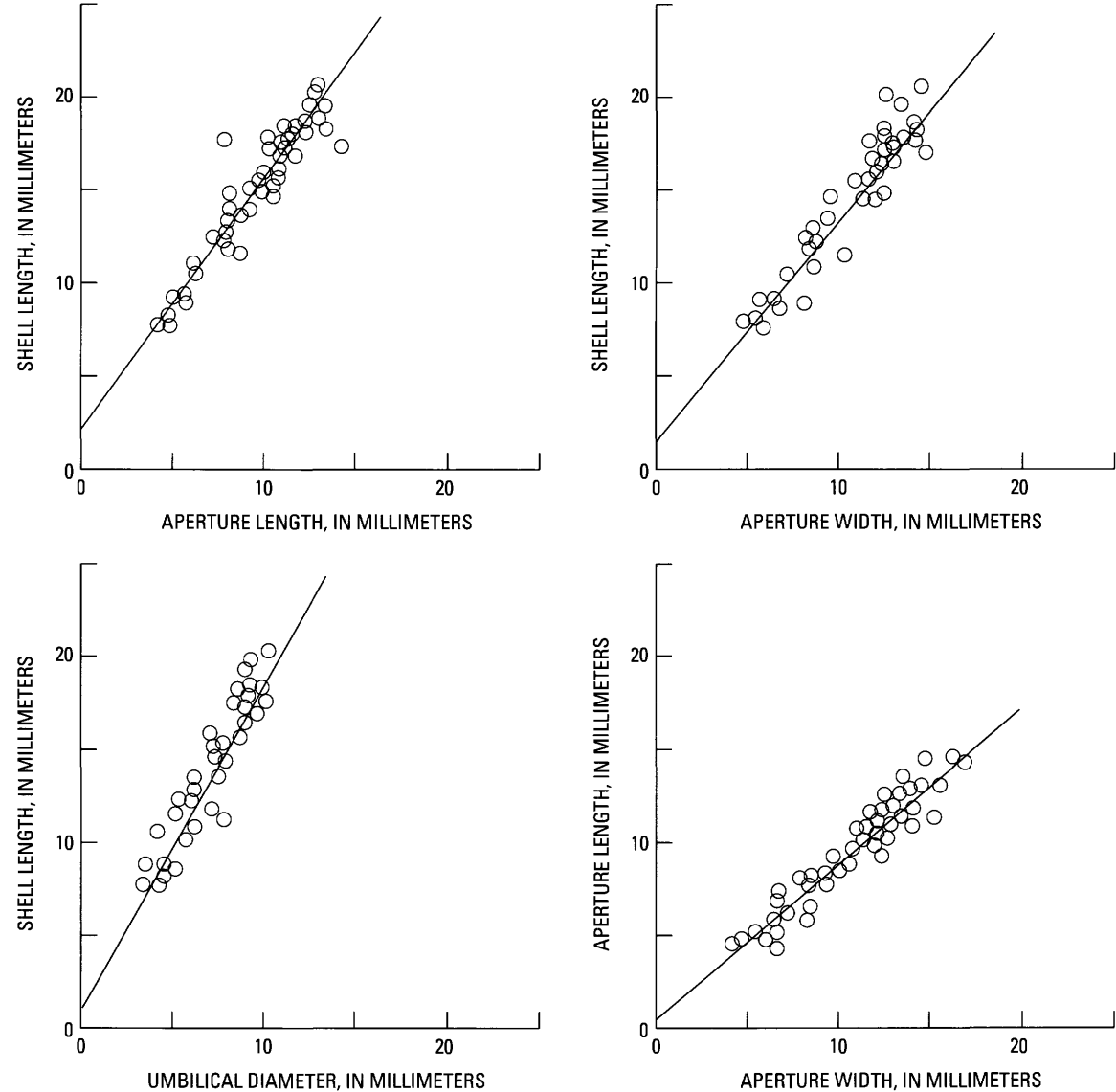


FIGURE 26.—Bivariate plots of measurements made on specimens of *Cyrtolites (Cyrtolites) retrorsus* from the Logana Member of the Lexington Limestone in central Kentucky.

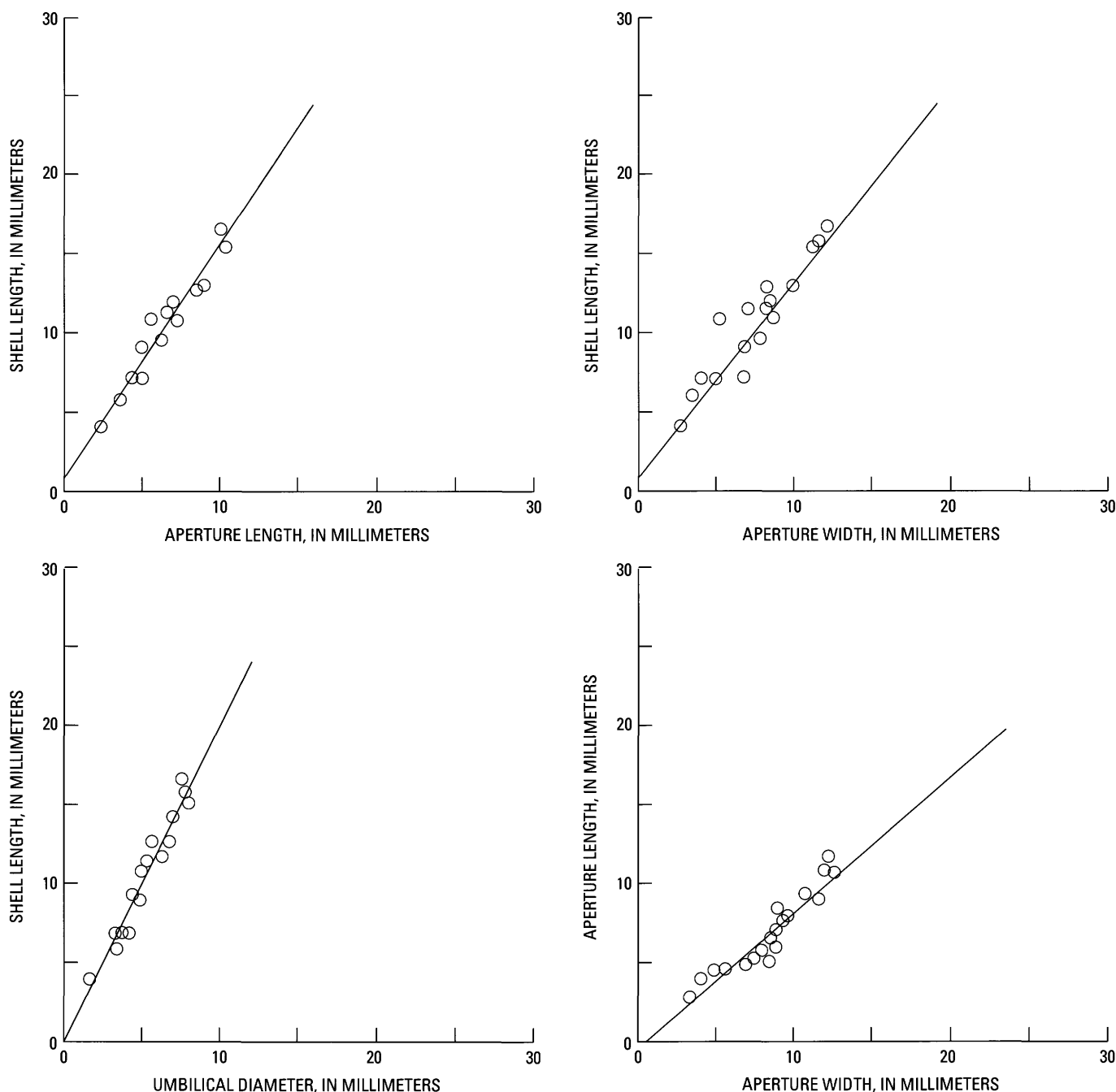


FIGURE 27.—Bivariate plots of measurements made on specimens of *Cyrtolites (Cyrtolites) retrorsus* from the Grier Limestone Member of the Lexington Limestone in central Kentucky.

study remain under the original museum number USNM 45790; the other three are figured here and are given the new numbers USNM 265938 (pl. 5, figs. 1, 2), USNM 265899 (pl. 5, figs. 3, 4), and USNM 265900 (pl. 5, fig. 13).

*Distribution.*—In the USGS silicified collections, *C. (C.) retrorsus* was recognized in the Curdsville Limestone (5022-CO, 5023-CO, 5080-CO, 5100-CO), Logana (D-1196-CO, 4865-CO, 5073-CO, 5086-CO, 5091-CO,

5092-CO, 6419-CO, 7791-CO), Grier Limestone (4073-CO, 4852-CO, 4876-CO, 4879-CO, 4880-CO, 4883-CO, 5067-CO), Millersburg (7344-CO, 7353-CO, 7455-CO), and Perryville Limestone (5015-CO) Members of the Lexington Limestone (Kirkfieldian-Shermanian). The most and best preserved specimens came from the Logana Member; fairly good specimens came from the Grier Limestone Member; and the other members of

the Lexington Limestone contained few specimens, and those are fair to poor in preservation.

Two calcitic specimens of *C. (C.) retrorsus* (USNM 265909 and 265910; pl. 7, figs. 11–13, 14–16), which are well preserved but have variable form, came from the Edenian portion of the Kope Formation at Covington, Ky.

Thus, *C. (C.) retrorsus* is known in Kentucky from the Lexington Limestone (Kirkfieldian-Shermanian) to the Kope Formation (Edenian). A supposed subspecies (*C. retrorsus fillmorensis*) was described by Ulrich and Scofield (1897) from Blackriveran strata of Minnesota. Because this supposed "subspecies" is very poorly known and does not seem clearly distinct from the stock as known in the type area, and because *C. (C.) retrorsus* is shown here to have a variable shell morphology, the Minnesota "subspecies" is synonymized with *C. (C.) retrorsus*.

In Tennessee, Bassler (1932) and Wilson (1949) reported the species from (1) the *Ctenodonta* member of the Hermitage Formation, (2) the Bigby, Cannon, and dove-colored facies of the Bigby-Cannon Limestone, and (3) the upper Catheys Formation. The first two occurrences are Kirkfieldian-Shermanian in age, and the third is either Shermanian or Edenian in age, probably the latter (Sweet and Bergstrom, 1976, text-fig. 3).

*Comparison.*—*C. (C.) retrorsus* is quite variable in shape, but, as shown in figures 26 and 27, its whorl dimensions are notably consistent. The only other Kirkfieldian-Shermanian species currently recognized in North America is *C. (P.) subplanus* (pl. 7, figs. 26–35); it can be readily distinguished by its noncarinate dorsal crest, its lack of rugae, and its much weaker growth lines, with revolving threads absent or only barely discernible, so that no reticulate sculpturing is obvious.

The latest Shermanian-Edenian species, *C. (C.) clay-sferryensis* n. sp. (pl. 8, figs. 11–20), is very similar to *C. (C.) retrorsus*, but the former species has a slightly wider aperture and sharply angular umbilical shoulders. In the Edenian, juveniles of *C. (C.) retrorsus* might easily be confused with *C. (P.) carinatus* (pl. 7, figs. 18–25), which is a small species; these two should be distinguishable by the difference in the number of whorls present in the juveniles of the former versus the adults of *C. (P.) carinatus*.

Specimens of *C. (C.) retrorsus* (pl. 7, figs. 11–16) from the Edenian portion of the Kope Formation vary in shell form, but the character of their surface markings suggests that they are conspecific with the specimens from Kirkfieldian-Shermanian-age strata.

*Discussion.*—In their discussion of the species *C. retrorsus*, Ulrich and Scofield (1897, p. 861, 862) were confident of its specific distinctiveness, but they expressed concern about the inclusion of some speci-

mens, particularly those from the basal beds of what they called the Trenton Group in Kentucky and Tennessee. They stated: "So far as the form of the shell and the volutions are concerned, the specimens in question certainly agree very closely with *C. retrorsus*, and if appearances are not deceptive, they are like it also in the backward swing of the surface markings. The evidence at hand, therefore, seems to indicate that all of the Tennessee and Kentucky specimens hitherto referred to *C. ornatus* really belong to *C. retrorsus*."

It is not surprising that Ulrich and Scofield were apprehensive about this species, because it exhibits a high degree of intraspecific variation in shape. It is recognized mainly on the basis of its distinct reticulate ornament pattern (in adult shells), the gentle curving of its growth lines over the dorsal crest of the shell, and its aperture height/width ratio regardless of the apertural outline. As shown on plate 5, figures 14, 18, and 22, the aperture shape of *C. (C.) retrorsus* can vary from quadrangular to nearly circular in a single population. All three of these figured specimens are from a single sample from the Logana Member of the Lexington Limestone (USGS sample 6419-CO) in central Kentucky. This sample is considered to represent a single population because of (1) its occurrence in a single sampled bed, (2) the presence of a gradational growth series, and (3) the quality of preservation, which suggests very little transport. It appears that this intraspecific variability in whorl shape is largely genetic, rather than ecophenotypic, in origin. However, there also appears to be ecophenotypic variation between populations from different stratigraphic units. For example, when some of the more rounded, inflated forms from the Logana Member of the Lexington Limestone (pl. 5, figs. 18–25) are compared directly with more angular forms, such as Ulrich and Scofield's (1897) type specimens from Tennessee (pl. 5, figs. 5–12), there appear to be two possible species. However, Ulrich and Scofield's type specimens from Kentucky (pl. 5, figs. 1–4, 13) are intermediate in form, as are many other specimens, including some of the Logana specimens (pl. 5, figs. 14–17). Such marked variation makes the formulation of a concise description of the species difficult. Equally frustrating are ontogenetic changes in shell form. Most juvenile specimens are quite angular, some even being carinate dorsally and laterally, and the dorsal slopes can be slightly concave. These small, smooth, angular specimens resemble *C. (P.) carinatus*, but can be distinguished by their narrower form and fewer whorls. This situation is not uncommon when dealing with isotrophic molluscan univalves. Ulrich and Scofield (1897) claimed that immature specimens of *Cyrtolites* and *Carinaropsis* are virtually indistinguishable. Thein and Nitecki (1974, p. 55) encountered a similar problem with Chesterian bellerophonitids,

TABLE 27.—Measurements (in millimeters) of *Cyrtolites* (*Cyrtolites*) *claysferryensis*

USNM No.	Shell length	Aperture length	Aperture width	Umbilical diameter	Ventral width	Wave length of rugae	No. of growth lines per mm
265923	16.9	9.7	13.0	9.1	3.4	1.5–2.0	4
265924	15.0	9.0	12.7	8.6	3.0	1.5	5–6
265925	19.0	12.8	16.2	9.5	4.5	2.0–3.0	4
265973	16.1	10.4	14.4	8.1	3.6	1.5–2.0	—
265973	—	10.4	14.6	—	—	2.0	5
265973	—	12.2	13.8	11.2	—	—	—
265973	14.1	10.7	12.5	—	—	—	—
265973	16.9	11.5	16.4	8.0	3.5	—	—
265970	17.3	13.1	17.1	10.1	4.7	—	5–6
265970	16.7	10.9	15.8	8.0	3.7	2.0	—
265970	15.8	10.7	13.0	8.9	2.8	2.0	4
265970	15.1	—	13.2	9.1	3.0	2.0	4–5
265972	13.5	7.6	10.5	7.7	3.0	1.5	4
265976	15.2	—	—	6.9	3.6	1.5–2.0	5–6

finding that the differentiation of three subgenera of *Knightsites* by looking at immature specimens was impossible.

During adult and gerontic growth, shell form may change continuously. Some shells retain some of the angularity of youth (pl. 5, fig. 11), but the aperture broadens and the dorsal whorl slopes become convex. Other shells lose their angularity completely in the final evolution, with the dorsal crest becoming almost rounded, so that a more inflated shell results (pl. 5, figs. 22–25).

Also, the coarseness of the rugae can be quite variable, and does not vary in concert with the degree of angularity or roundness of the shell. For example, the lectotype (pl. 5, figs. 5–7) and a paralectotype (pl. 5, figs. 8–10) from the same collection from Tennessee are very similar in general form, but the former specimen has more distinct ridgelike rugae, similar to some of the inflated *Logana* forms (pl. 5, figs. 22–25). Regardless of shell form, all adult specimens of the species have distinct reticulate shell sculpturing, with abaperturally curved growth lines reflecting a broad, shallow, dorsal labral sinus.

*C. (C.) retrorsus* apparently gave rise to a fairly diverse group of Late Ordovician descendants. The two specimens of *C. (C.) retrorsus* from the Edenian Kope Formation (pl. 7, figs. 11–13, 14–16) previously discussed may represent the last surviving populations of *C. (C.) retrorsus* in the study area, possibly struggling for existence under the more turbid conditions of the early Cincinnati seas.

***Cyrtolites* (*Cyrtolites*) *claysferryensis* new species**

Plate 4, figures 15–17; Plate 8, figures 11–20

**Diagnosis.**—Shell moderate in size (up to 19 mm long), angular; aperture wide and subquadrangular, dorsal crest and umbilical shoulders sharply angular, dorsal

slopes convex, ventral slopes concave; reticulate ornament distinct; sinus shallow.

**Description.**—Shell moderate in size for genus, broad angular; coiling moderately loose; umbilicus wide and rather deep. Aperture subquadrangular and broad, aperture height/width ratio 0.76; dorsum carinate in juveniles, becoming sharply angular in adults; dorsal slopes broadly convex, draping slightly at umbilical shoulders in some large specimens; umbilical shoulders sharply angular; ventral slopes distinctly concave. Rugae distinct, thin, regularly spaced, forming small nodes at umbilical shoulder and extending dorsally for about three-fourths the width of dorsal slope; rugae do not influence ventral slopes. Growth lines swing quite gently abaperturally over dorsal crest of shell, reflecting a broad, shallow, dorsomedian labral sinus; short, alternating, revolving threads of near equal prominence, resulting in distinct reticulate surface sculpturing.

**Measurements.**—Measurements of *C. (C.) claysferryensis* are listed in table 27 and shown graphically in figure 28. For all parameters plotted, growth appears to be highly coordinated; correlation coefficients are 0.97–0.98. All regression lines approach the graph origins quite closely.

**Types.**—The new species was found in the following USGS silicified samples from the Clays Ferry Formation: 6143-CO, 6990-CO, 7343-CO, 7348-CO, 7349-CO, 7350-CO, 7458-CO, 7461-CO, and 7812-CO. The specimen here designated the holotype for *C. (C.) claysferryensis* is USNM 265924 (pl. 8, figs. 14–18) (shell length 15.0 mm; aperture length 9.0 mm; aperture width 12.7 mm) from USGS 6143-CO, from the upper tongue of the Clays Ferry Formation in a road exposure on the eastern side of Kentucky Route 982, 0.4 mi south of the junction of Kentucky Routes 32, 36, and 982 in Cynthiana, Ky. Two silicified paratypes are also figured, USNM 265923 (pl. 8, figs. 19, 20), from the same collection as the

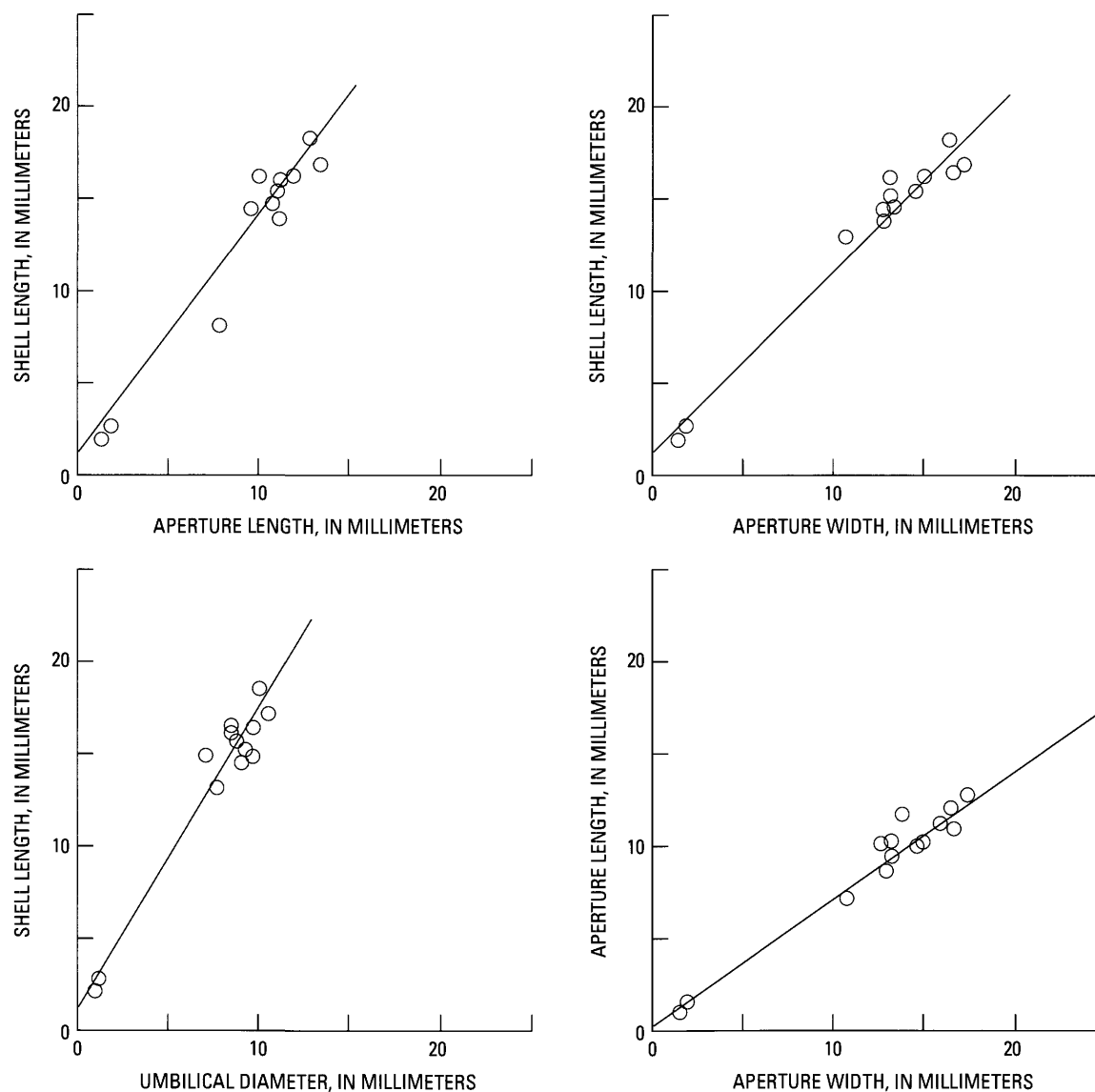


FIGURE 28.—Bivariate plots of measurements made on specimens of *Cyrtolites* (*Cyrtolites*) *claysferryensis* new species from the Clays Ferry Formation in north-central Kentucky.

holotype, and USNM 265925 (pl. 8, figs. 11–13), from USGS sample 6990-CO. About 60–70 specimens and fragments are present in the silicified collections, but only 14 were sufficiently preserved to be measured.

Two calcitic specimens collected by me are also designated paratypes. Paratype USNM 265959 (pl. 4, figs. 15, 16) was found in a mollusk bed composed predominantly of small pelecypods and gastropods, in the Kope Formation at the Carrollton, Ky., exit from Interstate I-71 (locality KY-1). Paratype USNM 315609 (pl. 4, fig. 17) was found in a mollusk bed dominated by *Sinuities granistriatus* in the lower Kope Formation, about 10 ft above the contact with the Point Pleasant Tongue of the Clays Ferry Formation, just north of Ohio Route 52

along the north shore of the Ohio River, at Bear Creek Quarry, between Neville and Chilo, Ohio (locality OH-1).

*Distribution.*—The new species is known from the lower Kope Formation (Edenian) in Kentucky and southwestern Ohio.

*Comparison.*—*C. (C.) claysferryensis* is very similar to some of the more angular forms of *C. (C.) retrorsus*, but it differs in several ways: its aperture height/width ratio is smaller, reflecting its relatively broader aperture; its umbilical shoulders are consistently more sharply angular, this impression being accentuated by the concave slopes of the broad umbilicus; its growth lines generally do not swing abaperturally as deeply (reflecting a shallower sinus) (pl. 8, fig. 18); and its rugae

are generally thinner and sharper (pl. 8, fig. 14), and never extend onto the upper ventral slopes. *C. (C.) claysferryensis* is also quite similar in some respects to *C. (C.) hornyi* n. sp. from the Richmondian Dillsboro Formation of southeastern Indiana, but the latter species has flatter whorl slopes (pl. 8, fig. 1) and straight growth lines (pl. 8, fig. 2), and it attains a somewhat larger size (pl. 8, figs. 1-4).

**Discussion.**—It is clear that *C. (C.) claysferryensis* evolved directly from *C. (C.) retrorsus*, which not only closely resembles the former species in many morphological features, but also immediately precedes and partially overlaps it stratigraphically. *C. (C.) retrorsus* thrived in the dominantly carbonate environments of the upper Middle Ordovician Lexington Limestone, and apparently only barely survived into the overlying Edenian Kope Formation. *C. (C.) claysferryensis* first appears in the Clays Ferry Formation, which straddles the Middle-Upper Ordovician boundary and is adjacent to both the upper Lexington Limestone and the lower Kope Formation, having more shale than the former and less than the latter. The new species is also recognized in the Kope Formation. Apparently, the evolution of a wider, more angular aperture, with a shallower dorsomedian sinus, helped *C. (C.) claysferryensis* survive the more turbid conditions of the early Cincinnati seas. This apertural modification may have enabled better channeling of currents through the mantle cavity and thus prevented clogging of the ctenidia by fine sediments, or may have assisted in supporting the shell on softer substrates.

It should be noted that whereas the dorsal slope of *C. (C.) retrorsus* is relatively well developed, that of *C. (C.) claysferryensis* is somewhat shallower, and later species lack the sinus altogether. It is difficult to understand why this lineage would show this trend toward reduction of a labral sinus, because an emargination is known to be highly efficient as an exhalant canal in pleurotomariacean gastropods, and it would seem to be likewise useful in monoplacophorans. Perhaps its absence allowed a tighter seal when the animal clamped down onto the substrate for protection.

As noted above, *C. (C.) claysferryensis* is similar to *C. (C.) hornyi* from the Richmondian part of the Dillsboro Formation of Indiana. The species inhabited similar depositional environments of alternating carbonate and shale sedimentation, and *C. (C.) hornyi* is likely the end product of slow intrafacies evolution, but at present intermediate forms are not known.

***Cyrtolites (Cyrtolites) minor* Ulrich, 1897**

Plate 7, figures 2-10

*Cyrtolites ornatus minor* Ulrich in Ulrich and Scofield, 1897, p. 860, pl. 62, figs. 30, 31; Weller, 1903, p. 174, 175, pl. 12, figs. 6, 7.

**Diagnosis.**—Shell small (up to 13.5 mm long), narrow; dorsal carina high and sharp, umbilical shoulders rounded to narrowly rounded; rugae distinct; growth lines pass over dorsal carina with little or no deflection; reticulate ornament distinct.

**Description.**—Shell small and narrow in form, umbilicus fairly wide. Aperture subquadrangular; dorsal carina well developed, high, and sharp; dorsal slopes concave for short distance near dorsal carina, becoming convex through most of their extent; umbilical shoulders rounded to narrowly rounded; ventral slopes flat to slightly concave. Rugae well developed, particularly at umbilical shoulder, over which they extend onto upper ventral slope; rugae thick and rounded at umbilical shoulder, becoming weaker dorsally to near dorsal carina. Growth lines generally at right angle to dorsal carina, but may be slightly deflected abaperturally; revolving threads of near equal strength to growth lines, together forming a distinct reticulate shell sculpture.

**Measurements.**—Measurements of three specimens, including the holotype, of *C. (C.) minor* are listed in table 28 and shown graphically in figure 29. The fourth set of measurements listed in table 28 were taken from Weller's (1903, pl. 12, figs. 6, 7) figure of the species from New Jersey. Although only a few specimens were available for measurement, growth appears highly coordinated, with high correlation values, but the regression lines do not approach the graph origins very closely. It is likely that this picture would change greatly with the measurement of more specimens.

**Material.**—Only three specimens of *C. (C.) minor* are known from the study area, the holotype (USNM 45787), a specimen from the Kope Formation (UC 19668), and a specimen from the Fairview Formation collected by Steve Felton of Cincinnati (UC 44275). All three specimens are calcitic casts, and the Kope specimen is encrusted by bryozoans.

**Distribution.**—The holotype (USNM 45787) is from the *Clitambonites* bed of the Prosser Formation at Cannon Falls, Minn., which Ulrich and Scofield (1897) considered the base of the "Trenton Series" and which Templeton and William (1963, figs. 19A-B) considered the basal beds and formation of the Galena Group. Weiss (1957) split off the lower Prosser into a new unit, the Cummingsville Formation, which Sweet and Bergstrom (1976, text-fig. 3) considered Kirkfieldian-Shermanian in age. Ross and others (1982) listed the Cummingsville and Prosser Members of the Galena Formation as Kirkfieldian to Shermanian in age. Weller (1903) reported the species from the "Trenton Series" of New Jersey. In Kentucky and Ohio, *C. (C.) minor* is known from the Kope Formation (Edenian) and the Fairview Formation (Maysvillian) in the vicinity of Cincinnati, Ohio.



TABLE 28.—Measurements (in millimeters) of *Cyrtolites* (*Cyrtolites*) *minor*

Museum No.	Shell length	Aperture length	Aperture width	Umbilical diameter	Ventral width	Wave length of rugae
USNM 45787	9.8	6.4	6.2	4.7	1.4	1.0
UC 19668	13.5	8.0	7.0	6.2	2.0	2.0
UC 44275	12.0	7.0	6.5	6.5	2.0	2.0
Weller (1903)	11.5	—	8.5	—	—	—

*Comparison.*—*C. (C.) minor* is quite similar in form to *C. (C.) ornatus*, of which it was originally considered a “variety” by Ulrich and Scofield (1897). However, *C. (C.) minor* is much smaller than *C. (C.) ornatus*, and there can be no doubt that the specimens assigned to *C. (C.) minor* are adults and not juveniles of the *C. (C.) ornatus*, as they possess at least two whorls and have well-developed rugae and reticulate shell sculpturing. Two observations have prompted me to regard *C. (C.) minor* as a distinct species. First, it is consistent in its forms over a wide geographic area (Minnesota to Kentucky to New Jersey) and through a distinct stratigraphic range

(Kirkfieldian-lower Maysvillian). Second, besides its smaller size, it differs from *C. (C.) ornatus* in its slightly narrower shell form, and by having the growth lines slightly deflected abaperturally over the dorsal crest (at least in the geologically older forms of the species), showing a possible transitional relationship with *C. (C.) retrorsus*.

It is easy to confuse *C. (C.) minor* with *C. (P.) carinatus* (pl. 7, figs. 18–25), as the general shell form of the two species can be quite similar. Both are small species having distinct dorsal carinae, and the two occur in the same stratigraphic interval (Edenian) in the study

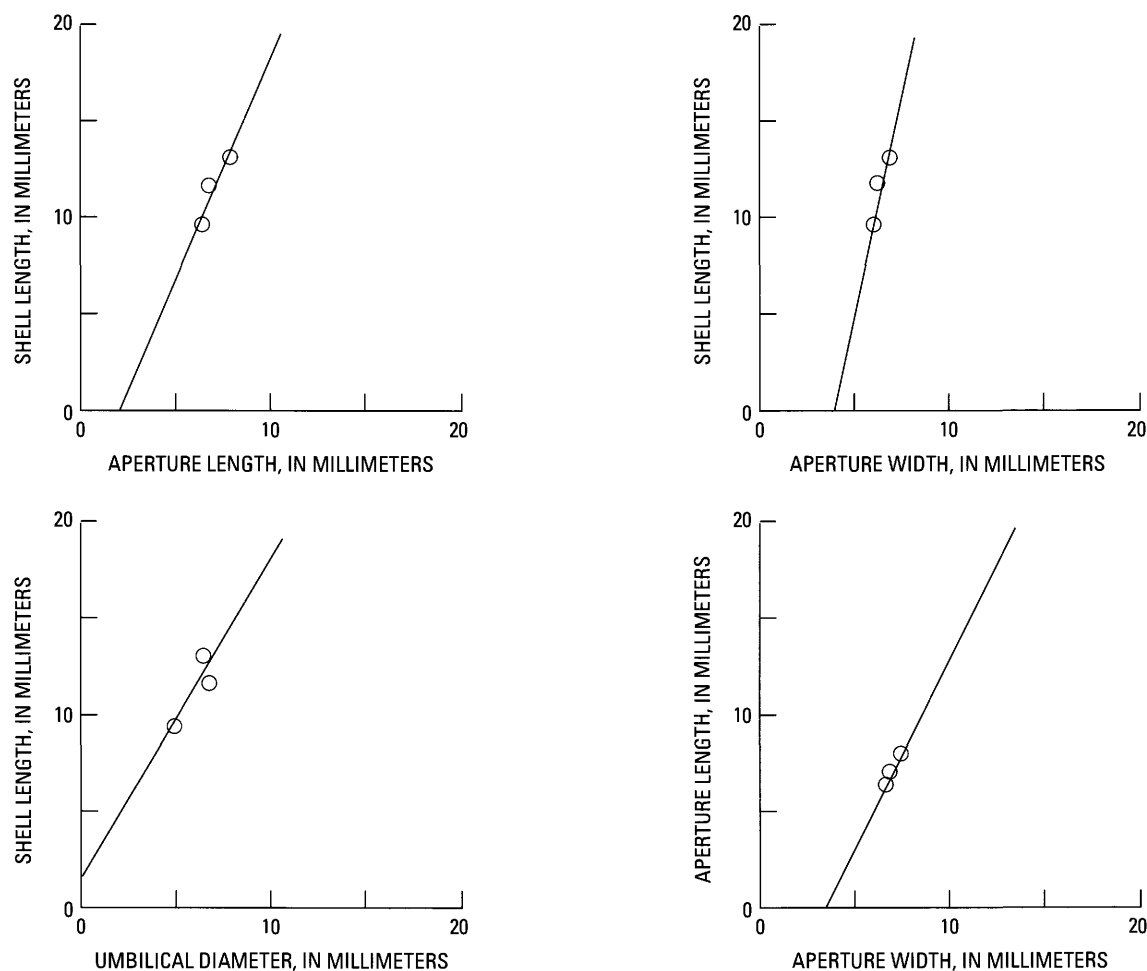
FIGURE 29.—Bivariate plots of measurements made on specimens of *Cyrtolites* (*Cyrtolites*) *minor*.

TABLE 29.—Measurements (in millimeters) of *Cyrtolites* (*Cyrtolites*) *hornyi*

USNM No.	Shell length	Aperture length	Aperture width	Umbilical diameter	Ventral width	Wave length of rugae	No. of growth lines per mm
265920	26.9	17.9	21.9	14.6	2.4	3.0	4
265921	22.7	14.5	17.2	11.35	2.7	3.0	4-5
265922	22.9	15.0	18.1	13.0	—	2-3	4
265978	12.8	8.65	10.4	7.0	—	—	—

area. *C. (P.) carinatus* differs in lacking rugae and a distinct reticulate ornament, as well as in having sharply angular to carinate umbilical shoulders.

*Discussion.*—*C. (C.) minor* may be an intermediate species between *C. (C.) retrorsus* and *C. (C.) ornatus*. Not only does the stratigraphic range of *C. (C.) minor* overlap with the upper part of the stratigraphic range of *C. (C.) retrorsus* and the lowest part of the range of *C. (C.) ornatus*, but the curvature of the growth lines of *C. (C.) minor* is also intermediate between these two other species. The holotype (pl. 7, figs. 2-4) of *C. (C.) minor* from the uppermost Champlainian strata (Prosser Formation) of Minnesota has surface markings that are essentially identical with those of *C. (C.) ornatus*, "except the transverse striae in crossing the dorsal carina are sometimes bent slightly backward" (Ulrich and Scofield, 1897, p. 861). Weller (1903, p. 174), in the description of his specimens from the "Trenton" of New Jersey, noted that the growth lines ran "almost straight across the volutions." The Cincinnati (Edenian and lower Maysvillian) specimens from the present study area appear to show no abapertural deflection of the growth lines dorsally (pl. 7, figs. 5-7, 8-10). Therefore, there appears to be a gradual evolutionary trend within the species *C. (C.) minor* toward the final and complete reduction of an apertural sinus in the *C. (Cyrtolites)* lineage.

#### *Cyrtolites* (*Cyrtolites*) *hornyi* new species

Plate 8, figures 1-10

*Diagnosis.*—Shell large (up to 27 mm long), with broad, angular shell form and relatively rapid rate of whorl expansion; aperture diamond shaped, dorsally and laterally sharply angular, dorsal and ventral slopes nearly flat; rugae thin, growth lines not deflected anteriorly over dorsum, revolving lines weak.

*Description.*—Shell relatively large for genus, having broad, angular form; relatively rapid rate of whorl expansion, whorls barely contiguous, even showing slight tendency toward uncoiling in largest specimens; adult shell with two or three whorls. Aperture quadrangular and diamond shaped; dorsal and ventral slopes slightly concave in juveniles, becoming nearly flat in adults; dorsum and umbilical shoulders slightly carinate in juveniles, becoming sharply angular in adults. Rugae

thin, distinct, with regularly spaced ridges, in many specimens forming nodes along umbilical shoulders and extending to near dorsal crest. Growth lines directed straight over dorsal crest of shell without any abapertural deflection, stronger than revolving connecting threads, so that reticulate surface sculpturing is not conspicuous.

*Measurements.*—Measurements of *C. (C.) hornyi* are listed in table 29 and shown graphically in figure 30. All parameters plotted for this species have very high correlation coefficients (nearly perfect), and the regression lines approach the graph origins closely. Although only four specimens were measurable, the species appears to have nearly isometric growth, as the ratios between the plotted parameters stay constant throughout growth.

*Type material.*—*C. (C.) hornyi* n. sp. is known from about 16 specimens, most of which are fragmentary, from USGS silicified collection 6139-CO, which is from the upper Dillsboro Formation along the southern bank of Salt Creek, 900 ft upstream from the covered bridge on Enochsburg-Oldenburg Road, in the New Point quadrangle, Indiana. The holotype (USNM 265920) (shell length 26.9 mm; aperture length 17.9 mm; aperture width 21.9 mm) is here designated the specimen shown on plate 8, figures 1-4. Two paratypes are also figured (USNM 265921 and 265922 on pl. 8, figs. 5-10). All other paratypes are placed together under the number USNM 265978.

*Distribution.*—The new species is known only from the single locality given above in the Richmondian part (upper Upper Ordovician) of the Dillsboro Formation of southeastern Indiana. The single sample came from the part of the Dillsboro Formation previously termed the "Liberty Formation" (and even earlier termed "the *Strophomena* beds"). This portion of the formation is referred to herein as the "Liberty biofacies."

*Comparison.*—*C. (C.) hornyi* is clearly distinguishable from all other Richmondian species of *Cyrtolites*. *C. (C.) ornatus* has a somewhat narrower, more rounded shell form, and its rugae are much more strongly expressed (pl. 6, figs. 1-18). *C. (C.) disjunctus* is even more distinct, being disjunctly coiled and even more rounded than *C. (C.) ornatus* (pl. 6, figs. 19-22). *C. (C.) hornyi* (pl. 8, figs. 1-10) most closely resembles *C. (C.) claysferryensis* (pl. 8, figs. 11-20). However, the whorl slopes of *C. (C.) hornyi* are much flatter, giving a

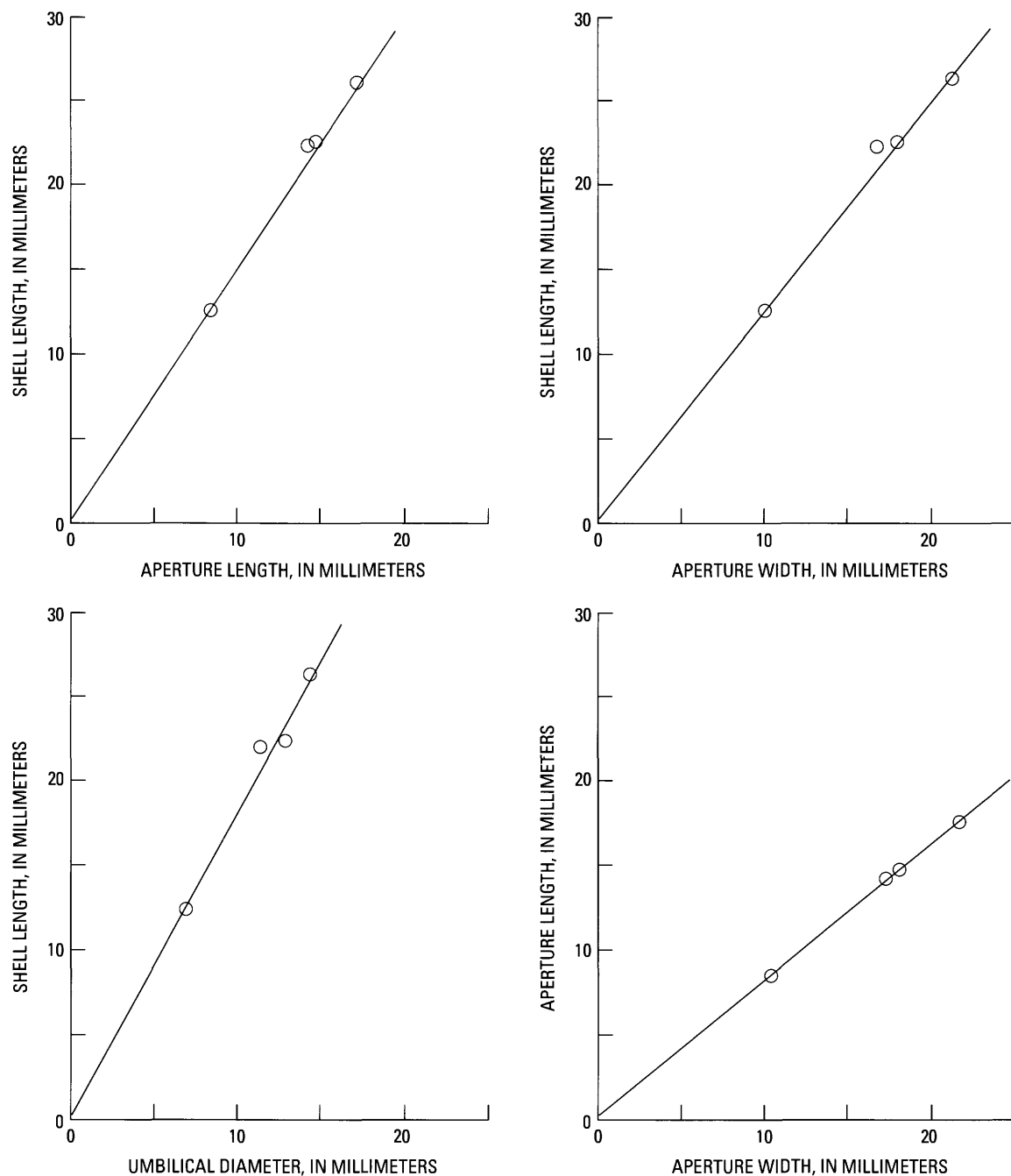


FIGURE 30.—Bivariate plots of measurements made on specimens of *Cyrtolites (Cyrtolites) hornyi* new species.

distinctly diamond shaped aperture, and its growth lines are straight rather than deflected abaperturally over the dorsal crest, demonstrating the lack of an apertural sinus as is clearly present in *C. (C.) claysferryensis*. Figures 28 and 30 show that the modes of growth in the two species are also very similar, the most striking difference being in the larger size attained by the Richmondian species.

*Discussion.*—*C. (C.) hornyi* almost certainly is descended from *C. (C.) claysferryensis*. Not only are the two species quite similar morphologically, but they apparently inhabited similar depositional environments (see "Discussion of subgenera"), which were characterized by intermittent carbonate and shale deposition. Both stratigraphic units in which the respective species are found are characterized in part by the presence of

TABLE 30.—Measurements (in millimeters) of *Cyrtolites* (*Cyrtolites*) *disjunctus*

USNM No.	Shell length	Aperture length	Aperture width	Umbilical diameter	Ventral width	Wave length of rugae	No. of growth lines per mm
45785	23.0	12.1	11.0	11.2	—	2-3	4-5

large, flat strophomenid brachiopods. Although it is not known whether either species inhabited these brachiopod communities, the widespread presence of these environments indicates a similar depositional system operating during deposition of the formations. I collected *C. (C.) claysferryensis* from two localities, one in the Clays Ferry Formation and one in the lower Kope Formation, and in both places the species was restricted to thin horizons characterized by almost entirely molluscan assemblages. Given our current knowledge, and considering the apparent rarity of *C. (C.) hornyi* and the lack of known intermediate Maysvillian forms, it is inferred that this species was more specialized in its habits than the more abundant Maysvillian-Richmondian-agespecies *C. (C.) ornatus*.

*Cyrtolites* (*Cyrtolites*) *disjunctus* Ulrich and Scofield, 1897

Plate 6, figures 19-22

*Cyrtolites disjunctus* Ulrich and Scofield, 1897, p. 864, pl. 62, figs. 48, 49.

[?] *Cyrtolites* cf. *C. disjunctus* Ulrich and Scofield, Wilson, 1951, p. 23, pl. 2, figs. 3, 4.

**Diagnosis.**—Shell with disjunct coiling; aperture ovoid; rugae well developed as rounded ridges; growth lines not deflected over dorsal crest, revolving threads of near equal strength with growth lines, and the two forming distinct reticulate surface sculpture.

**Description.**—Shell moderate in size for genus (up to 23 mm long), disjunctly coiled, whorls rapidly expanding in size; narrow in dorsal view. Aperture broadly ovoid, narrowing dorsally to a low dorsal carina; dorsal slopes convex; umbilical shoulders broadly rounded; ventral slopes convex and shorter than dorsal slopes. Ventral side of whorl bears revolving, elevated, tapering band, with squared-off raised margins bordering depressed central furrow. Rugae strongly developed as broadly rounded ridges, which extend from lower ventral slopes to near dorsal carina. Distinct reticulate shell ornament formed by straight growth lines, which are not deflected abaperturally over dorsal crest, and revolving connecting threads of equal strength. Shell thin.

**Measurements.**—Measurements of the holotype of *C. (C.) disjunctus* are listed in table 30.

**Material.**—The only known specimen of this species is the holotype (USNM 45785), but that single specimen preserves the shell and its markings excellently.

**Distribution.**—The holotype is from Upper Ordovician strata near Spring Valley, Minn. Wilson (1951) reported *Cyrtolites* cf. *C. disjunctus* from the Rockland beds (Rocklandian-upper Middle Ordovician) of the Ottawa-St. Lawrence Lowland, Canada, but emphasized: "The specimens at hand are too poorly preserved for certain identification, but they show the free final whorl." She figured only a copy of the drawing of the holotype given by Ulrich and Scofield (1897, pl. 62, figs. 48, 49), and did not show any of her material. I doubt very strongly that Wilson's specimens belong to *C. (C.) disjunctus*, mainly because of their much lower stratigraphic position. I suspect that she might have been looking at internal molds of another species of *Cyrtolites*, many of which, because of the loose coiling of the genus, are disjunct (see pl. 7, fig. 1, for an example of a disjunct internal mold of *C. (C.) ornatus*).

**Comparison.**—Even though *C. (C.) disjunctus* is not known from the Cincinnati arch region, it is treated herein so that it could be compared with the disjunct internal molds of *C. (C.) ornatus*, which are quite common in the Upper Ordovician of the study area (pl. 6, fig. 18; pl. 7, fig. 1). The whorls of *C. (C.) disjunctus* expand at a different and somewhat more rapid rate, and the volutions increase their distance from the axis of coiling at a much higher rate. This mode of coiling results in a shell having a relatively small initial whorl and a relatively large adult whorl that is exposed on all sides, including the venter. Moreover, the ovoid whorl shape of *C. (C.) disjunctus* is much more rounded.

**Discussion.**—It is important to note that *C. (C.) disjunctus* retains the ventral "saddle" on the venter of the whorl which would fit over the dorsal crest of the preceding whorl in conjunctly coiled species (pl. 6, figs. 20, 22). This would seem to indicate that this species developed directly from a conjunct species. *C. (C.) ornatus* most likely is the ancestor. The two species have similar whorl shapes, although *C. (C.) disjunctus* has more rounded umbilical shoulders. Their external sculpturing is especially similar. Both have well-developed, thick, ridgelike rugae and a distinct reticulate sculpture pattern, with nearly equally strong, straight growth lines and revolving threads. Furthermore, some gerontic specimens of *C. (C.) ornatus* show a tendency to uncoil in the last quarter-whorl or so. Disjunct coiling is generally considered an adaptation to a more sessile mode of life

in the Gastropoda, and this may also apply to the Monoplacophora.

**Subgenus CYRTOLITES (PARACYRTOLITES) new subgenus**

*Description*.—Shell having no rugae developed on whorl slopes, and having no, or only weakly developed, reticulate ornament. Aperture sinuate, with V-shaped growth lines deflected abaperturally over dorsal crest of shell.

*Distribution*.—Kirkfieldian (upper Middle Ordovician)-Edenian (lower Upper Ordovician) of Eastern North America.

*Type species*.—*C. (P.) subplanus* Ulrich in Ulrich and Scofield, 1897.

*Other species*.—*C. (P.) subplanus* Ulrich in Ulrich and Scofield, *C. (P.) carinatus* Miller, and *C. (P.) parvus* Ulrich in Ulrich and Scofield.

**Cyrtolites (Paracyrtolites) subplanus Ulrich, 1897**

Plate 7, figures 26–35; Plate 8, figures 22–27

*Cyrtolites subplanus* Ulrich in Ulrich and Scofield, 1897, pl. 62, figs. 40–44; Bassler, 1932, pl. 20, figs. 8, 9; not Foerste, 1924, p. 204, pl. 34, fig. 5; not Wilson, 1951, p. 23, pl. 2, figs. 5, 6.

*Diagnosis*.—Shell medium in size (up to 12.4 mm long), narrow, rounded; umbilicus small and nearly circular; aperture subquadrangular, dorsum sharply rounded, dorsal slopes and umbilical shoulders rounded, ventral slopes flat to slightly concave; no distinct rugae developed; growth lines fine, deflected strongly abaperturally over dorsum, revolving threads weak or lacking.

*Description*.—Shell medium in size for genus, narrow in dorsal view, rather tightly coiled; umbilicus relatively small, nearly circular. Aperture rounded, subquadrangular, height and width nearly equal; dorsum sharply rounded with no carina developed, dorsal slopes gently convex, umbilical shoulders rounded, ventral slopes flat to slightly concave. Dorsal slopes smooth, lacking distinct rugae, but may have some gentle wrinkling, particularly near aperture of larger specimens. Growth lines fine but distinct, becoming slightly stronger with growth; lines turn sharply abaperturally over dorsum, increasing in angle near crest, reflecting relatively deep labral sinus. Very faint revolving connecting threads, barely visible on adult specimens, not distinct enough to create reticulate pattern, but can give a faint impression of pitting. Shell thin.

*Measurements*.—Measurements of the types of *C. (P.) subplanus* are listed in table 31. Because the species is relatively thin shelled and therefore is not generally completely preserved, the measurements are open to greater error than those of thicker shelled species. Although it is difficult to determine actual proportions of the species and their variation, the measurements should

TABLE 31.—Measurements (in millimeters) of *Cyrtolites* (Paracyrtolites) subplanus

USNM No.	Shell length	Aperture length	Aperture width	Umbilical diameter
45792	—	13.3	12.1	—
265914	12.4	—	7.5	6.3

be accurate enough to give a general impression of size and trends.

*Material*.—Ulrich and Scofield's (1897) types include two silicified specimens (USNM 45792) collected from the Bigby-Cannon Formation at Snow's Hill, 4 mi east of Liberty, Tenn. A note in the box containing the two types indicates that the specimens came from the *Lophospira sumnerensis* zone of the "Upper Trenton." Wilson (1949, p. 129) listed *L. sumnerensis* as a typical fossil of the Cannon facies of the Bigby-Cannon Formation. The larger of these two types is here designated the lectotype (USNM 45792) (pl. 7, figs. 26, 27); the other is designated the paralectotype (USNM 265914) (pl. 7, figs. 28, 29). It is noted that Ulrich and Scofield (1897, pl. 62, figs. 40–43) showed a partial reconstruction of the lectotype.

The species was recognized for the first time in Kentucky from USGS silicified collections D-1196-CO from the Logana Member and 4852-CO from the Grier Limestone Member of the Lexington Limestone. The best of these specimens is from the Logana collection (pl. 7, figs. 30–32, 34) (USNM 265915); it preserves the aperture shape and surface ornament very well. Specimen USNM 265917 (pl. 8, fig. 27) also comes from this collection. The collection from the Grier Limestone Member includes forms that compare favorably with *C. (P.) subplanus*. Specimens USNM 265918 (pl. 7, fig. 33) and USNM 265916 (pl. 8, figs. 22–24) are fragmentary, and their shells seem a bit too broad for the species. Specimen USNM 265919 (pl. 8, figs. 25, 26) has the same features, but is also worn nearly smooth and is bored.

*Distribution*.—The species is known from strata of Kirkfieldian-Shermanian ages (late Middle Ordovician) in Tennessee and Kentucky. In Tennessee the species is known from the Cannon facies of the Bigby-Cannon Formation, according to the label with the types and to Wilson (1949). Bassler (1915) listed the species from the Catheys Formation (Shermanian-Edenian). Foerste (1924, p. 204) confirmed the occurrence of the species in the Catheys, and he further cited a possible specimen from Edenian strata of Manitoulin Island, Canada. He did not figure the latter specimen, but from his description it is more like *C. (P.) carinatus*, having angular umbilical shoulders. In Kentucky *C. (P.) subplanus* is known for certain from the Logana Member (Kirkfieldian) of the Lexington Limestone, and probably also from

the Grier Limestone Member (early Shermanian) of the same formation.

*Comparison.*—This distinctive species is separable from the cooccurring *C. (C.) retrorsus* (pl. 5, figs. 1–26) in several ways: it is narrower in dorsal view (pl. 7, figs. 27, 29, 30); it has a nearly smooth, rounded, but not inflated form, lacking rugae (pl. 7, figs. 26, 28, 32); the dorsal crest of the shell (pl. 7, figs. 34, 35) has a more deeply cut V-shaped sinus; and the short, revolving connecting threads between the growth lines are so weak that there is no apparent reticulate sculpture.

*Discussion.*—Bassler (1915, p. 386) listed a page number in Ulrich and Scofield's (1897) on which the original description of the species is supposed to be found, and the latter authors gave the same page reference in their plate description for the species. However, there is no description of *Cyrtolites subplanus* on that or any other page in Ulrich and Scofield (1897), so the new species was only figured by them. Therefore, the description given herein is the first published for the species. This is the oldest species known for *C. (Paracyrtolites)* and is the type species for the subgenus. It is believed to be ancestral to the Edenian species *C. (P.) carinatus* and *C. (P.) parvus*.

The ecological requirements of the *C. (P.) subplanus* species appear to have been the same as for *C. (C.) retrorsus*, with which it cooccurs in USGS silicified samples D-1196-CO from the Logana Member and 4852-CO from the Grier Limestone Member of the Lexington Limestone.

***Cyrtolites (Paracyrtolites) carinatus* Miller, 1874**

Plate 7, figures 18–25; Plate 8, figure 21

*Cyrtolites carinatus* Miller, 1874, p. 311, fig. 32; Miller, 1889, p. 401, text-fig. 67; Ulrich and Scofield, 1897, p. 862, pl. 62, figs. 50–51; Grabau and Shimer, 1909, p. 610, figs. 815e–g; Foerste, 1924, p. 205, pl. 34, figs. 2a–c, pl. 35, figs. 5a, b

*Diagnosis.*—Shell moderate in size (up to 22 mm long), angular, narrow; aperture quadrangular and nearly equidimensional; dorsal carina high and sharp, lateral carinae not as prominent, dorsal and ventral whorl slopes essentially flat; distinct rugae lacking; growth lines very fine, swing abaperturally over dorsum; revolving threads very faint.

*Description.*—Shell moderate in size; form angular and narrow, tightly coiled; umbilici large, open, and nearly circular. Aperture quadrangular; dorsum with high, sharp carina; lateral angles with low, sharp carinae; dorsal whorl slopes nearly flat, but can be slightly convex or concave; ventral whorl slopes flat to slightly concave. Distinct rugae lacking, but weak wrinkling of shell visible on dorsal slopes of some specimens, particularly in gerontic specimens. Growth lines very fine and closely spaced, swinging gently abaperturally over dorsum;

TABLE 32.—*Measurements (in millimeters) of Cyrtolites (Paracyrtolites) carinatus*

Museum No.	Shell length	Aperture length	Aperture width	Umbilical diameter	Ventral width
USNM					
49993	22.00	14.30	11.6	11.0	3.0
265913	17.95	10.25	12.2	8.7	3.5
265912	13.05	7.00	7.6	7.5	2.1
265911	8.20	5.60	6.0	5.0	1.1
47499	12.90	—	7.2	7.3	—
45783	13.80	9.25	8.7	6.9	2.5
45783	11.25	—	—	—	—
45783	11.10	—	—	6.7	—
UCGM					
44277	12.5	7.3	7.0	6.9	2.1
44278	12.8	7.4	7.4	6.2	2.5
44279	13.1	—	—	7.2	—

revolving threads lacking or very faintly developed, particularly in immature specimens.

*Measurements.*—Measurements of *C. (P.) carinatus* are listed in table 32.

*Material.*—No specimens of this species were recognized in the new USGS silicified collections. The holotype (pl. 7, figs. 18, 19) is specimen UC 8895. Twelve specimens listed under three museum numbers (USNM 45783, 47499, 49993) and labeled as Ulrich and Scofield's (1897) "plesiotypes" were also examined. Four specimens from suite 47499 are figured herein: USNM 265913 (pl. 7, figs. 24, 25), which is a fairly large specimen with part of the shell preserved; USNM 265912 (pl. 7, fig. 21); USNM 265911 (pl. 7, fig. 23); and USNM 47499 (pl. 7, fig. 22). The largest specimen, USNM 49993, is not figured; nor are specimens of the suite USNM 45783. This collection of specimens was labeled as being from the Kope Formation (Edenian) at Newport, Ky.

A few specimens of the species were found in the University of Cincinnati Geological Museum under UCGM 19658. Steve Felton of Cincinnati made a number of specimens from the Kope Formation near Carrollton, Ky., available. These latter specimens were collected from a thin bed made up almost entirely of a molluscan assemblage (pl. 8, fig. 21). These calcitic specimens are UCGM 44277 (pl. 7, fig. 20), UCGM 44278, and UCGM 44279 (pl. 8, fig. 21). These specimens are better preserved than any others examined.

*Distribution.*—Ulrich and Scofield (1897) stated that the species was to be found in the lower shales of the Cincinnati in the Cincinnati, Ohio, area, as well as probably in Wisconsin, Iowa, and Minnesota. More recent collections confirm that the species appears restricted to the Kope Formation (Edenian) of the study area. Foerste (1924) reported the species from the Edenian Sheguiandah Formation on Manitoulin Island, Ontario, Canada.

*Comparison.*—This species can be distinguished from all other species of *C.* (*Paracyrtolites*) by its possession of both dorsal and lateral carinae. It does resemble *C.* (*C.*) *claysferryensis*, but it (1) does not attain as large a size, (2) lacks distinct rugae on the whorl slopes, (3) has finer growth lines, and (4) has such fine revolving lines that they are generally not even discernible.

*Discussion.*—Miller (1874) did not mention any revolving connecting threads in his original description of the species, but Ulrich and Scofield (1897, p. 863) observed a faint but distinct reticulate pattern on the inner volutions of some well-preserved specimens. They claimed that the connecting threads are present in young growth stages, but become weaker through growth and are removed by even minimal abrasion.

To my knowledge, *C.* (*P.*) *carinatus* always occurs in a molluscan assemblage in thin limestone beds of the Kope Formation (pl. 8, fig. 21). The molluscan association recalls the usual occurrence of *C.* (*C.*) *claysferryensis* and *C.* (*C.*) *ornatus*.

*Cyrtolites* (*Paracyrtolites*) *parvus* Ulrich, 1897

Plate 7, figure 17

*Cyrtolites parvus* Ulrich in Ulrich and Scofield, 1897, p. 846, pl. 62, figs. 45–47; Foerste, 1924, p. 204–205, pl. 34, figs. 4a, b.

*Description.*—Shell small (up to 8.5 mm long), tightly coiled; umbilicus relatively small. Aperture subquadrangular; dorsum with low carina; dorsal slopes gently convex; umbilical shoulders rounded; ventral slopes nearly flat. Rugae absent. Growth lines fine but distinct, swinging abaperturally over dorsum; no revolving threads known.

*Measurements.*—The only measurements possible on the single specimen examined were shell height (8.55 mm) and maximum umbilical diameter (3.75 mm).

*Material.*—The only specimen available is the holotype, USNM 45788, which is a small, rather poorly preserved calcitic cast (pl. 7, fig. 17).

*Distribution.*—The holotype, USNM 45788, is from “near the top of the Trenton group at Covington, Kentucky,” according to a museum label. The specimen most likely was collected before the submergence of sub-Kope (Edenian) outcrops along the Ohio River Valley near Cincinnati by the damming of the Ohio River. In present-day stratigraphic nomenclature, these beds probably would be assigned to the Point Pleasant Tongue of the Clays Ferry Formation of latest Shermanian age. Foerste (1924, p. 204) cited the species as from the “Cynthiana Formation,” now included in the Clays Ferry Formation, at Covington, Ky. He also noted specimens “resembling this species” in the Maysvillian strata of Manitoulin Island, Ontario, Canada.

*Comparison.*—Ulrich and Scofield (1897) claimed that this species is characterized by stronger surface markings than any other member of the genus. The holotype does not support this contention (pl. 7, fig. 17). The holotype bears some resemblance to small specimens of *C.* (*C.*) *retrorsus* (pl. 5, figs. 1, 2), but is less carinate dorsally and laterally than juveniles of that species, and also than juveniles of *C.* (*P.*) *carinatus*.

*Discussion.*—The holotype of this species does not support the contention in the original description that the species bears stronger surface markings than any other species of the genus. Because the holotype does not support the original description, the validity of the species may be suspect. Nevertheless, the single, rather poorly preserved specimen does not fit readily into any other known species, so the name *C.* (*P.*) *parvus* is retained herein. On the basis of the faint ornament of the holotype, the species is placed in the subgenus *C.* (*Paracyrtolites*).

Family SINUITIDAE Dall in Eastman, 1913

*Diagnosis.*—Shell tightly involute to convolute; umbilicus moderately small to lacking; whorls rounded to globose; sinus relatively wide, U-shaped to rounded V-shaped; lateral apertural margins rounded to distinctly lobate; surface markings generally very fine col-labral lines; thin inductural deposits in some cases extending slightly beyond parietal area.

*Stratigraphic range.*—As defined, in the Ordovician the family is known with certainty from Blackriveran-Richmondian-age strata in Eastern North America. However, it may extend into the Lower Ordovician (Bassler, 1915, p. 1160, 1161). Rollins and Batten (1968) reported the genus *Sinuitopsis* from Devonian rocks.

*Genera included.*—*Sinuities* Koken, 1896; *Sinuitopsis* Perner, 1903; *Strangulites* Horny, 1962; *Sylvestrosphaera* Peel, 1980.

*Discussion.*—As defined herein, the family Sinuitidae is more restricted than ever before and consists of four closely related genera. Previously, authors such as Knight and others (1960) included many genera that had little more in common with *Sinuities* and its phylogenetic allies than a similarly shaped sinus. With the discovery of discrete paired muscle scars in *Sinuitopsis*, *Sinuities*, and *Sylvestrosphaera* by Rollins and Batten (1968), Peel (1980), and Runnegar (1982), these genera were transferred to the Monoplacophora. Muscle scars are not yet known in *Strangulites*. The other genera previously placed in the Sinuitidae by Knight and others (1960) and Horny (1963a) are tentatively assigned to the Bucanellidae of the superfamily Bellerophonacea. Runnegar and Jell (1976, p. 121) included such genera as *Cloudia* and *Strepsodiscus* in the Sinuitidae, but I do not think these



genera are evolutionarily closely related to the sinuitid genera cited herein.

**Genus SINUITES Koken, 1896**

*Diagnosis.*—Shell tightly coiled, convolute, umbilicus closed or very small; dorsum generally rounded, flattened somewhat in some cases, with dorsomedian ridge in very few; aperture large, generally longer than wide, with deep, rounded, median sinus and lateral margins projecting downward as rounded or subangular lobes; parietal deposits thin, ornamented in many cases; growth lines fine, closely spaced, in many cases intersected by faint revolving lines.

*Type species.*—*Bellerophon bilobatus* Sowerby, 1839, by subsequent designation of Bassler (1915, p. 1159).

*Distribution.*—Middle and Upper Ordovician of North America, Europe, and North Africa.

*Comparison.*—Most species placed in the genus *Sinuities* are quite distinctive, and confusion with other genera is likely only when poorly preserved internal molds are encountered. In that case, there may be confusion with species of *Sphenosphaera* Knight or *Bellerophon* Montfort.

Knight and others (1960, p. I177) treated *Sinuitopsis* Perner as a subgenus of *Sinuities*, but Horny (1963a, p. 76, 77) strongly contested this assignment. He claimed that their hand-drawn figures 93/7a, b (Knight and others, 1960, p. I176) misinterpreted the lateral lobes of *Sinuitopsis*, and show a circumumbilical structure not present in the type species or related species. Important features distinguishing *Sinuitopsis* are its higher, rounder shell shape on lateral view, its distinctly open umbilicus, its rounded, but not lobate, lateral apertural margins, and its narrower apertural sinus.

Horny (1962, p. 473; 1963a, p. 75) proposed the genus *Strangulites*, stating that it differs from *Sinuities* by having more rounded, closely involuted whorls with characteristic deep constrictions of the adult body whorl. He noted (1963a) that a number of the British Upper Ordovician species of *Sinuities* described by Reed (1921) also bear body whorl constrictions, but that these species are laterally compressed and have lobate lateral apertural margins. The type species, *Strangulites strangulatus* (Perner), is certainly globose, but no more so than the Kentucky species *Sinuities obesus* (Ulrich) (compare Horny, 1963a, pl. 6, figs. 1-3, with pl. 9, figs. 1-12, herein). Furthermore, Horny's (1963a, pl. 6, fig. 2, and pl. 5, fig. 4) figures seem to show that the lateral lips of *S. strangulatus* actually are mildly lobate (note growth lines). Horny admitted that *Strangulites* might be considered a subgenus of *Sinuities*. It is concluded here that the two are synonymous.

*Discussion.*—Species of *Sinuities* described prior to 1896-97 were generally assigned to *Bellerophon*. Koken

(1896, p. 392) erected the new genus *Sinuities* to contain European Ordovician species. Unaware of this new genus, Ulrich and Scofield (1897, p. 848) proposed the genus *Protowarthia* for American species. Bassler (1915, p. 1159) recognized the synonymy and the priority of *Sinuities* Koken, and formally designated *Bellerophon bilobatus* Sowerby the type species of *Sinuities*. Reed (1921, p. 5) pointed out that "unfortunately, the species *B. bilobatus* has been made to comprise a somewhat miscellaneous assortment of forms, and the customary usage of the specific name has become loose and unsatisfactory." Therefore, he subdivided *B. bilobatus* into three new species and restricted the definition of the original taxon.

The American species *Sinuities cancellatus* (Hall) may be plagued by the same problem pointed out by Reed for *S. bilobatus*. Specimens of *Sinuities* are fairly common in the Upper Ordovician of the Cincinnati arch region, but just as in other areas of occurrence, these specimens are nearly always internal molds. *S. cancellatus* has become the usual receptacle for these specimens. At least three subspecies have been named (Bassler, 1915, p. 1159), but their validity is questionable (see discussions of species below).

The genus *Sinuities* is greatly in need of a comprehensive specific review. It is an important taxon not only because of its broad geographic and stratigraphic distribution and its relative abundance in some strata, but also because of its phylogenetic significance (see sections on "Functional Morphology" and "Phylogeny and Classification").

***Sinuities pervoluta* (Ulrich and Scofield, 1897)**

*Protowarthia pervoluta* Ulrich and Scofield, 1897, p. 871, pl. 63, figs. 21-27; Grabau and Shimer, 1909, p. 611, figs. 817d-f.

*Sinuities pervolutus* (Ulrich and Scofield), Bassler, 1915, p. 1160.

*Diagnosis.*—Shell small (less than 15 mm long), tightly enrolled, rather globose; dorsum uniformly rounded, without ridge or flattening; aperture wider than long; parietal deposits granistriate; growth and revolving lines exceedingly fine.

*Material.*—The type material (USNM 45968-45970) was adequately illustrated by Ulrich and Scofield (1897, pl. 63, figs. 21-27) and is not figured herein. No new material is known.

*Distribution.*—Ulrich and Scofield (1897, p. 871) listed the species from the "Black River group and in the lowest bed (*Orthis* or *Modiolodon* bed) of the Trenton group" in Kentucky and equivalent strata in Minnesota (Decorah Formation). In modern terms, the Kentucky occurrences are in the Tyrone Limestone (Rocklandian) and the Logana Member of the Lexington Limestone (Kirkfieldian).

TABLE 33.—Measurements (in millimeters) of *Sinuities cancellatus*

UCGM No.	Shell length	Shell height	Aperture length	Aperture width	Dorsal width	Posterior width	Ventral width	Sinus depth	Sinus width
44304	24.4	16.3	16.3	21.9	14.4	11.8	9.7	10.8	14.2
44307	24.6	16.5	17.4	21.0	16.0	13.7	—	9.8	9.9

*Comparison.*—Ulrich and Scofield (1897, p. 871) noted that *S. pervoluta* might be a “variety” of *S. granistriatus* (Ulrich). However, *S. pervoluta* is smaller (the shell being less than 15 mm long), more tightly coiled, and more globose, and has a wider aperture than *S. granistriatus*. *S. pervoluta* also lacks a dorsal ridge or a flattening of the dorsum.

In their discussion of *S. obesus* (Ulrich), Ulrich and Scofield (1897, p. 875) stated: “Very young specimens may look much like the largest of *P. pervoluta*, but the adult form, which is all we have seen, is certainly quite distinct.” A number of small specimens of a globose species of *Sinuities* were found in USGS silicified samples 5023-CO, 5084-CO, and 5100-CO from the Curdsville Limestone Member of the Lexington Limestone. These small, poorly preserved silicified specimens are probably not *S. pervoluta*, because some show a small umbilicus, as cited for *S. obesus*; as a result, they were placed in the latter species. Unless well-preserved material is available, juveniles of *S. obesus* and adults of *S. pervoluta* are extremely difficult to distinguish.

*Sinuities cancellatus* (Hall), 1847

Plate 11, figures 6–12

*Bellerophon bilobatus* Emmons (not Sowerby), 1842, p. 392, fig. 6; Hall, 1847, p. 184, pl. 40, figs. 3a-d; Miller, 1874, p. 306; Lesley, 1889, p. 81, figs.; Miller, 1889, p. 396, fig. 652.

*Cyrtolites bilobatus* Emmons, 1855, p. 166, figs. 2, 3, 22, 24; pl. 17, fig. 10c.

*Bellerophon cancellatus* Hall, 1847, p. 307, pl. 83, figs. 10a-c.

*Protowartha cancellata* (Hall), Ulrich and Scofield, 1897, p. 872, pl. 63, figs. 1–14; Weller, 1903, p. 175, pl. 12, figs. 3–5; Cumings, 1908, p. 971, pl. 39, figs. 6a, b; Grabau and Shimer, 1909, p. 611, figs. 817g-i; Knight, 1941, p. 279, pl. 6, figs. 3a, b.

*Sinuities cancellatus* (Hall), Bassler, 1915, p. 1159; Bassler, 1919, p. 313, pl. 50, figs. 37–39; pl. 55, figs. 12–21; Foerste, 1924, p. 205, pl. 34, fig. 6; Ruedemann, 1926, p. 62, pl. 8, fig. 6; Bassler, 1932, pl. 21, figs. 16–18; Shimer and Shrock, 1944, p. 441, pl. 176, figs. 24, 25; Wilson, 1951, p. 25, pl. 2, figs. 11, 12; Caster, Dalve, and Pope, 1955, pl. 1, figs. 16, 17; Pope and Martin, 1977, pl. 1, figs. 16, 17.

*Diagnosis.*—Shell medium in size, smoothly rounded dorsally and laterally, subglobose, involute, umbilicus closed; sinus moderately shallow, lateral aperture lobes well rounded; growth lines fine, revolving lines even finer.

*Description.*—Shell medium in size (adult about 25 mm long), involute, with closed umbilicus, generally subglobose, smoothly rounded dorsally and laterally, degree of convexity variable. Sinus moderately shallow, V-shaped,

having well-rounded apex; lateral apertural margins merge into well-rounded lobes. Aperture distinctly wider than long. Parietal inductura thin, folding over venter of coil onto umbilical region, marked by fine, wavy revolving lines. Shell ornament of fine, closely spaced growth lines crossed by even finer revolving lines, giving a faint cancellate appearance.

*Measurements.*—Measurements of *S. cancellatus* are listed in table 33.

*Material.*—The holotype was adequately figured by Knight (1941, p. 6, fig. 3a). Specimens preserving the shell examined here are UCGM 44304 and UCGM 44307. Numerous internal molds of the species, most of which are unnumbered, were examined in the collections of the geology museums of the University of Cincinnati and Miami University.

*Distribution.*—The species has been reported from “Trenton through Richmond groups” (Kirkfieldian-Shermanian to Richmondian) throughout the eastern half of the United States and Canada (Ulrich and Scofield, 1897; Bassler, 1915; Shimer and Shrock, 1944). Herein, the species is recognized from Shermanian- through Richmondian-age strata in the Cincinnati arch region.

*Comparison.*—*S. cancellatus* is distinguished from *S. planodorsatus* (Ulrich) and *S. granistriatus* (Ulrich) by its smoothly rounded dorsum, being neither flattened nor bearing a ridge. It is further distinguished from these species, as well as from *S. rectangularis* (Ulrich and Scofield), by its more broadly rounded lateral aperture lobes and its shallower apertural sinus.

*Discussion.*—*S. cancellatus* is long ranging stratigraphically and widely distributed geographically for species of *Sinuities*. It is difficult to evaluate the species properly without examining specimens from its entire distribution. All specimens examined for this study were from the Shermanian- through Richmondian-age strata of the Cincinnati arch province. Nearly all were internal molds, and none of the few specimens retaining the shell preserved the shell ornament satisfactorily. Furthermore, many of the internal molds were badly compressed, apparently owing to the animal's thin, probably aragonitic shell, which must have dissolved prior to compaction of the generally fine grained encasing sediment. Such specimens are commonly weathered out of Cincinnati shales.

Even dealing only with Cincinnati arch material, and mainly with internal molds, the morphological variation

of specimens included in this species was quite apparent. However, no consistent pattern could be discerned which could provide a basis for subdividing *S. cancellatus* with confidence. A number of subspecies have been named by previous authors. Bassler (1915, p. 1159) recognized *S. cancellatus acutus* (Hall, 1847) and *S. cancellatus corrugatus* (Hall, 1847). These were originally named subspecies of *S. bilobatus* Emmons, which was placed in synonymy with *S. cancellatus* by Bassler. Ulrich and Scofield (1897, p. 872) named *S. cancellatus trentonensis* for specimens from the "Trenton group" which "are almost constantly a trifle more narrowly rounded dorsally than is the geologically higher typical form of the species." It should be noted that the species was originally described from the Trenton Group of New York, so the Trenton material is actually "typical." Wilson (1951) persisted in using *S. bilobatus corrugatus* (Hall), and named two new subspecies, *S. cancellatus angularis* and *S. cancellatus liratus* (the latter being equivalent to *S. cancellatus acutus*). I do not believe any specimens bearing a dorsal ridge should be included in *S. cancellatus*, and therefore I regard *S. liratus* Wilson as a distinct species. However, based on her illustration, the specimen's placement in *Sinuities* is uncertain.

In the Cincinnati arch material, three general variants of *S. cancellatus* are recognized as end members in a maze of morphological gradations. The first end member would be placed in *S. cancellatus corrugatus* (Hall) of some authors. However, the distal corrugations of this variant are variable in strength and number (1-3) and were seen only in internal molds. Furthermore, corrugated specimens occur in collections in which most of the internal molds lack corrugations, and I strongly suspect that the corrugations are the result of compaction. The other two variants have more narrowly rounded (*S. cancellatus acutus*) or more broadly rounded (*S. cancellatus cancellatus*) dorsal shell forms (pl. 11, figs. 10-12 and 6-9, respectively). Even though these two general forms were seen in specimens preserving the shell as well as in internal molds, there was much gradation between the two end members, and such a feature can be influenced by compaction. Therefore, at present it is not possible to subdivide *S. cancellatus* from the Cincinnati arch region into subspecies, and *S. cancellatus acutus*, *S. cancellatus corrugatus*, *S. cancellatus trentonensis*, and *S. cancellatus angularis* are treated as synonyms of *S. cancellatus cancellatus*.

The specimens shown herein (pl. 11, figs. 6-12) are slightly worn and preserve only a trace of the growth lines. Knight (1941, pl. 6, fig. 3a) illustrated the holotype, which although unfortunately distorted by crushing, preserves the cancellate shell ornament very well. Knight's (1941, pl. 6, fig. 3b) hypotype has the more typical preservation.

### *Sinuities obesus* (Ulrich), 1897

Plate 9, figures 1-12

*Protowarthia obesus* Ulrich in Ulrich and Scofield, 1897, p. 874, 875, pl. 63, figs. 45-47. *Sinuities obesus* (Ulrich), Bassler, 1915, p. 1160.

**Diagnosis.**—Shell large (up to 36 mm long), obese; umbilicus closed; sinus broad and shallow, lateral lobes rounded.

**Description.**—Shell large, involute, with umbilicus closed; whorl form obese, broadly and uniformly rounded; dorsum smooth. Aperture distinctly wider than long, fairly semicircular in outline around outer margins, inner margins angling inward. Aperture lip thickened near contact with coil, thinning outward around periphery. Parietal deposits quite thin, ornamentation unknown. Sinus broad, moderately shallow; lateral lobes broadly rounded. Growth lines very fine.

**Measurements.**—As seen on plate 9, figures 1-12, specimens of this species are generally too badly fragmented for many reliable measurements. Measurements listed in table 34 are meant to give only general relative dimensions.

**Material.**—Ulrich and Scofield's (1897, p. 874, 875, pl. 63, figs. 45-47) type specimens (USNM 45961, 45962) are internal molds from the Curdsville Limestone Member of the Lexington Limestone.

New USGS silicified material from Kentucky comes from the Curdsville Limestone Member (4940-CO, 5022-CO, 5023-CO, 5072-CO, 5084-CO, 5100-CO, and 7785-CO) and the Logana Member (4865-CO, 5073-CO, 5086-CO, 5092-CO, 6419-CO, and 7791-CO) of the Lexington Limestone. Essentially all silicified specimens are incomplete, so that accurate counts and measurements were not possible. The most prolific samples (5092-CO, 6419-CO, and 7791-CO) contained more than 100 specimens and fragments. Specimens cataloged under USNM 315634, 315635, 315636, and 315637 were selected for illustration herein (pl. 9, figs. 1-12).

**Distribution.**—The species occurs in the Curdsville Limestone and Logana Members of the Lexington Limestone (Kirkfieldian), and is currently known only from central Kentucky.

**Comparison.**—In the smooth roundness of the whorls, *S. obesus* matches *S. cancellatus*, but *S. obesus* is much larger and more obese. As discussed under *S. pervoluta*, adults of that species might be confused with juveniles of *S. obesus*.

**Discussion.**—Ulrich and Scofield (1897, p. 875) cited a shallow sinus as characteristic of this species, but that conclusion is the result of looking at poor material. USNM 315636 (pl. 9, fig. 5) clearly shows by its growth lines that the sinus is at least moderately deep. This growth-line evidence further points out that even new silicified material that appears to have a nearly complete

TABLE 34.—Measurements (in millimeters) of *Sinuities obesus*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Dorsal width	Posterior width	Ventral width
315658	23.4	17.0	10.5	—	—	—	—
315634	31.2	21.5	17.7	30.7	20.5	17.3	14.0
315659	28.5	20.3	17.1	26.0	—	—	11.1
315659	—	8.7	5.8	12.1	8.4	6.9	5.2
315659	16.1	—	9.4	20.6	—	—	7.4
315659	—	—	12.7	22.2	—	—	10.0
315660	10.4	—	6.2	10.6	—	—	—
315661	9.9	8.0	5.0	10.8	—	—	—
315635	11.6	9.0	7.1	10.9	7.5	6.3	4.6
315635	36.1	—	22.1	36.3	23.0	17.4	14.4
315667	29.0	—	17.5	27.7	—	—	—
315663	—	—	—	19.4	13.7	10.9	—
315663	26.0	18.2	16.0	25.4	18.8	15.4	11.6
315663	16.9	11.6	9.2	16.8	11.2	9.5	8.1
315663	15.9	—	9.5	16.4	11.9	—	—
315664	12.9	13.4	10.5	18.4	12.3	10.1	8.1
315664	—	—	—	29.1	18.9	16.3	11.9
315664	17.0	—	9.4	16.0	11.6	9.8	8.2
315664	13.4	10.1	8.1	12.9	—	—	6.3

apertural margin (pl. 9, figs. 1–4, 6–12) actually has had the thin outer apertural margin completely broken away.

Another distinctive feature of *S. obesus* is the transverse furrows on the outer whorls of internal molds. These are much like the furrows of so-called *S. cancellatus corrugatus* (Hall). No such furrows were seen on the silicified material, either externally or internally. As in *S. cancellatus corrugatus*, such wrinkles in *S. obesus* internal molds may be a response in local populations to some environmental stress, may be a gerontic feature, may reflect actual internal soft parts such as bandlike muscles, or may be due to deformation from compaction of the encasing sediments. In any case, the use of transverse wrinkles on internal molds as a diagnostic species level taxobasis is not advocated here.

Ulrich and Scofield (1897) also noted a faint dorsomedian ridge on internal molds. Like the wrinkles on internal molds, this is not seen on silicified replicas of the shells.

#### *Sinuities planodorsatus* (Ulrich)

*Protowartha planodorsata* Ulrich in Ulrich and Scofield, 1897, p. 871, pl. 63, figs. 31–35.

*Sinuities planodorsatus* (Ulrich), Bassler, 1915, p. 1160; Ruedemann, 1926, p. 61, pl. 8, fig. 5.

**Diagnosis.**—Shell medium in size; dorsum narrowly and smoothly rounded in submaturity, becoming broad and flattened in maturity.

**Material.**—Ulrich and Scofield's (1897) type suite (USNM 45960) consisted of six specimens, three of which they illustrated (their pl. 63, figs. 31–35). Their illustrations are adequate, and the species is not illustrated here. No definite new material was found, though some

unnumbered internal molds in the University of Cincinnati Geology Museum collections from the Kope Formation may be assignable to this species.

**Distribution.**—The type material comes from the Southgate biofacies of the Kope Formation (middle Edenian) at Covington, Ky. (Ulrich and Scofield, 1897; Bassler, 1915). Ruedemann (1926, p. 61) reported the species from Edenian-age strata in New York.

**Comparison.**—Ulrich and Scofield (1897, p. 871) stated that this species might be a "variety" of *S. granistriatus* (Ulrich), the two species being similar in general shell form and ornamentation. However, *S. planodorsatus* differs in having a much more emphasized dorsal flattening and lacking a dorsal ridge.

**Discussion.**—This species seems to be valid and is distinct from *S. granistriatus*, though the two certainly are closely related. Ruedemann (1926, p. 61) noted that *S. planodorsatus* "fills a thin band" at one stratigraphic section he studied. Such an occurrence is typical of other species of *Sinuities* this author has collected from Edenian strata (*S. cancellatus* and *S. granistriatus*).

#### *Sinuities granistriatus* (Ulrich), 1897

Plate 11, figures 1–5; Plate 21, figure 1; Plate 45, figures 1–9

*Protowartha granistriata* Ulrich and Scofield, 1897, p. 870, pl. 63, figs. 28–30.

*Sinuities granistriatus* (Ulrich), Bassler, 1915, p. 1160; 1919, p. 314, pl. 50, figs. 40–41; pl. 55, figs. 9–11; Ruedemann, 1926, p. 63, pl. 8, figs. 7, 8.

**Diagnosis.**—Shell medium in size (up to 30 mm long), involute; dorsomedian ridge distinct through submaturity, weakening or disappearing in maturity.

**Description.**—Shell medium in size, rather tightly involute; umbilicus closed. Whorls relatively narrow in

TABLE 35.—*Measurements (in millimeters) of Sinuites granistriatus*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Dorsal width	Posterior width	Ventral width
44295	30.0	20.2	22.0	22.0	16.7	13.0	10.3
44296	29.5	—	21.3	21.7	15.3	12.2	10.2
44297	27.0	19.0	—	—	—	11.3	9.5

early growth, broadening dorsally and inflating somewhat laterally toward maturity. Dorsomedian ridge distinct, rounded, marked by faint revolving striae in submaturity; in maturity, dorsum flattens, dorsomedian ridge becomes lower and broader, eventually disappearing completely in some specimens. Dorsomedian ridge bordered by shallow furrows in some compressed specimens. Aperture width and length (from inner lateral lip contact with whorl) nearly equal, or width slightly greater. Labral sinus moderately deep; lateral aperture lobes distinctly projecting, lobe margins apparently rounded but bending rather sharply inward in adults at contact with flattened dorsum. Shell thin except at inner apertural margins; parietal deposits fairly thin, with fine pitting. Shell surface marked by fine growth lines and very delicate revolving lines.

*Measurements.*—The measurements in table 35 are of three of the largest and best preserved specimens from locality OH-1 (Bear Creek Quarry); however, because of the consistently fragmented aperture lip, the four measurements of the shell and aperture are only approximations. Ulrich and Scofield (1897, p. 870) presented a series of average measurements apparently from smaller specimens (average shell 19 mm long). Their aperture length was taken from a median point, whereas measurements reported herein were taken at the lateral extremity, where the lip reaches the coil.

*Material.*—Ulrich and Scofield's (1897) type suite is USNM 45959. These specimens are from the Kope Formation (Edenian) at Cincinnati, Ohio. The new specimens described here are UCGM 44295, 44296, 44297, 44298 (pls. 11, 21, 45), and a number of unfigured specimens cataloged under UCGM 44299. Almost all these specimens retain at least part of the shell, but none is complete. All these new specimens were collected from a single limestone lens in the Kope Formation (Edenian) at Bear Creek Quarry (locality OH-1), Ohio. UCGM 44306 (pl. 45, figs. 5-7), another specimen retaining the shell, was collected from the Kope Formation (Edenian) at locality KY-1, Carroll County, Ky.

*Distribution.*—The species is known only from the Edenian portion of the Kope Formation in southwestern Ohio and northern Kentucky.

*Comparisons.*—*S. granistriatus* resembles *S. planodorsatus* in shell size and form, particularly in the flattening of the dorsum in maturity, but the former can

be easily distinguished from that species, as well as from *S. cancellatus*, by its submature dorsomedian ridge. *Sinuities globularis* (Miller and Faber) is smaller and broader, and has a flattened dorsum with a median ridge and two diverging lateral ridges throughout growth.

*Discussion.*—Ulrich and Scofield (1897, p. 870) described the dorsomedian ridge of *S. granistriatus* as continuing to the apertural margin and as being bounded by wide furrows. Their specimens averaged only 19 mm in shell length. Larger adult specimens described herein show that the dorsomedian ridge becomes lower and broader, and even disappears completely in many mature specimens (pl. 11, figs. 1-5; pl. 45, figs. 3-9). The adult specimens described herein also show that the dorsomedian ridge is not bounded by true furrows; rather, furrows commonly result from vertical compression owing to the thinner shell material on either side of the thickened ridge.

A collection of more than 100 specimens of this species was found in a lenticular argillaceous limestone bed enclosed by shale in the lower Kope Formation at Locality OH-1. *Tetranota bidorsata* is associated with *S. granistriatus* but occurs in small numbers. Other associated skeletal fragments include sparse trilobite (*Cryptolithus*) and crinoid debris (pl. 21, fig. 1). The shale encasement may have been responsible for preservation of the thin, delicate shells, but even such an ideal circumstance did not allow preservation of any complete specimens. This case demonstrates why well-preserved specimens of this species, and of other species of *Sinuities*, are so rare.

#### *Sinuities globularis* (Miller and Faber), 1894

Plate 10, figures 1-13

*Bellerophon globularis* Miller and Faber, 1894, p. 28, pl. 1, figs. 21, 22.  
*Sinuities globularis* (Miller and Faber), Bassler, 1915, p. 1160.

*Diagnosis.*—Shell moderately small, umbilicus closed; dorsum broad; rounded dorsomedian ridge and two lateral, low, diverging ridges present throughout growth.

*Description.*—Shell moderately small (up to 20 mm long), tightly coiled; umbilicus closed. Whorls broad, inflated; dorsum with distinct, round dorsomedian ridge, bounded by shallow widening furrows, which in turn are bordered by low, rounded, diverging ridges. Aperture broad, semicircular in general outline; parietal deposits

TABLE 36.—*Measurements (in millimeters) of Sinuites globularis*

Museum No.	Shell length	Shell height	Aperture length	Aperture width	Dorsal width	Posterior width	Ventral width
UC 8811a	19.6	12.0	12.8	17.6	11.2	8.4	—
UC 8811b	20.0	14.0	—	18.4	12.0	8.8	—
UCGM 44305	16.5	11.1	9.8	14.3	9.9	8.7	6.4

unknown; sinus deep, lateral aperture lobes well rounded. Growth lines fine, closely spaced; revolving lines not known.

*Measurements.*—Measurements of *S. globularis* are listed in table 36.

*Material.*—The lectotype (UC 8811a) and paralectotype (UC 8811b) (pl. 10, figs. 1–7 and 11–13, respectively) are calcareous replicas. One other similar specimen, UCGM 44305 (pl. 10, figs. 8–10), was collected during the course of this study from locality KY-1.

*Distribution.*—The type specimens are from the Kope Formation (Edenian) at Cincinnati, Ohio. The new specimen cited above is from the same Kope Formation at locality KY-1, near Carrollton, Ky.

*Comparison.*—The dorsomedian ridge of this species is broader than that of *S. granistriatus*. The latter species also appears in some specimens to have lateral furrows, but this seems to be simply a result of vertical compaction of the thin shell adjacent to the thickened median ridge. Further, *S. globularis* is broader and more globular than *S. granistriatus*, and has true dorsolateral ridges.

#### *Sinuites subcompressus* (Ulrich, 1897)

*Protowartha subcompressa* Ulrich in Ulrich and Scofield, 1897, p. 873, pl. 63, figs. 40–44; Cumings, 1908, p. 972, pl. 39, figs. 5–56.

*Sinuites subcompressus* (Ulrich), Bassler, 1915, p. 1161.

*Diagnosis.*—Shell large, well-rounded dorsally, somewhat compressed laterally, umbilicus closed; aperture semioval, sinus width and depth nearly equal, lateral lobes gently rounded; growth lines fine, revolving lines not known.

*Material.*—Ulrich's types are USNM 45973 and 45974. No additional material is known. The original illustrations are adequate, and the species is not figured here.

*Distribution.*—The species is known only from the Waynesville biofacies of the Dillsboro Formation (Richmondian) in Butler County, Ohio, and near Versailles, Ind. (Bassler, 1915).

*Comparison.*—*S. subcompressus* differs from *S. cancellatus* (Hall) in its greater size, narrower and flatter sides, and apparent lack of revolving shell ornament.

#### Class GASTROPODA Cuvier, 1797

*Diagnosis.*—Mollusks having a distinct head, a radula, a solelike foot adapted for creeping, and a visceral mass that has been rotated up to 180 degrees with respect to

the head-foot, so that the gut becomes twisted, the left and right gills come to lie, respectively, on the right and left sides of the body, and the nervous system forms a "figure eight" (Runnegar and Pojeta, 1974).

#### Subclass PROSOBRANCHIA Milne-Edwards, 1848

*Diagnosis.*—Gastropods displaying the full effects of torsion as defined by Knight and others (1960, p. I171).

#### Order ARCHAEOGASTROPODA Thiele, 1925

*Diagnosis.*—Prosobranchia having aspidobranth ctenidia (that is, bipectinate, with filaments alternating on two sides of axis) that are free at one end; organs of pallial complex, including ctenidia, paired primitively, the right set generally partly or completely reduced; no siphon or proboscis, and thus no siphonal canal at shell margin.

*Discussion.*—Knight and others (1960, p. I155, I156) preferred the term "Archaeogastropoda" over earlier used names (that is, Scutibranchia, Aspidobranthia, Streptoneura, and Diotocardia) because of inconsistency in the use of those names and because the present term embraces the desired groups of fossil snails without the restriction of implying the existence of certain anatomical conditions. The Archaeogastropoda is a fairly diverse assemblage of taxa that exhibit the primitive features attributed, in varying degrees, to the hypothetical newly tortured ancestral form (Knight and others, 1960).

The morphological characteristics used to define archaeogastropods are largely anatomical, but have direct bearing on the form of the shell containing them. Yonge (1947) described the features of the aspidobranth condition in detail. He noted that the possession of paired gills by the pleurotomariaceans is reflected by a labral emargination. This labral emargination, in the form of a sinus or slit, acts as an exhalant passage midway between the pair of gills, affecting the more efficient expulsion of deoxygenated water (which has passed over the gills), fecal wastes, and sediment contaminants. Knight (1952) strongly supported homology between the pleurotomariaceans and the bellerophonaceans in this regard. Yonge (1947) cited four aspidobranth conditions in living prosobranchs: (1) asymmetrical shell with two asymmetrical ctenidia (Zeugobranthia), (2) secondarily symmetrical shell with two symmetrical ctenidia (Fissurellidae), (3) asymmetrical shell with loss of one or both ctenidia (Neritacea, Valvatacea, Trochacea), and (4) sec-

ondarily symmetrical shell with loss of one or both ctenidia (Patellacea, Cocculinacea, some Neritacea).

Knight (1952) envisioned the Bellerophontacea as evolutionary intermediates between untorted mollusks and the asymmetrically coiled Pleurotomariacea. Recent observations of Early and Middle Cambrian molluscan univalves place some doubt on this interpretation and suggest that torsion was a slow adaptive process resulting from the asymmetrical coiling of primitive untorted mollusks (Runnegar and Pojeta, 1974; Pojeta and Runnegar, 1976; Runnegar, 1983). However, even if this view is excepted, it does not mean that the Bellerophontacea were untorted, as secondary symmetry is common in the Archaeogastropoda. Pojeta and Runnegar (1976, p. 32) noted that the earliest pleurotomariaceans, such as the sinuopeids, raphistomenids, and eotomariids of the Late Cambrian, were low spired shell forms. The nearly synchronous appearance of the bellerophontaceans and these low spired pleurotomariaceans in the Late Cambrian might also be significant in this matter. In any case, the homology of the labral emargination and other features of the shell are considered herein to support a close relationship between the pleurotomariaceans and bellerophontaceans. Therefore, the Bellerophontacea is assigned to the Archaeogastropoda, not to the Monoplacophora. (See section on "Phylogeny and Classification" for complete discussion.)

#### Suborder BELLEROPHONTINA Ulrich and Scofield, 1897

*Diagnosis.*—Shell isostrophic, bilaterally symmetrical; coiling generally contiguous, involute to convolute, but disjunct coiling is known; apertural margin with median sinus or slit, the latter generating a selenizone, the former resulting in the development of tremata in some cases; no opercula known; presence of paired aspidobranth ctenidia implied by presence of labral emargination; circumumbilical muscle scars infer single pair of retractor muscles.

*Stratigraphic range.*—Upper Cambrian-Lower Triassic.

#### Superfamily BELLEROPHONTACEA McCoy, 1851

*Diagnosis.*—Same as for order.

*Stratigraphic range.*—Same as for order.

*Discussion.*—Table 17 gives a summary of the higher taxonomic classification of the Bellerophontacea used herein. The first four families listed (Bucanellidae through Euphemitidae) have a labral emargination in the form of a sinus. The next four families (Tropidodiscidae through Carinaropsidae) have a true slit. In all other ways, the shell morphologies of the eight families are quite similar. Knight and others (1960) placed considerable taxonomic emphasis on the presence or absence of a slit in bellerophontaceans. However, Horny (1963a)

noted the likelihood of a gradation between a sinus and a slit, and their application as features of great taxonomic significance has been questioned.

The families Cyrtolitidae and Sinuitidae are here assigned to the Monoplacophora; both families are sinus-bearing and were assigned to the Bellerophontacea by Knight and others (1960). This change in class-level assignment resulted from the discovery of dorsally discrete multiple paired muscle scars in species of *Cyrtolites* and *Sinuitopsis* (Horny, 1963c; Rollins and Batten, 1968). Runnegar (1982) reported monoplacophoranlike muscle scars in *Sinuities*, in contrast to Knight's (1947a) claim of columellar muscle scars in that genus. Runnegar's discovery is not surprising, because *Sinuities* and *Sinuitopsis* are close morphologically; Knight and others (1960) treated these two taxa as subgenera. Rollins and others (1971) reported gastropodlike columellar scars in a species of the sinus-bearing genus *Sinuitina*. Because of the general overall conchological similarities of many sinus-bearing and slit-bearing symmetrical univalved mollusks, and because some have muscle scars here interpreted as monoplacophoranlike whereas others have gastropodlike columellar muscle scars, I believe it is premature to transfer all sinus-bearing species to the Monoplacophora.

Thus, until new information indicates otherwise, I will treat the sinus-bearing families Bucanellidae, Grandostomatidae, Tremanotidae, and Euphemitidae as bellerophontacean gastropods. No members of these families are present in the faunas described herein; however, a brief discussion of each family follows.

The family Bucanellidae (Koken, 1925) occurs in rocks ranging in age from Late Cambrian to Middle Permian. It is characterized by a relatively broad phaneromphalous shell having a sinus-bearing apertural margin, fairly fine collabral threads, and, in some cases, spiral threads. The genera here included in the Bucanellidae were placed by Knight and others (1960) in three family-level taxa—Cyrtolitidae, Bucanellinae, and Sinuitinae. As mentioned previously, *Cyrtolites* and *Sinuities*, and close allies, are now classified as monoplacophorans, not as gastropods. *Sinuitina* closely resembles *Cyrtolites* in its conchology, but because of its gastropodlike columellar muscle scars, it is here placed in the family Bucanellidae. The trilobate shell of *Bucanella* also suggests gastropod affinities, based on the convincing functional analyses of such shells done by Peel (1974). Other genera placed in the Bucanellidae are *Owenella* and, with question, *Trigyna*, *Anconochilus*, and *Crenistriella*.

The family Grandostomatidae is characterized by an explanate adult shell that is phaneromphalous and sinuate and has transverse and spiral ornament. The family ranges from the Middle Ordovician to the Devonian, and is made up of the genera *Grandostoma*, *Ptomatis*, and



?*Patellostium*. Horny (1962) proposed this grouping as a subfamily of the Sinuitidae in order to distinguish sinuate forms having a greatly expanded body whorl. This shell form seems convergent with some slit-bearing bellerophontaceans, such as members of the Carinaropsidae. Peel (1977b) has interpreted such expanded shell forms as adaptations to life on soft substrates, the broad surface area inhibiting sinking into the mud.

The Tremantotidae includes sinuate shells having dorsal tremata developed in association with an expanded aperture. The family is represented by the Middle Silurian and Lower Devonian genera *Tremantotus* and *Boiotremus*, respectively. Peel (1972, p. 419) erected the subfamily Tremantotinae of the family Sinuitidae, demonstrating that the previous close association of these genera to *Salpingostoma* was due to homeomorphy. He showed that the tremata of *Tremantotus* and *Boiotremus* were formed by the periodic expansion of the aperture and closing off of a deep sinus, and that no slit was present. Peel pointed out that the periodic expansions of the shell aperture in *Tremantotus* commenced only in later ontogenetic stages, whereas in *Boiotremus* they occurred throughout ontogeny. He assumed that the successive flared apertures were resorbed with continuation of growth.

The family Euphemitidae is characterized by a shell entirely covered by inductural layers, with a narrow sinus that nearly becomes a slit in some species. The family is known from the Mississippian to the Permian, with questionable members in the Devonian. The family includes the genera *Euphemites*, *Paleuphemites*, *Euphemitopsis*, *Warthia*, and ?*Stachella*. The exact position of this family in the phylogeny of the bellerophontaceans is uncertain, and its relationships to other sinuate and slit-bearing families needs to be evaluated carefully. Rollins (1967) interpreted this group as being "ploughers" that ploughed through the surface sediments in search of food, similarly to the modern moon snail *Polinices*.

The sinuate forms appeared during the Late Cambrian along with the slit-bearing bellerophontaceans, but in greater diversity and abundance. Both groups maintained low diversities through the Early Ordovician. The Middle Ordovician was a time of great radiation for the slit-bearing group. The only sinus-bearing group to become truly abundant and diverse seems to be the late Paleozoic euphemitids; their success may be related to their specialized morphology. All slit-bearing families, and most of the subfamilies, are present in the faunas considered herein.

#### Family TROPIDODISCIDAE Knight, 1956

*Diagnosis*.—Shell small to moderate in size, whorls laterally compressed and narrow, though somewhat

expanded in some cases; umbilicus wide; slit deep, extending as much as one-half whorl from the apertural margin; parietal inductura not developed; posterior train present in few cases.

*Stratigraphic range*.—Upper Cambrian-Lower Devonian.

*Discussion*.—Most American species of *Tropidodiscus* Meek and Worthen, 1866, and *Phragmolites* Conrad, 1838, were described under the synonymous names *Oxydiscus* deKoninck, 1882, and *Conradella* Ulrich and Scofield (1897), respectively. Ulrich and Scofield (1897, p. 851, 852) assigned these two genera (under the names *Oxydiscus* and *Conradella*) to the family Bucaniidae, believing they were allied to *Bucania* through the common possession of a deep slit, a wide umbilicus, and the lack of a parietal callosity. Dall, in Eastman (1927), and Wenz (1938) continued this practice.

Knight (1956, p. 42) erected the new subfamily Tropidodiscinae, and Knight and others (1960) placed it in the family Bellerophontidae (adjacent to the Bucaniinae). They included the genera *Tropidodiscus*, *Phragmolites*, *Temnodiscus* Koken, 1896, and *Chalarostrepsis* Knight, 1948, in the Tropidodiscinae. All but the last of these genera occurs in the Ordovician faunas of the Cincinnati arch region. Horny (1963a, p. 70) supported the classification of Knight and others (1960), but Golikov and Starobogatov (1975, p. 207) elevated the Tropidodiscinae to the family level, a change that is supported here.

The familial assignment of the genus *Temnodiscus* is a matter of some controversy. Koken had associated the genus with sinuate forms, as did Horny (1962), who claimed the genus did not bear a true slit. However, I agree with the classification of Knight and others (1960), as Knight's (1941, pl. 10, figs. 3a-d) figures clearly show a true slit and selenizone in the type species of the genus, which is *Temnodiscus lamellifer* (Lindstrom, 1884).

The tropidodiscids seem to have played a significant role in the ancestry of other early Paleozoic bellerophontaceans. *Chalarostrepsis praecursor* Knight, 1947b, from the Upper Cambrian of Quebec, and ?*Tropidodiscus* sp., from the Middle or Upper Cambrian of Bolivia, are the earliest known bellerophontaceans (Curry and Morris, 1967, p. 426). *Chalarostrepsis* is exemplary of the primitive morphological traits of the Bellerophontacea: a loose style of coiling, a wide-open umbilicus, and a deep anteromedian apertural slit (see "Functional Morphology" section). *Chalarostrepsis* is apparently ancestral to the other genera of the family, which show a trend toward tighter involute coiling.

The Lower Ordovician *Eobucania* Kobayashi, 1955, seems to have descended from the tropidodiscids, or at least from the same stock, both having deep slits and well-defined selenizones. Also, like *Chalarostrepsis* and *Tropidodiscus*, *Eobucania* has only collabral shell orna-

ment, except for threads bordering the selenizone. The more primitive members of the genus *Bucania* (the *B. sulcatina* group of Ulrich and Scofield, 1897) also are characterized by a wide-open umbilicus and a deep slit, as are species of the new genus *Undulabucania*, these forms differing from the tropidodiscids mainly in their more broadly rounded, depressed whorl forms. It seems likely that the tropidodiscids are ancestors of the bucaniids.

Such traits as the narrow whorl form and the presence of a posterior train in some tropidodiscids could suggest a link to the Early and Middle Cambrian helcionellaceans, but such a connection is not actively supported here. At present, relations between Upper Cambrian molluscan univalves and those earlier forms remain a matter of some controversy and require a great deal more study.

#### Genus TROPIDODISCUS Meek and Worthen, 1866

**Diagnosis.**—Shell laterally compressed, whorls gradually expanding, barely contiguous; umbilicus large; slit deep, selenizone as thin keel, with or without lunulae; growth lines only ornament.

**Description.**—Shell small to moderate in size, strongly compressed laterally; whorls gradually expanding throughout growth, barely contiguous, resulting in large, open umbilicus exposing all previous volutions. Apertural outline subtriangular to lanceolate; sinus broadly curved, rather deep; slit deep, narrow; selenizone on high, thin keel, which may be sharp or slightly truncated and with lunulae. Growth lines as fine threads or fine imbricating lamellae. No revolving ornament.

**Type species.**—*Bellerophon curvilineatus* (Conrad, 1842), by original designation (Knight, 1941, p. 360, 361).

**Distribution.**—The genus is known from the Early Ordovician (Canadian) to the Late Devonian. Species are present in upper Middle Ordovician (Kirkfieldian-Shermanian) and Late Ordovician (Richmondian) strata in the Cincinnati arch region.

**Comparison.**—*Tropidodiscus* could be confused only with species of *Phragmolites*, the latter differing mainly in its consistent strong, wavy lamellae, which do not curve over the surface of the shell, thus reflecting the absence of an apertural sinus.

**Discussion.**—Knight (1941, p. 360, 361) wrote a detailed review and opinion on the complex nomenclatural history of this genus. The genus originally was named *Tropidiscus* Meek (1866), but this was an invalid homonym. Meek and Worthen (1866, p. 160) emended the name to *Tropidodiscus* (whether purposely or not is a matter of question). DeKoninck (1882, p. 81) erected the genus *Tropidocyclus* as an objective synonym of *Tropidiscus*, designating *Bellerophon curvilineatus* Conrad, 1842, the type species. Koken (1889, p. 390)

erected the genus *Oxydiscus* to replace the homonym *Tropidiscus* and its emendation, and *Tropidocyclus*, which he rejected because it encompassed unrelated species. Knight (1941, p. 361) strongly disagreed with Koken's action. He favored the adoption of *Tropidocyclus* as the valid genus name, but reluctantly accepted the principles of the International Commission of Zoological Nomenclature, which dictated retention of the emended name *Tropidodiscus* Meek and Worthen (1866).

*Tropidodiscus* shows relationship to the Bucaniidae in its large umbilicus, lack of a parietal callosity, and deep slit, but this evidence is offset by its lack of any spiral ornament. Nevertheless, the genus probably is a representative of a primitive stock of bellerophontaceans that gave rise to the Bellerophontidae and Bucaniidae. The earliest known bucaniid genus, *Eobucania* Kobayashi (1955), agrees with *Tropidodiscus* in its open umbilicus and deep apertural slit, and, significantly, its spiral ornament consisting of only two threads bordering the selenizone.

#### *Tropidodiscus subacutus* (Ulrich), 1897

Plate 41, figures 9–13

*Oxydiscus subacutus* Ulrich in Ulrich and Scofield, 1897, p. 913, pl. 62, figs. 62–65; pl. 82, figs. 23–25; Weller, 1903, p. 179, pl. 12, figs. 8, 9; Grabau and Shimer, 1909, p. 616, 826; Bassler, 1932, p. 222, pl. 20, figs. 11, 12.

*Cyrtolites subacutus* Miller, 1897, p. 767.

*Tropidodiscus subacutus* (Ulrich), Shimer and Shrock, 1944, p. 443, pl. 178, figs. 8, 9.

**Diagnosis.**—Shell moderately small (up to 13 mm long), lenticular, with 3.5–4.5 volutions, each embracing one-third to one-half the preceding one; whorl floor keel distinct, narrow, sharply rounded.

**Description.**—Shell moderately small, lenticular, the greatest width about one-half the shell height; 3.5–4.5 volutions in adult, each volution embracing one-third to one-half the preceding one. Shell width and thickness greatest at narrowly rounded umbilical shoulder; dorsal slopes slightly concave to flat; dorsum acutely carinate, but with narrow truncation at crest for selenizone. Umbilici wide, all earlier volutions visible; umbilical slopes cut inward essentially horizontally. Whorl floor keel distinct, narrow, sharply rounded. Slit deep, narrow; sinus narrow, V-shaped, relatively deep. Growth lines fine, closely and fairly regularly spaced.

**Measurements.**—Measurements of *T. subacutus* are listed in table 37.

**Material.**—The lectotype is from the original type suite (USNM 45952) and is herein designated USNM 387021 (pl. 41, figs. 11–13). It and 20 paralectotypes (USNM 45952), as well as all of the new USGS collections cited above, are silicified. No complete specimens are known, all having at least the anteromedian, slit-bearing,

TABLE 37.—Measurements (in millimeters) of *Tropidodiscus subacutus*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter
387021	12.95	9.9	6.4	5.2	3.8

area broken away. As in *Salpingostoma*, the shell adjacent to the deep slit must have been thinnest and weakest, and thereby most easily broken.

*Distribution.*—Ulrich and Scofield (1897) reported this species from the upper beds of the "Trenton Group" near Danville, Ky., and their 21 type specimens are labeled as coming from the "Flanagan" beds of that vicinity, which are now considered to be in the upper Lexington Limestone (Shermanian). The name "Flanagan chert beds" was abandoned after it was found that the name had been used for different silicified limestone horizons at various stratigraphic levels within the Lexington Limestone. Ulrich and Scofield also claimed possible recognition of the species "in Tennessee and in the *Fusispira* beds in Minnesota." Weller (1903, p. 46) reported the species from talus blocks from "the upper Black River and the lower Trenton beds" of New Jersey.

In the USGS silicified collections, *T. subacutus* was identified from the Salvisa Bed of the Perryville Limestone Member (6915-CO, 6916-CO) and the upper Devils Hollow Member (5087-CO, 5095-CO) of the Lexington Limestone. Fragmentary specimens assigned to *T. cf. T. subacutus* were found in the Tyrone Limestone (5075-CO) and the Faulconer Bed of the Perryville Limestone Member (6136-CO) of the Lexington Limestone. Additional fragmentary specimens classifiable only to *T. sp. indet.*, but probably belonging to this species, were found in the Curdsville Limestone Member (6134-CO, 7784-CO), the Grier Limestone Member (4880-CO), and the Devils Hollow Member (5036-CO, 7789-CO) of the Lexington Limestone.

Therefore, *T. subacutus* is certainly recognized from the upper Lexington Limestone (Shermanian), but probably occurs also in the Tyrone Limestone (Rocklandian) and in the lower Lexington Limestone (Kirkfieldian).

*Comparison.*—The only other species in the fauna warranting comparison is *T. cristatus* (Safford), which differs in its somewhat larger size, its more rapid expansion and fewer number of volutions at maturity, its looser coiling (volutions embrace only about one-sixth the height of the preceding whorl), resulting in a larger umbilicus, and its more rounded whorl floor keel (Ulrich and Scofield, 1897, p. 914).

*Discussion.*—*T. subacutus* appears to have been a geographically widespread, and possibly stratigraphically long ranging, species. Its rather thin, delicate, small shell makes its preservation and recognition diffi-

TABLE 38.—Measurements (in millimeters) of *Tropidodiscus cristatus*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter
45950	21.9	17.0	8.7	8.0	6.5
45950	22.8	20.2	8.8	9.1	8.4

cult. It appears to have inhabited a wide range of normal marine shallow-water carbonate environments.

#### *Tropidodiscus cristatus* (Safford), 1869

Plate 41, figures 6–8

*Cyrtolites cristatus* Safford, 1869, p. 289.

*Oxydiscus cristatus* Ulrich and Scofield, 1897, p. 914, pl. 82, figs. 26–28.

*Diagnosis.*—Shell moderately large (up to 23 mm long), with 3.0–3.5 volutions in adult, each embracing about one-sixth the previous one; whorl floor keel relatively low and rounded.

*Measurements.*—Measurements of *T. cristatus* are listed in table 38.

*Material.*—Only the two type specimens (USNM 45950) are known. Both of these are silicified and have the last one-third whorl broken away. The specimen figured on plate 41, figures 6–8, is here designated the lectotype.

*Distribution.*—The type specimens are from the Cannon facies of the Bigby-Cannon Limestone (Kirkfieldian-Shermanian) of Jackson County, Tenn.

*Comparison.*—The most similar species is *T. subacutus*; for comparisons between the two, see "Comparison" under that species. (Also see Ulrich and Scofield, 1897, p. 814.)

#### *Tropidodiscus magnus* (Miller), 1878

Plate 42, figures 1, 2

*Cyrtolites magnus* Miller, 1878, p. 103, pl. 3, fig. 10.

*Oxydiscus magnus* Ulrich and Scofield, 1897, p. 859; Cumings, 1908, p. 970, pl. 41, fig. 5.

*Diagnosis.*—Shell large (up to 27 mm long), narrow, lenticular, dorsal slopes gently convex, dorsum rounded; three or more volutions, each embracing about one-third of previous one; sinus narrow and deep.

*Measurements.*—Measurements of the holotype of *T. magnus* are listed in table 39.

*Material.*—The holotype (UC 10838; pl. 42, figs. 1, 2) is a very weathered calcitic specimen. A few other poorly preserved unnumbered specimens are in the University of Cincinnati Geology Museum collections.

*Distribution.*—The holotype is from Richmondian-age strata near Richmond, Ind. (Miller, 1878). Unnumbered specimens in the University of Cincinnati collections are

TABLE 39.—Measurements (in millimeters) of *Tropidodiscus magnus*

UC No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter
10838	27.0	24.0	18.5	10.0	8.0

labeled as coming from the Saluda Formation at Madison, Ind.

*Comparison.*—The convex dorsal slopes and rounded dorsum of *T. magnus* distinguish it from any other known species of the genus.

*Discussion.*—Although *T. magnus* is known from only a small number of specimens, no other species has such a rounded (rather than carinate) dorsum (pl. 42, figs. 1, 2). *T. magnus* is the only species of *Tropidodiscus* recognized from the Upper Ordovician of the Cincinnati arch region. However, I note that 16 poorly preserved silicified fragments assignable only to *T. sp. indet.* were recognized in four USGS samples (6411-CO, 6412-CO, 6414-CO, 7843-CO) from the Gilbert Member of the Ashlock Formation (Maysvillian) of Kentucky.

#### Genus PHRAGMOLITES Conrad, 1838

*Diagnosis.*—Shell generally rather small (in most cases less than 10 mm long); sinus lacking, slit half a revolution deep; growth increments lamellose, corrugated, scalloped; fine revolving threads present.

*Description.*—Shell rather small, generally narrow and gradually expanding, but in a few cases broad and rapidly expanding; whorl slopes gently convex; umbilicus wide; apertural outline elliptical, subcordate to subtriangular; parietal deposits lacking. Sinus lacking; slit half a revolution deep; selenizone narrow, lunulate, bordered by revolving threads, in many cases elevated on a carina. Growth lines fine, straight; periodic growth increments lamellose, corrugated, scalloped, evenly spaced; fine revolving threads generally present.

*Type species.*—*Phragmolites compressus* Conrad, 1838, by monotypy.

*Distribution.*—Middle and Upper Ordovician (Blackriveran-Richmondian) in North America and Europe.

*Comparison.*—The lamellose, corrugated, scalloped, and uncurved (nonsinuate) growth increments readily distinguish *Phragmolites* from *Tropidodiscus*, which has a similar shell form and a deep slit. *Temnodiscus* can have many lamellose growth increments similar to those of *Phragmolites*, but it differs by having a sinus and a relatively shallow slit.

*Discussion.*—Conrad (1838) thought *P. compressus* to be a chambered shell, hence the genus name, translating “partitioned stone.” Hall (1847) asserted that the species was not chambered and placed it in the genus *Cyrtolites*.

Ulrich and Scofield (1897, p. 905) recognized the species’ generic distinctiveness, but chose not to revive the name *Phragmolites* as it gave “an incorrect idea of the fossil.” They concluded, “Had the name [*Phragmolites*] ever attained currency, we would feel ourselves bound to revive it, on the score of priority, despite its inappropriateness, but as no one, so far as we can learn, ever adopted it, we thought it best to view the name as one that has failed of being established because of incorrect and insufficient definition.” Hence, they renamed the genus *Conradella*, but curiously made *C. obliqua* Ulrich and Scofield the type species, even though Conrad’s original type species was recognized as a member of the new genus. Bassler (1915) used the name *Phragmolites* rather than *Conradella*, but numerous other authors, including Koken (1898, 1925) and Reed (1921), used *Conradella*. Wenz (1938, p. 102) placed *Conradella* in synonymy with *Phragmolites*. Knight (1941) described the type species of both genera, and Knight and others (1960, p. 1179) followed Wenz (1938). All modern authors agree with the priority of *Phragmolites*.

Ulrich and Scofield (1897, p. 905), citing a long apertural slit, large umbilicus, generally gradually expanding whorls, and surface sculpture as phylogenetic morphological characteristics, proposed that *Phragmolites* and *Bucania* Hall were derived from the same stock. This viewpoint is heartily supported here. Among the Tropidodiscidae, *Phragmolites* shows the closest morphological connection to the Bucaniidae. Especially comparable to *Phragmolites* is *Undulabucania* n. gen., which includes species whose general form resembles that of the *Bucania sulcatina* group, but which have very deep slits and distinctly wavy, intersecting or nearly intersecting, growth lines. In the latter two characteristics, *Undulabucania* shows common morphologic traits with *Phragmolites*.

#### *Phragmolites compressus* Conrad, 1838

Plate 42, figure 14; Plate 44, figures 1–4

*Phragmolites compressus* Conrad, 1838, p. 119; Weller, 1903, p. 178, pl. 12, figs. 16, 17; Knight, 1941, p. 242, pl. 9, fig. 2; Shimer and Shrock, 1944, p. 443, pl. 178, fig. 5; Wilson, 1951, p. 29, pl. 2, figs. 17, 18.

*Cyrtolites compressus* (Conrad), Hall, 1847, p. 188, pl. 40A, figs. 2a–f; 1862, p. 40, fig. 4; Chamberlin, 1883, p. 158, fig.; Lesley, 1889, p. 182, fig.

*Conradella compressa* (Conrad), Ulrich and Scofield, 1897, p. 906, not described or figured.

*Conradella similis* Ulrich in Ulrich and Scofield, 1897, p. 906, not figured.

*Diagnosis.*—Shell narrow, very gradually expanding; whorls barely contiguous, lanceolate-shaped, longer than wide; corrugated growth lamellae widely spaced, with five or six reentrants per side.

TABLE 40.—Measurements (in millimeters) of *Phragmolites compressus*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Lamellae spacing
387019	12.7	—	5.5	4.7	1.0
387020	9.0	7.3	4.8	—	0.7–1.0

*Description.*—Shell small (up to 13 mm long), narrow, very gradually expanding; whorls barely contiguous, embracing only the dorsal carina of the preceding whorl. Dorsal carina prominent, slightly rounded, with faint lunulae; dorsal slopes briefly concave near carina, then becoming evenly convex; umbilical shoulders sharply rounded; ventral slopes slightly convex to nearly flat. Apertural outline lanceolate, higher than wide. Umbilici wide. Slit deep, apparently about one-half a volution. Growth lines fine, closely spaced; very fine revolving lines visible in some specimens. Periodic corrugated growth lamellae rather widely spaced, with five or six square reentrants from shoulder to carina.

*Measurements.*—Measurements of *P. compressus*, listed in table 40, are estimates based on fragmentary material (pl. 44, figs. 1–4).

*Material.*—Three specimens from Kentucky were examined. The holotype of *P. similis* (USNM 47568; pl. 42, fig. 14) is a fragmentary silicified specimen. USNM 387020 (pl. 44, figs. 2–4) is a broken silicified shell having a well-preserved exterior. USNM 387019 (pl. 44, fig. 1) is a calcitic specimen embedded in a limestone with brachiopod and bryozoan fragments.

The whereabouts of Conrad's (1838) type is unknown, but Knight (1941, p. 242, pl. 9, fig. 2) described and figured Hall's (1847, p. 188, pl. 40A, figs. 2a, b) hypotype. Knight assumed that because Conrad was a colleague of Hall, Hall was familiar with the species, and his description might well be based on the type material. Knight believed that Hall's figured specimen may have been part of Conrad's type suite.

*Distribution.*—This species has been reported from the "Trenton Group" of New York, New Jersey, Pennsylvania, and Ontario. The label included with the Kentucky hypotype (pl. 44, figs. 1–4) described here reads: "Lower part of Trenton and perhaps Black River, 2–4 miles north of Burgin, Mercer Co., Kentucky." These specimens are Kirkfieldian-Shermanian, and probably Rocklandian, in age. The holotype of *P. similis* is probably Blackriveran in age. Thus, the total stratigraphic range is Blackriveran-Shermanian.

*Comparison.*—*P. compressus* has a lanceolate apertural outline that is longer than wide, whereas *P. obliqua* has a nearly circular aperture, and *P. grandis* and *P. triangularis* have apertures that are wider than long.

*Discussion.*—*Conradella similis* Ulrich is put in synonymy with this species. The holotype (USNM 47568) of *C. similis* is a poorly preserved fragment (pl. 42, fig. 14) that is closest to *P. compressus*, and no other specimens were located. A label in the museum tray containing the holotype of *C. similis*, initialed by Ulrich, reads: "Two other specimens formerly in this box are of *C. compressa* and have been removed." The single remaining specimen resembles *P. compressa* in its size and general shell form, and in the obliquity of its corrugated growth lamellae and the number of reentrants on those lamellae. This specimen is from the High Bridge Group (Blackriveran) of Kentucky.

#### *Phragmolites grandis* (Ulrich), 1897

Plate 42, figures 7–13; Plate 43, figures 1–3

*Conradella grandis* Ulrich in Ulrich and Scofield, 1897, p. 908, pl. 62, fig. 67; pl. 67, figs. 16–18.

*Phragmolites grandis* (Ulrich), Bassler, 1932, p. 194, pl. 6, figs. 11, 12.

*Diagnosis.*—Shell relatively large (up to 30.5 mm long) and rapidly expanding; aperture subtriangular, wider than long; corrugated lamellae with five or six reentrants per side.

*Description.*—Shell large and rapidly expanding for genus, lateral flaring of aperture increases in adulthood. Dorsal slopes gently convex, umbilical shoulders sharply rounded, umbilical slopes nearly flat and horizontal; umbilicus moderate in size, deep. Apertural outline subtriangular, width becoming increasingly greater than length through growth. Slit about one-half volution deep, rather wide; selenizone on truncated dorsum, bordered by revolving threads. Growth lines fine, closely spaced, crossed by fine, widely spaced revolving lines; periodic corrugated growth lamellae distinct, with five or six reentrants from whorl crest to shoulder.

*Measurements.*—Measurements of the lectotype and a paralectotype of *P. grandis* are listed in table 41.

*Material.*—Five calcitic specimens are in the original type suite (USNM 45756). The specimen shown on plate 42, figures 10–13, is here designated the lectotype, because it was Ulrich and Scofield's (1897, pl. 67, figs. 16–18) figured specimen; it is given the number USNM 315667. The paralectotypes figured here (pl. 42, figs. 7–9; pl. 43, figs. 1–3) are numbered USNM 315668 and 387018, respectively. The remaining two unfigured paralectotypes retain the number USNM 45756.

*Distribution.*—The species is known only from the Lebanon Limestone (Blackriveran) in the vicinity of Lebanon, Tenn.

*Comparison.*—*P. grandis* is similar to *P. triangularis* Ulrich and Scofield from Blackriveran strata of the Upper Mississippi Valley, but it is larger and more rapidly expanding, and has more convex dorsal slopes, a

TABLE 41.—Measurements (in millimeters) of *Phragmolites grandis*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Ventral width	Wave length of lamellae
315667	30.5	23.0	16.0	—	9.8	8.8	1.5–2.0
315668	20.0	13.7	11.4	19.0	5.4	7.2	1.5

relatively wider aperture, fewer corrugated lamellae folds, and more distinct revolving lines (Ulrich and Scofield, 1897, p. 908–909).

*Discussion.*—The smaller, submature specimens of this species, as shown by the paralectotype USNM 387018 (pl. 43, figs. 1–3), are proportionately narrower. The increase in whorl expansion rate apparently was an adult occurrence. The two adult specimens figured here (pl. 42, figs. 7–9 and 10–13) at first glance appear different; however, this difference seems to be a result of preservation. The paralectotype (pl. 42, figs. 7–9) has the expanded aperture broken away, its right side is an internal mold, and the preserved shell material on the left side is worn. The lectotype, USNM 315667 (pl. 42, figs. 10–13), preserves the aperture and shell sculpturing much better. The broad expanded aperture of this species is uncharacteristic of the genus and suggests a phylogenetic relationship to *Bucania* and *Undulabucania*.

***Phragmolites cellulosus* (Ulrich and Scofield), 1897**

Plate 43, figures 4–12

*Conradella dyeri* var. *cellulosa* Ulrich and Scofield, 1897, p. 910, pl. 67, figs. 27–29; Cumings, 1908, pl. 39, fig. 9.

*Phragmolites dyeri cellulosus* (Ulrich and Scofield), Bassler, 1915, p. 972.

*Diagnosis.*—Shell small, gradually expanding, whorls somewhat inflated in adults; aperture subcordate; corrugated lamellae closely spaced, spiral threads weak.

*Description.*—Shell small (up to 11.5 mm long), gradually expanding, narrow; whorls becoming somewhat inflated in adulthood. Dorsal slopes moderately convex; umbilical shoulders rather narrowly rounded; ventral slopes slightly convex, angled downward. Apertural outline subcordate. Slit deep; selenizone on prominent, elevated, rounded dorsomedian keel, lunulae faint. Corrugated growth lamellae very closely spaced (four per millimeter), scalloping generally not distinctly squared; revolving threads moderately distinct on well-preserved surface, generally three per millimeter.

*Measurements.*—Measurements of *P. cellulosus* are listed in table 42.

*Material.*—Three specimens were examined. USNM 47562 is a complete shell whose surface is worn (pl. 43, figs. 7–9). USNM 61029 is a specimen whose surface is well preserved (pl. 43, figs. 4–6). USNM 79250 is a

specimen whose ventral whorl is broken away (pl. 43, figs. 10–12). The holotype (USNM 45753) is not figured.

*Distribution.*—The specimens examined here are all from the Hermitage Formation (Kirkfieldian) of central Tennessee. Ulrich and Scofield (1897, p. 910) reported this species from the “*Clitambonites* bed” at St. Paul and Cannon Falls, Minn., which was their basal “Trenton” unit. Bassler (1915, p. 972) stated that the species occurred in the Prosser Formation at the same localities, which, according to Sweet and Bergstrom (1976, text-fig. 3), is Shermanian-Edenian in age. Ross and others (1982) showed the unit as Shermanian in age.

*Comparison.*—Ulrich and Scofield (1897, p. 910) distinguished *P. dyeri* var. *cellulosus* from *P. dyeri dyeri* by the former's much smaller dorsal keel and by differences in their surface markings. I recognize *P. cellulosus* as a distinct species on the basis of these characteristics. The Tennessee specimens assigned to *P. cellulosus* have a very prominent dorsal keel, but their surface markings are subtly different from *P. dyeri*. The lamellae of *P. cellulosus* are more distinctly scalloped and are not quite as closely spaced as in *P. dyeri*. The Tennessee specimens also attain a slightly larger size, and their whorls become more inflated, compared with typical Richmondian *P. dyeri*.

*Discussion.*—As implied above, the differences between *P. cellulosus* and *P. dyeri* are subtle, but they are recognizable. Confusion between the two species should not be a problem, and their stratigraphic ranges are not known to overlap.

*P. cellulosus* occurs in Safford's (1869) “*Orthis* bed” (Hermitage Formation) in Tennessee and in Ulrich and Scofield's (1897) “*Clitambonites* bed” (Prosser Formation) in Minnesota, each considered the base of the “Trenton” by those authors. Both formations are interbedded shales and argillaceous limestones containing abundant brachiopod faunas.

TABLE 42.—Measurements (in millimeters) of *Phragmolites cellulosus*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Ventral width
47562	8.5	7.30	3.6	4.3	3.5	1.9
79250	10.0	—	4.1	5.5	—	1.9
61029	11.5	9.25	6.5	6.0	4.6	3.0

TABLE 43.—Measurements (in millimeters) of the holotype of *Phragmolites bellulus*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Ventral width
45751	10.75	9.1	4.5	4.0	1.9

***Phragmolites bellulus* (Ulrich), 1897**

Plate 44, figures 5–7

*Conradella bellulus* Ulrich in Ulrich and Scofield, 1897, p. 910, pl. 67, figs. 23–26.

*Phragmolites bellulus* (Ulrich), Bassler, 1915, p. 971.

**Diagnosis.**—Shell small (up to 11 mm long), narrow; slit only one-quarter whorl deep; selenizone with distinct lunulae; corrugated growth lamellae moderately closely spaced, with eight or nine reentrants per side.

**Description.**—Shell small, very gradually expanding, narrow throughout. Dorsal slopes broadly convex, umbilical shoulders rather well rounded, umbilical slopes gently convex; apertural outline subovate to subcordate. Dorsal carina elevated, truncate, with distinct lunulae. Slit apparently open only one-quarter whorl. Corrugated growth lamellae moderately closely spaced (three per millimeter), with eight or nine reentrants from shoulder to crest, but losing corrugations within the umbilicus. Revolving lines fairly distinct, about six from shoulder to crest (two lines per millimeter).

**Measurements.**—Measurements of the holotype of *P. bellulus* are listed in table 43.

**Material.**—The holotype (USNM 45751) (pl. 44, figs. 5–7), and only known specimen, of *P. bellulus* is a well-preserved calcitic specimen.

**Distribution.**—The holotype came from the Fairmount biofacies of the Fairview Formation at Covington, Ky. (Maysvillian).

**Comparison.**—Ulrich and Scofield (1897) placed *P. bellulus* in an intermediate position between *P. elegans* Miller and *P. dyeri* Hall. *P. bellulus* differs from *P. elegans* in its “more slender whorls and less coarsely marked surface,” and from *P. dyeri* in its narrower shell and less crowded corrugated lamellae, and in having distinct lunulae on the slitband.

***Phragmolites elegans* (Miller), 1874**

Plate 44, figures 11–15; Plate 45, figure 10

*Cyrtolites dyeri* Hall (part), Meek, 1873, p. 149, pl. 13, figs. 2d, e.

*Cyrtolites elegans* Miller, 1874, p. 310, fig. 31; 1889, p. 402, fig. 668.

*Conradella elegans* (Miller), Ulrich and Scofield, 1897, p. 911, pl. 67, figs. 12–15.

*Phragmolites elegans* (Miller), Bassler, 1915, p. 972.

**Diagnosis.**—Shell small (up to 11.4 mm long); apertural outline lanceolate with angular shoulders; seleni-

TABLE 44.—Measurements (in millimeters) of *Phragmolites elegans*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Ventral width
315669	8.0	6.6	4.5	4.0	3.3	1.7
315671	11.4	8.2	5.6	25.6	4.5	2.0
315670	6.0	5.3	—	3.3	2.7	—
315672	4.4	3.8	2.5	2.2	1.8	0.8

zone with distinct lunulae; corrugated growth lamellae moderately spaced, with five or six shallow reentrants per side.

**Description.**—Shell small, gradually expanding, relatively tightly enrolled, with each volution embracing one-third to one-half the previous one, and consisting of about three whorls. Dorsal slopes very gently convex and quite acute to one another; umbilical shoulders subangular; ventral slopes nearly flat and sloping inward; apertural outline lanceolate. Slit one-half whorl deep; selenizone on moderately elevated dorsomedian keel, flat topped, with bordering threads and distinct, closely spaced lunulae. Corrugated growth lamellae moderately spaced, with five or six shallow reentrants per side. Growth lines very fine; revolving threads apparently lacking.

**Measurements.**—Four of Ulrich and Scofield's (1897) hypotypes were measured (table 44).

**Material.**—Four of twelve calcitic specimens in Ulrich and Scofield's (1897) hypotype suite (USNM 45754) are figured here: USNM 315669 (pl. 44, figs. 11–13), USNM 315670 (pl. 44, fig. 14), USNM 315671 (pl. 44, fig. 15), and USNM 315672 (pl. 45, fig. 10). Other calcitic specimens examined were UCGM 19819 and 19820.

**Distribution.**—The species is known only from the Corryville biofacies of the Grant Lake or Bull Fork Formation (late Maysvillian) in the vicinity of Cincinnati, Ohio.

**Comparison.**—*P. grandis* (Ulrich) and *P. triangularis* Ulrich and Scofield have shell forms similar to *P. elegans*, but both of these Blackriveran species attain much greater size and have coarser ornament. The early Maysvillian species *P. bellulus* Ulrich differs in its more rounded whorl form and its generally more closely spaced and more scalloped lamellae. The Richmondian species *P. dyeri* (Hall) differs similarly, but also lacks distinct lunulae and bears distinct revolving threads.

**Discussion.**—*P. elegans* is a distinctive species related to both *P. bellulus* and *P. dyeri*. *P. bellulus* apparently is ancestral to *P. dyeri*. *P. elegans* seems to have evolved separately, as shown by the different character of its shell lamellae. *P. elegans* may be descended from *P. grandis*, which, while larger, had a similar whorl form and corrugated lamellae.



Meek (1873) thought this species bore revolving threads, but Miller (1874, p. 310, 311) claimed that what Meek described "were merely the rows formed by the flexures of the transverse lamellae." Miller's point is demonstrated in specimen USNM 315669 (pl. 44, fig. 11) in the last few visible corrugated lamellae near the apertural margin.

It is to be noted that like other Cincinnati species of the genus, *P. elegans* is associated with ramose bryozoa. Plate 45, figure 10, is only one of three of Ulrich and Scofield's specimens found "attached" at the aperture to a ramose bryozoan fragment. Two possibilities other than chance could explain this repeated association and position. The bellerophont could have used the elevated position for a site from which to suspension feed, or it may have been actually feeding at the surface of contact, either preying on the bryozoan itself or possibly grazing on algae growing on a dead colony. In any case, such occurrences probably reflect essentially instantaneous burial, in which the bellerophont clamped down, clinging to the bryozoan branch, and was entombed.

***Phragmolites dyeri* (Hall), 1872**

Plate 44, figures 8–10; Plate 45, figure 11

*Cyrtolites dyeri* Hall, 1872, p. 230, pl. 8, figs. 7, 8; Meek, 1873, p. 149, pl. 13, figs. 2a–c, not figs. 2d, e; Miller, 1874, p. 309.

*Conradella dyeri* (Hall), Ulrich and Scofield, 1897, p. 909, pl. 67, figs. 30–33; Cumings, 1908, p. 957, pl. 39, figs. 8a–c.

*Phragmolithes dyeri* (Hall), Grabau and Shimer, 1909, p. 618, figs. 823e, f.

*Phragmolites dyeri* (Hall), Bassler, 1915, p. 972.

**Diagnosis.**—Shell small (up to 9.0 mm long); apertural outline cordate; dorsal carina elevated, rounded, lacking distinct lunulae; corrugated growth lamellae very closely spaced, with about 10 reentrants per side; revolving threads prominent.

**Description.**—Shell small, rarely greater than 10 mm in diameter, gradually expanding, each whorl embracing about one-third of previous one. Apertural outline cordate; dorsal slopes broadly rounded, becoming more tightly enrolled at umbilical shoulders, ventral slopes convex, angled downward. Slit depth uncertain, but apparently less than one-half whorl; selenizone on elevated dorsomedian carina, crest rounded, lunulae lacking. Corrugated growth lamellae very closely spaced (four or five per millimeter), notched at contact with prominent spiral threads (about three per millimeter), straight to round or square between threads, about 10 notches from whorl shoulder to crest.

**Measurements.**—Measurements of *P. dyeri* are listed in table 45.

**Material.**—Ulrich and Scofield's (1897) hypotype material (USNM 45752) consists of four calcitic specimens and a small slab containing two additional speci-

TABLE 45.—Measurements (in millimeters) of *Phragmolites dyeri*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Ventral width
315673	8.0	6.5	4.0	4.5	3.0	1.6
45752	9.0	7.6	4.3	4.4	3.0	1.8
45752	5.7	—	2.5	2.8	2.0	—

mens. USNM 315673 (pl. 44, figs. 8–10) and USNM 315674 (pl. 45, fig. 11) were selected from the USNM 45752 suite for illustration of the species herein. Numerous unnumbered specimens in the collections of the University of Cincinnati and Miami University Geology Museums were examined.

**Distribution.**—Ulrich and Scofield (1897, p. 910) reported this species from the "Richmond Group" of southeastern Indiana, southwestern Ohio, north-central Kentucky, and near Spring Valley, Minn. Specimens examined here came from the Arnheim, Waynesville, and Liberty biofacies of the Bull Fork Formation (Richmondian) of the Indiana-Ohio-Kentucky area.

**Comparison.**—*P. dyeri* is readily distinguished from *P. bellulus* and *P. elegans* by its more cordate shaped aperture, its more closely spaced lamellae, its prominent spiral threads, and the absence of lunulae on its selenizone.

**Discussion.**—This species is rather uncommon, probably largely as a result of being overlooked because of its small size; when found, it is never abundant. Many specimens are quite well preserved, and they are generally found in association with a brachiopod-ramose bryozoan-trilobite assemblage. The small slab (USNM 315674) shown on plate 45, figure 11, is typical. The implications of the association between Cincinnati species of *Phragmolites* and ramose bryozoans are presented in the discussion of *P. elegans*.

Ulrich and Scofield (1897, p. 910) claimed that the revolving threads of *P. dyeri* were "as a rule not ridges at all, but only an appearance due to the elevation and longitudinal arrangement of the closely following loops of the transverse lamellae." Contrary to this claim, and in agreement with other descriptions, specimens examined here, including those of the Ulrich and Scofield collection (pl. 44, figs. 8–10), appear to have distinct revolving ridges independent of the scalloping of the lamellae.

Although lunulae generally appear to be lacking on the selenizone of this species, there is a suggestion of lunulae on the specimen shown on plate 44 (fig. 9).

From material examined, it appears that *P. dyeri*'s slit is much shorter than the general depth of one-half whorl, but at present an exact slit depth for the species cannot be given. It should be noted that the most closely related species, *P. bellulus* (Maysvillian), has a slit only one-

quarter whorl deep. It seems a reduction of slit depth may be characteristic of this latest Ordovician lineage of *Phragmolites*.

Genus *TEMNODISCUS* Koken, 1896

*Diagnosis*.—Shell small, disjunct to loosely coiled, relatively rapidly expanding; whorl slopes convex; aperture sinuate, with shallow slit; selenizone generally on truncated dorsum, narrow to broad, with lunulae, without distinct borders, can be ridgelike in submaturity; growth lines sublamellose to distinctly lamellose, finely crenulated in some cases, with fine revolving threads between growth lines.

*Type species*.—*Cyrtolites lamellifer* Lindstrom, 1884, by subsequent designation of Reed (1921, p. 47).

*Distribution*.—*Temnodiscus* is known from the Silurian of Sweden (Lindstrom, 1884) and Great Britain (Reed, 1921), and possibly from the Late Ordovician and Silurian of Bohemia (Horny, 1963a). The single known North American species is from late Middle Ordovician (Shermanian) strata near Cincinnati, Ohio.

*Comparison*.—*Temnodiscus* is distinguished from *Tropidodiscus* by its lamellose growth increments and revolving threads, from *Phragmolites* by its curved (sinuate), more finely crenulated lamellae, and from both by its generally more rapid rate of whorl expansion, its occasionally disjunct coiling, and its relatively shallow slit.

*Discussion*.—Koken (1896, p. 100) erected the genus *Temnodiscus* for five species placed in *Cyrtolites* that were described by Lindstrom (1884) from the Silurian of Sweden. Unaware of Koken's genus name, Ulrich (1897) proposed the genus *Cyrtolitina* for a single American species, *C. nitidula*, and the five species assigned by Koken to *Temnodiscus*; he also designated *Cyrtolites lamellifer* Lindstrom the type species. Reed (1921, p. 47) correctly recognized the validity of *Temnodiscus* indicating *C. lamellifer* as the type species (Knight, 1941, p. 345).

The familial placement of *Temnodiscus* is a subject of some uncertainty. Lindstrom (1884) and Ulrich and Scofield (1897) clearly described and figured slitbands in the species they described. Koken (1896) agreed with these descriptions, but then in 1897 gave a new description of the genus, in which he stated that no slitband was present (Reed, 1921, p. 47). Horny (1963a, p. 90), after describing three new species of *Temnodiscus* from the Ordovician-Silurian of Bohemia and examining Knight's (1941, pl. 10, figs. 3a-d) photographs of the type species, concluded that there was no real selenizone in *T. lamellifer* and congeneric species. He stated (p. 90), "The apparent selenizone originates from the very narrow and deep true sinus with nearly parallel sides." I also examined Knight's (1941) figures, and believe that the species

does have a true selenizone with distinct lunulae. However, the species described by Horny do not appear to have true selenizones; rather, they have sharp dorsal carinae. The species described by Reed (1921) are said to have narrow slitbands (with lunulae) mounted on flat-topped carinae; in one case (*T. monilifer*), the slitband is flattened in maturity, but becomes "narrower and completely (?) closed to form an acute keel in proximal part of shell" (p. 48).

The presence of a slit in *T. nitidula* (Ulrich) is also problematical. Its truncate dorsum seems to have distinct "lunulae," but some of these "lunulae" appear continuous with growth lines, whereas others do not (pl. 42, figs. 4, 6). There are no distinct bordering threads separating the selenizone from the dorsal slopes of the shell, and the emargination present is not nearly as deep as in species of *Tropidodiscus* and *Phragmolites*. This "pseudoselenizone" is similar to those of some other bellerophonacean species, such as *Tetranota bidorsata* (Hall) and *T. sexcarinata* Ulrich and Scofield (pls. 21, 22). Furthermore, the "pseudoselenizone" is relatively well defined compared with species such as *Sphenosphaera troosti* (d'Orbigny) (pl. 29) that have only a dorsomedian ridge but are clearly closely related to *S. clausus* (Ulrich) (pl. 30), which has an excellently defined slitband with lunulae.

In light of these observations, *Temnodiscus* is retained in the Tropidodiscidae. Direct comparison of specimens of species from the various areas is needed to determine the uniformity and validity of composition of the genus *Temnodiscus*.

*Temnodiscus nitidula* (Ulrich) 1897

Plate 42, figures 3-6

*Cyrtolites nitidula* Ulrich, 1879, p. 12, pl. 7, figs. 7, 7a.

*Cyrtolitina nitidula* Ulrich in Ulrich and Scofield, 1897, p. 866, pl. 62, figs. 53-55.

*Temnodiscus nitidula* Knight, 1941, p. 345.

*Diagnosis*.—Shell small (up to 9 mm long), rapidly expanding, relatively tightly coiled; dorsum broadly truncated, selenizone broad, with distinct lunulae; growth lines sublamellose; revolving threads fine.

*Description*.—Shell small, expanding rather rapidly to about two volutions; relatively tightly coiled for genus, the outer volution embracing about half of the inner one; umbilicus moderate in size, with rounded shoulders. Dorsal slopes entirely gently convex; dorsum broadly truncated; parietal deposits not seen; apertural outline subcordate. Selenizone broad, borderless, with distinct lunulae. Sinus deep, slit relatively shallow. Growth lines strong, apparently sublamellose, closely and evenly spaced, strongly curved. Fine revolving threads.

*Measurements*.—Measurements of *T. nitidula* are listed in table 46.

TABLE 46.—Measurements (in millimeters) of *Temnodiscus nitidula*

USNM No.	Shell length	Aperture length	Aperture width	Umbilical diameter	Ventral width	Selenizone width
315542	9.0	5.5	5.4	5.0	2.0	1.1
315543	7.8	5.1	4.9	4.0	1.5	1.1

**Material.**—The four specimens located were Ulrich's types, all cataloged under USNM 45793. Shell material is lacking in all, but external ornament is well preserved, and thus the specimens probably are composite molds. From this suite, USNM 315542 (pl. 42, figs. 3, 4) is designated the lectotype, and USNM 315543 (pl. 42, figs. 5, 6) and the other two specimens (left under the original number) are paralectotypes.

**Distribution.**—Ulrich and Scofield (1897, p. 867) cited the species as occurring in the "upper part of the Trenton Group, in the river quarries just west of Covington, Kentucky." These beds are now assigned to the Point Pleasant Tongue of the Clays Ferry Formation (Shermanian).

**Comparison.**—Probably the species most easily confused with *T. nitidula* would be the monoplacophorans *Cyrtolites* (*Paracyrtolites*) *carinatus* and *C. (P.) parvus*. Both can be readily distinguished from *T. nitidula* by their carinate, rather than distinctly truncate, dorsal sides.

**Discussion.**—This species is rare, possibly because of its small size and the apparent lack of preservation of its shell. It cannot be confirmed, but the uniform preservation of the type suite suggests collection from a single bed.

#### Family BUCANIIDAE Ulrich and Scofield, 1897

**Diagnosis.**—Shell having numerous volutions that are barely contiguous to slightly overlapping, with early volutions visible in moderately narrow to wide umbilicus; generally having shallow labral slit that generates a selenizone; shell surface having collabral growth lines or lamellae, which generally are crossed by revolving lines varying from angular ridges to threads.

**Stratigraphic range.**—Lower Ordovician-Devonian.

**Discussion.**—Ulrich and Scofield (1897) erected this family and included some genera that have since been removed. Knight (1956) recognized the distinctiveness of some of the genera and moved them to the Tropicodiscidae. Peel (1972), demonstrating that the genus was sinuate and did not possess a true slit, placed *Tremanotus* in the Tremanotidae.

There has never been significant disagreement about the distinctiveness of this family, only about how the distinctiveness should be expressed in the classification scheme within the Bellerophontacea. Koken (1925),

Knight and others (1960), and Horny (1963a) considered the grouping to be a subfamily of the Bellerophontidae. Ulrich and Scofield (1897), Dall in Eastman (1913), Wenz (1938), and Golikov and Starobogatov (1975) have considered the grouping to be an independent family, as is done herein. The separation of the Bucaniidae from the Bellerophontidae expresses more clearly that the former group is a distinct and more primitive phylogenetic entity.

The Bucaniidae encompasses four recognized subfamilies—Bucaniinae (Ulrich and Scofield, 1897), Salpingosomatinae (Koken, 1925), Plectonotinae (Boucot and Yochelson, 1966), and Undulabucaniinae new subfamily.

As is obvious from its name, the Lower Ordovician genus *Eobucania* Kobayashi, 1955, was from its inception considered to be closely related to *Bucania*. Knight and others (1960) placed *Eobucania* in the Bucaniinae, thus supporting such a relationship. However, *Eobucania* bears as much, or more, resemblance to the Tropicodiscidae as to the Bucaniidae. Like *Tropicodiscus*, *Eobucania* has a deep slit and only fine, closely spaced collabral shell markings. The aperture in *Eobucania* does flare and expand like that of a bucaniid, but its whorl form is quite distinct. *Eobucania* is intermediate in morphology and phylogeny between *Tropicodiscus* and *Bucania*, and probably represents a group of early bellerophontaceans some species of which gave rise to *Bucania* and its relatives. Thus, it is understandable that *Eobucania* would be difficult to classify at the family level; however, as noted below, it is here placed in the Bucaniinae.

#### Subfamily BUCANIINAE Ulrich and Scofield, 1897

**Diagnosis.**—Shell with apertural margins tending to flare, mainly laterally; slit relatively short, open at apertural margin; collabral growth lines in many cases crossed by revolving threads.

**Stratigraphic range.**—Lower Ordovician-Devonian.

**Genera included.**—*Bucania* Hall, 1847, *Kokenospira* Bassler, 1915, ?*Megalomphala* Ulrich and Scofield, 1897, and *Eobucania* Kobayashi, 1955 are members of this subfamily. Horny (1963a) removed *Coelocyclus* Perner, 1903, from the Bucaniinae, where it had been placed by Knight and others (1960), and assigned it to the subfamily Cymbulariinae Horny of the Bellerophontidae. However, *Coelocyclus*'s open umbilicus and depressed whorls suggest that it should remain with the bucaniids.

**Genera considered here.**—*Bucania*, *Kokenospira*.

**Discussion.**—Bucaniinae is the core grouping of the family Bucaniidae; it encompasses nearly the same grouping of genera considered the tribe Bucaniides by Knight and others (1960). The group apparently descended from the tropicodiscids through an intermediate stock such as that represented by the Lower

Ordovician genus *Eobucania*. It would seem that the other subfamilies of the Bucaniidae, as well as possibly the subfamily Bucanopsinae of the Bellerophontidae, evolved from the Bucaniinae during the Early to Middle Ordovician radiation of the bellerophontaceans.

#### Genus BUCANIA Hall, 1847

*Diagnosis.*—Shell having medium to large umbilicus; revolving ornamentation running normal to, and generally interrupted by, growth lines or lamellae.

*Description.*—Shell size from small to large, the whorls rounded or depressed and generally gradually expanding; umbilicus medium to large. Outer aperture lip thin, with broad, V-shaped sinus and central slit; slit shallow to quite deep; selenizone generally narrow, being slightly elevated, flat, or channellike; inner aperture of lip thickened in many cases. Shell surface marked by transverse growth lines or lamellae and revolving threads; revolving threads run normal to, and are generally interrupted by, growth lines; growth lines in many specimens become lamellose in maturity, accompanied by a general thickening of the whorl laterally and posterolaterally.

*Type species.*—*Bellerophon sulcatus* Emmons, 1842, by subsequent designation of Waagen (1880, p. 130).

*Distribution.*—Lower Middle Ordovician (Chazy) to Middle Silurian (Niagaran) in Eastern North America (Bassler, 1915), and Middle Ordovician to Silurian in Europe and northeast Asia (Knight and others, 1960).

*Comparison.*—*Salpingostoma* Roemer, 1876, differs from *Bucania* in having abrupt expansion of the adult whorls and a long, distally closed off slit. *Tetranota* Ulrich and Scofield, 1897, differs in having the selenizone mounted on a broad, elevated dorsomedian band, in many cases with one or two lateral ridges. Members of the new genus *Undulabucania* resemble species of the *Bucania sulcatina* group (see discussion below) in shell form, but differ in lacking revolving threads and having the more *Phragmolites*-like features of a deep slit and regularly wavy growth lines.

*Discussion.*—Hall (1847, p. 32) erected the genus *Bucania* for those species previously assigned to *Bellerophon* Montfort (1808) that have an umbilicus of sufficient size to reveal the earlier volutions. In the following years, most authors found it impossible to mark a proper boundary between *Bucania* and *Bellerophon* based solely on umbilical size, and therefore generally considered the two names synonyms. Nevertheless, Hall (1861, p. 93) reaffirmed his contention that *Bucania* was a useful genus; unfortunately, he offered no further supportive evidence.

Waagen (1880, p. 150) asserted that the primary taxobasis of the genus *Bucania* was its spiral ornamentation.

He noted that the umbilicus was generally larger in species of *Bucania* than in species of *Bellerophon*, but he believed that the overlap between the two genera excluded that characteristic as the primary taxobasis. Waagen also emphasized the presence of distinct transverse growth lines crossing the revolving threads, and the general thinness of the shell, except for the massive thickening of the inner lip in many species.

Ulrich and Scofield (1897, p. 883, 884) commended Waagen's definition of the genus, but showed that it was too broad, encompassing a variety of distinct forms that also bear revolving ornament (such as *Salpingostoma*, *Kokenospira*, and *Bucanopsis*). Until now, Ulrich and Scofield's review and redefinition of the genus was the most definitive statement on *Bucania*. They believed that *Bucania* should be restricted to species that have fairly large umbilici, a broad, V-shaped sinus with a central slit, and the characteristic shell markings. They emphasized that these shell markings differed from other genera having revolving lines, in that both the revolving and transverse markings in *Bucania* were oblique to the direction of coiling. All other comparable genera are characterized by revolving lines parallel to the direction of coiling.

Ulrich and Scofield (1897, p. 851) recognized two informal "groups" of species. The first, their "typical section" (the *B. sulcatina* group herein), was characterized by a thin shell, a broad umbilicus, broad whorls with a slow expansion rate, no massive parietal thickening, and a long slit. The second group, referred to as both the "*B. nashvillensis* section" (p. 851) and the "*B. lindsleyi* section" (p. 884), was described as having a thicker shell, a smaller umbilicus, more rapidly expanding whorls with a relatively longer aperture, in many cases with massive parietal thickening, and a shorter slit. These two groups are left informal here because, although the two end members, *B. sulcatina* and *B. lindsleyi*, are distinct, some species are gradational between them and exhibit characteristics of both groups. For example, *B. rugatina* resembles *B. lindsleyi* in its small umbilicus and its surface markings, but was placed in the *B. sulcatina* group by Ulrich and Scofield (1897) because of its gradual whorl expansion and thin shell.

The *B. sulcatina* group is more primitive than, and ancestral to, the *B. lindsleyi* group. The former group is mainly Chazy and Blackriveran in age, with only two known Kirkfieldian-Shermanian species. The *B. lindsleyi* group first appeared during Kirkfieldian time and continued into the Silurian Period.

At one time, Knight (1942, p. 487) advocated placement of the *B. lindsleyi* group in the genus *Lorobucania* Knight, which he claimed was essentially the genus *Bucania* as conceived by Ulrich and Scofield (1897, p. 850). They had characterized *Bucania* largely by the

possession of revolving ornament that runs normal to the apertural margin (and thus the growth lines), converges inward upon the slit and selenizone, and is generally interrupted by the growth lines or lamellae (pl. 14, fig. 14; pl. 17, fig. 2; pl. 18, fig. 7). Knight (1942) pointed out that *B. sulcatina*, the type species of *Bucania*, differs from that definition by the possession of revolving ornament that meets the apertural margin at a slight angle, runs parallel to the selenizone, and continues uninterrupted by the growth lines (pl. 12, figs. 1-5). Examination of Knight's (1941, pl. 11, figs. 1a, b) figures of the holotype of *B. sulcatina* confirms these observations. However, Knight and others (1960, p. 1180) placed *Loxobucania* in synonymy with *Bucania*. I have found no explanation for this reversal in judgment; it might be explained in the following manner. The members of the *B. sulcatina* group do not have a deep, V-shaped sinus with broadly rounded anterolateral apertural margins, as do members of the *B. lindsleyi* group. Rather, members of the *B. sulcatina* group have nearly straight anterior apertural margins (as reflected by their straight dorsal growth lines) that angle back slightly to form a very broadly obtuse, shallow, anteromedian sinus (pl. 12, fig. 5). The revolving ornament seems to be nearly normal to this straight apertural margin. It appears that in the more advanced group the revolving threads came to converge on the selenizone at a higher angle by the curving of the anterior apertural margin and development of a deep, V-shaped sinus (pl. 18, fig. 7). *B. sulcatina* and its allies probably did not need a deep sinus to assist in efficient circulation of water through the mantle cavity because they had a deep slit.

As pointed out elsewhere in this paper, the broken dorsal shells of numerous specimens of other deep-slit-bearing genera, such as *Salpingostoma* and *Tropidodiscus*, suggest a structural weakness of the shell in that area. The shortening of the slit and development of a deeper V-shaped sinus may have been apertural modifications in more advanced species of the genus *Bucania*, modifications that allowed maintenance of efficient water circulation through the mantle cavity as well as strengthening of the shell dorsum. Because of the gradational morphologic progression between the end-member species of these two groups, the genus *Loxobucania* is not used herein.

The *B. sulcatina* group is thought here to have descended from the *Phragmolites* stock of the tropidodiscids. Both groups have wide umbilici, long slits, and revolving ornament. The new genus *Undulabucania* also appears to have developed from that common stock. *U. punctifrons* was included in the "*B. sulcatina* group" by Ulrich and Scofield, but it differs significantly from the other species in that group in its lack of spiral ornament

and its wavy growth lines reminiscent of the corrugated shell markings of *Phragmolites*.

The genus *Salpingostoma* undoubtedly is closely related to, and probably evolved from, a species of *Bucania*. Juveniles of species of *Salpingostoma* are very similar to the "*B. sulcatina* group" in their large umbilici, depressed whorls, thin shell, and deep slit. Upon adult expansion, these species take on a shell form similar to members of the "*B. lindsleyi* group," with a longer aperture and thickened parietal lip. Also, the two genera have very similar shell markings.

#### *Bucania emmonsi* Ulrich and Scofield, 1897

Plate 12, figures 1-4

*Bucania emmonsi* Ulrich and Scofield, 1897, p. 887, pl. 66, figs. 1-3.

**Diagnosis.**—Shell widely umbilicate, umbilical slopes gently convex, sutures deep with wavy indentations; shell width increases by 2.8 times in one volution; revolving threads strongly angled mediad over dorsum.

**Description.**—Shell relatively small (up to 18 mm long), thin, consisting of three or four volutions; rate of whorl expansion fairly rapid, the shell width increasing by about 2.8 times in one volution. Umbilici widely open, so that all earlier whorls are clearly visible; umbilical slopes gently convex, causing whorl sutures to be quite deep. Ventral whorl surface, as visible along suture lines, has numerous gentle, wavy indentations. Shell dorsum gently and evenly convex, and umbilical shoulders sharply to narrowly rounded, giving aperture a rounded, subtrapezoidal outline. Slit unknown, but selenizone narrow and channellike.

Shell ornament dominated by revolving threads, which are equal in strength but widen slightly in their spacing outward from the dorsomedian line and number about 12 on either side; revolving threads pass over shell dorsum with obvious obliqueness to direction of coiling, angling mediad at about 10 degrees toward selenizone, and angling laterad on ventral shell slopes, thus always remaining perpendicular to curved growth lines and growing shell margin; growth lines only faintly visible, reflecting a rather straight sided, slightly convex, V-shaped apertural sinus.

**Measurements.**—Measurements of *B. emmonsi* are listed in table 47.

**Material.**—The lectotype of *B. emmonsi*, numbered USNM 46049, is a silicified replica that was figured by Ulrich and Scofield (1897, pl. 66, figs. 1-3). The other syntype, USNM 46050, is now the paralectotype.

**Distribution.**—The lectotype, USNM 46049, was collected from the Murfreesboro Limestone (Blackriveran) at Murfreesboro, Tenn. Ulrich and Scofield (1897, p. 888) also cited the species from the *Vanuxemia* and *Ctenodonta* beds of Minnesota, which Weiss (1957, fig. 1)

TABLE 47.—Measurements (in millimeters) of lectotype of *Bucania emmonsi*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Dorsal width	Posterior width	Ventral width	Selenizone width
46049	18.4	14.25	10.0	17.0	12.15	11.45	7.85	6.1	0.5

considered parts of the Platteville (Rockfieldian) and Decorah (Kirkfieldian) Formations, respectively.

*Comparison.*—This species is distinguished from *B. halli* by its smaller size, its more rapid whorl expansion, and its larger number of revolving threads, which are more obtuse to the midline. *B. emmonsi* also resembles *B. intexta* Hall (Middle Ordovician, New York), but differs from that species, and all others, by the wavy indentations on its deep suture lines.

*Bucania halli* Ulrich and Scofield, 1897

Plate 12, figures 5–18

*Bucania halli* Ulrich and Scofield, 1897, p. 886, pl. 66, figs. 4–8; Grabau and Shimer, 1909, p. 614, fig. 822; Wilson, 1951, p. 27, pl. 2, figs. 15, 16.

*Diagnosis.*—Shell widely umbilicate, umbilical shoulders subangular, umbilical slopes nearly flat; shell width increases by about 2.25 times in one volution; revolving ribs equal in strength and spacing, angled very slightly toward selenizone.

*Description.*—Shell moderate in size (20–30 mm long); three or four volutions; depressed whorls increase in size gradually, the shell width increasing by about 2.25 times in one volution; umbilicus widely open, umbilical shoulders subangular to sharply rounded, and umbilical slopes nearly flat. Shell dorsum broadly and evenly convex, ventral whorl gently concave, reflecting opposing shape of previous whorl; aperture shape subtrapezoidal, length/width ratio 6.2.

Revolving threads dominate shell ornament, consisting of about 12 dorsal threads on either side of selenizone that angle very slightly toward midline; weaker growth lines interrupt revolving threads only slightly, and are only slightly curved across dorsal slopes, reflecting a broad, shallow, V-shaped sinus. Slit unknown; selenizone slightly elevated, but concave.

*Measurements.*—Measurements of *B. halli* are listed in table 48.

*Material.*—The lectotype designated herein is specimen USNM 45717 (pl. 12, figs. 5–9), which is apparently

a composite mold dorsally and an internal mold in the umbilical areas. This specimen from Minnesota was illustrated previously by Ulrich and Scofield (1897, pl. 66, figs. 4, 5).

The remainder of the syntypic suite consists of seven specimens from the Curdsville Limestone Member of the Lexington Limestone of Mercer County, Ky. Six of these are poorly preserved internal molds, and are here designated paralectotypes under the original number, USNM 45718. The seventh, also a paralectotype (USNM 315582), is a very weathered silicified specimen retaining some aspect of the shell on the posterior coil and around the aperture (pl. 12, figs. 10–14); it may be the specimen figured in outline by Ulrich and Scofield (1897, pl. 66, fig. 8).

Two specimens of *B. halli* were found in the USGS silicified collections from Kentucky. The first, USNM 315544 (pl. 12, figs. 15, 16), is from the Grier Limestone Member (4073-CO), and the second, USNM 315545 (pl. 12, figs. 17, 18), is from the lower Curdsville Limestone Member (5100-CO), both from the Lexington Limestone. The first is referred to *B. halli* with confidence. However, the second is referred to *B. cf. B. halli*; it is an internal mold, apparently with a very thick shell remnant. This latter specimen's shell form (depressed whorls, wide umbilicus) agree well with *B. halli*, and the apparently thick shell may reflect expansion during silicification.

*Distribution.*—The lectotype (USNM 45717) is from the Decorah Formation (Rocklandian) (Black River Group of Ulrich and Winchell, 1897) at Cannon Falls, Minn. The paralectotypes, USNM 45718 and 315582, are from the Curdsville Limestone Member (Kirkfieldian) of the Lexington Limestone of Mercer County, Kentucky. USNM 315544 is from USGS sample 4073-CO, Grier Limestone Member (Shermanian) of the Lexington Limestone, and USNM 315545 is from USGS sample 5100-CO, Curdsville Limestone Member of the same formation (Kirkfieldian). Wilson (1951, p. 27) reported *B.*

TABLE 48.—Measurements (in millimeters) of *Bucania halli*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Dorsal width	Posterior width	Ventral width	Selenizone width
45717	21.3	15.0	10.5	16.9	13.8	13.20	10.0	7.5	0.8
315582	37.0	23.1	23.7	30.0	14.9	16.75	14.8	12.3	—

TABLE 49.—*Measurements (in millimeters) of Bucania subangulata*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Dorsal width	Posterior width	Ventral width	Selenizone width
315559	22.55	19.0	19.5	30.0	11.5	11.5	7.1	6.3	—
315560	22.30	14.5	14.5	—	10.5	10.5	7.5	—	1.4
315575	13.35	9.2	6.4	10.2	6.1	7.0	5.4	3.3	—
315578	—	—	—	21.7	—	12.8	—	6.8	—
265989	9.60	6.3	6.4	7.8	4.5	5.5	4.0	—	0.6
315576	14.30	8.9	9.0	10.9	6.5	6.8	4.7	2.8	0.9
315577	—	—	—	16.8	—	10.7	—	—	—
315596	—	—	—	13.2	—	7.9	5.9	3.8	—

*halli* from the Lowville and Leray beds (Blackriveran) of eastern Canada.

*Comparison.*—*B. halli* resembles *B. emmonsii*, both having the broad umbilici and depressed whorls of the *B. sulcatina* group. However, the whorls of *B. halli* expand more slowly (the width increasing by about 2.25 times in one volution, compared with 2.8 times in *B. emmonsii*). The umbilical shoulders of *B. halli* are more angular, its umbilical slopes are flatter, and its revolving threads approach the dorsomedian selenizone at a smaller angle.

*Discussion.*—Specimen USNM 315544 (pl. 12, figs. 15, 16) confirms the occurrence of *B. halli* in the Ordovician of Kentucky. The internal molds of the type suite (USNM 45718) are questionable in their species assignment. The figured paralectotype (pl. 12, figs. 10–14), USNM 315582, shows differences from the lectotype cf. *B. halli*. It may be the specimen shown in Ulrich and Scofield's plate 66, figure 8, which they said was only doubtfully referred to the species, "the back being unusually convex and the sides too blunt." When one examines the photographs of this specimen, it appears that the whorls are depressed and less convex in the early portion of the last whorl, but about one-third through that volution the whorl begins to expand toward the anterior, making the whorl much more convex dorsally. The umbilical form of USNM 315582 (pl. 12, figs. 12, 13) is comparable to that of the lectotype (pl. 12, fig. 9), both having subangular shoulders and flat slopes, but the umbilical form of USNM 315582 appears slightly deeper. It should be noted that in the last one-third volution of the lectotype, the shell shows a tendency toward increased anterior expansion of the whorl. Finally, specimen USNM 315582 shows strong lamellose growth lines on the expanded aperture (pl. 12, figs. 13, 14), whereas the lectotype (which is a composite mold) shows only weak evidence of growth lines. However, it is common in bucaniids for growth lines to become stronger, and even lamellose, in maturity. Therefore, the specimen is assigned to *B. halli*. In doing so, it is shown that the *B. sulcatina* group may have undergone an expansion and thickening of the shell similar to that of the *B. lindsleyi* group in maturity. It might also be noted

that the mature *B. halli*, as shown by specimen USNM 315582, somewhat resembles the Richmondian species *B. crassa* (pl. 19, figs. 7–10) in its highly convex dorsum and angular, deep umbilicus. However, *B. crassa* is more globose.

***Bucania subangulata* Ulrich, 1897**

Plate 14, figures 15–19; Plate 15, figures 8–24;

Plate 38, figures 11, 12

*Bucania subangulata* Ulrich in Ulrich and Scofield, 1897, p. 891, pl. 66, figs. 20–23.

*Diagnosis.*—Shell small, rapidly expanding; umbilicus moderately wide; whorl shape cordate to subtriangular; aperture slightly flared in maturity; selenizone elevated, flat; growth lines sublamellose, scalloped.

*Description.*—Shell small (up to 22.5 mm long) but rapidly expanding, consisting of about 3.5 volutions at maturity; umbilicus moderately wide, clearly exposing earlier whorls; dorsum rounded in juveniles, but becoming increasingly angular with a greater rate of aperture length growth, resulting in a prominent dorsomedian angle with steep, gently convex dorsolateral slopes; umbilical shoulders narrowly rounded to angular, umbilical slopes cut inward sharply and nearly flat. Adult apertural outline cordate to subtriangular. Selenizone moderately wide and nearly flat topped, showing distinct lunulae in some specimens. Growth lines broadly sweeping, becoming sublamellose with scalloped margins in maturity; revolving threads fine and closely spaced.

*Measurements.*—Measurements of *B. subangulata* are listed in table 49.

*Material.*—The type suite, USNM 45731, consists of eight silicified syntypes. Six of these are small and too poorly preserved to yield significant data; they are designated paralectotypes, are not figured, and are cataloged under the type suite number. A seventh syntype, here designated a paralectotype, is figured under the number USNM 315560 (pl. 14, fig. 19). The eighth syntype is here designated the lectotype, USNM 315559 (pl. 14, figs. 15–18). I note that the anteromedian portion of the lectotype was reconstructed with plaster by the



TABLE 50.—Measurements (in millimeters) of *Bucania lindsleyi*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Dorsal width	Posterior width	Ventral width	Selenizone width
315550	~36.0	22.2	21.8	30.5	13.0	21.0	17.0	14.7	2.0
315551	19.8	14.3	10.6	18.0	7.6	13.2	11.0	8.0	1.5

original author, but the reconstruction appears correct to me.

A number of specimens belonging to this species were found in the USGS silicified collections. USGS sample 7785-CO yielded four specimens that appear to be silicified internal molds; one is figured as USNM 315575 (pl. 15, figs. 8–12). USGS sample 5094-CO contained six specimens, including USNM 265989 (pl. 38, figs. 11, 12), 315576 (pl. 15, figs. 13–15), 315577 (pl. 15, figs. 16–20), and 315596. USGS sample 5096-CO contained two fragments, including USNM 315578 (pl. 15, figs. 21–24).

*Distribution.*—The type material was collected from the “Flanagan beds,” an outdated unit in the upper Lexington Limestone (Shermanian) subsequently found to represent several silicified horizons, 1.5 mi south of Burgin, Ky. The type suite may be from the Grier or Perryville Limestone Members of the Lexington Limestone.

The species is recognized here from the Curdsville Limestone Member (7785-CO) and Grier Limestone Member (5094-CO, 5096-CO) of the lower part of the Lexington Limestone.

*Comparison.*—Ulrich and Scofield (1897, p. 891) stated that *B. subangulata* could be distinguished from the associated *B. rugatina* by its subtriangular apertural outline. The more similar species *B. frankfortensis* and *B. nashvillensis*, which also have an angular dorsum (though to somewhat different degrees), can be readily distinguished from *B. subangulata* by their larger shells and smaller umbilici.

Another feature that helps in recognizing this species is the sublamellose, scalloped growth lines on the adult dorsolateral slopes. The scalloping may be accentuated by weathering of the fine revolving threads along the margins of the sublamellose growth lines. The feature is present in both the lectotype (pl. 14, figs. 15–18) and the USGS material (pl. 15, figs. 14, 15, 21, 24), and is not as well developed in any other species.

*Discussion.*—The rapidly expanding shell and dorso-median angulation of *B. subangulata* indicate a relation to *B. frankfortensis* and *B. nashvillensis*. The larger umbilicus of *B. subangulata* may indicate that it is more primitive than these other species, because large umbilici are characteristic of the *B. sulcatina* group.

The lectotype, USNM 315559 (pl. 14, figs. 15–18), shows the overall morphology of the species better than any other known specimen. The paralectotype, USNM

315560 (pl. 14, fig. 19), shows two critical morphological features not clearly visible on the lectotype, the truncated slitband with lunulae and the fine revolving lines (on the right dorsolateral slope). A number of the USGS specimens exhibit the scalloping of the growth lines (pl. 15, figs. 14, 15) also seen in the lectotype (pl. 14, fig. 17). Specimen USGS 315577 (pl. 15, figs. 16–20) preserves the slitband; such preservation is unusual for such a small specimen.

Ulrich and Scofield (1897, p. 891) stated that this species was associated with *B. rugatina* in the upper Lexington Limestone. Specimen USNM 265989 (pl. 38, figs. 11, 12) shows that the species also occurs in association with *Carinaropsis cymbula*.

#### *Bucania lindsleyi* (Safford), 1869

Plate 18, figures 1–9

*Bellerophon lindsleyi* Safford, 1869, pl. 3(G), figs. 3a, b, d, e.

*Bucania lindsleyi* Safford, Ulrich and Scofield, 1897, p. 889, pl. 66, figs. 24, 25; Bassler, 1932, pl. 20, fig. 28.

*Diagnosis.*—Shell rapidly expanding, broadly and evenly convex dorsally; selenizone concave, lunulae strong; revolving threads and growth lines strong, latter becoming lamellose in adulthood.

*Description.*—Shell moderately large (up to 36 mm long), consisting of three to four fairly rapidly expanding whorls which are rather closely coiled; umbilicus of moderate size and deep, with rather narrowly rounded shoulders and steeply cut, slightly convex umbilical slopes; dorsum of shell broadly convex, becoming broader and more evenly convex through growth, becoming nearly semicircular; whorl outline distinctly wider than long, and rather flat ventrally. Aperture lips remain thin, even on inner side, and even in adulthood. Selenizone distinct, bordered by thin ridges, wide, broadly concave, and marked by strong lunulae; slit unknown. Revolving threads strongly developed over entire shell, including umbilical slopes; growth lines also distinct, being broadly curved, reflecting a rather deep apertural sinus, becoming very lamellose in adulthood, and being very regularly spaced throughout growth.

*Measurements.*—Measurements of the lectotype and a paralectotype of *B. lindsleyi* are listed in table 50.

*Material.*—The three syntypes of the species examined were cataloged as USNM 45719. No other specimens were found. Two of the syntypes are figured here. One is now numbered USNM 315550, and is designated

TABLE 51.—*Measurements (in millimeters) of Bucania nashvillensis*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Dorsal width	Posterior width	Ventral width	Selenizone width	Slit length
315557	25.8	15.3	18.1	26.0	9.2	14.4	11.4	~7.8	1.4	~5.3
315558	—	21.1	26.1	27.8	—	—	—	—	1.8	~6.6
45724	~36.0	21.7	~27.0	~33.0	~12.9	19.3	14.4	10.1	1.5	—
315566	—	~11.1	—	~16.2	~6.1	10.0	7.3	—	—	—
315567	—	~15.9	—	~19.8	~9.5	~11.3	~8.3	~6.3	~0.7	—
315569	—	16.2	—	~20.0	8.1	—	—	—	1.3	—

the lectotype (pl. 18, figs. 1–6). The other is now USNM 315551, and is designated a paralectotype (pl. 18, figs. 7–9). The third syntype, an unfigured paralectotype, remains cataloged under the original museum number. All three are brown, weathered, silicified replicas. The lectotype is quite well preserved, probably because it was largely encrusted by bryozoans, most of which have been broken away to reveal the shell.

*Distribution.*—Ulrich and Scofield (1897, p. 890) and Bassler (1915, p. 136) cited *B. lindsleyi* as coming from the Catheys Formation of Dekalb County, Tenn., and possibly from the Prosser Formation near Cannon Falls, Minn. Both occurrences are in Shermanian-Edenian-age strata.

Bassler (1932) listed the species from the *Stromatacearium pustulosum* bed of the Catheys Formation, and the Cannon Limestone (Kirkfieldian-Shermanian) of central Tennessee.

*Comparison.*—*B. lindsleyi* differs from the closely related *B. nashvillensis* in being somewhat less tightly coiled, resulting in a larger umbilicus, in having a broadly rounded rather than angled whorl dorsum, in having a depressed, channellike rather than elevated selenizone, a thinner shell, and stronger shell markings. *B. micronema* is similar to *B. lindsleyi*, but the former is much smaller, and its revolving threads are finer and slightly wavy. *B. lindsleyi* differs from *B. rugatina* in being larger, less tightly coiled, and less expanded and having a concave selenizone.

*Discussion.*—*B. lindsleyi* and *B. nashvillensis* are closely related. They are representative of the more advanced group of bucaniids, which was designated informally by Ulrich and Scofield (1897, p. 851, 844, 886). They are the earliest known members of this informal group of species and gave rise to a number of late Middle and Upper Ordovician species. *B. lindsleyi* apparently evolved from the *B. sulcatina* group by the lengthening of the whorl outline and the development of a tighter coil, which was probably an adaptation facilitating the carrying and balancing of the shell.

#### *Bucania nashvillensis* Ulrich, 1897

Plate 13, figures 15–21; Plate 14, figures 1–14;  
Plate 15, figures 1–7; Plate 27, figures 21, 22

*Bucania nashvillensis* Ulrich in Ulrich and Scofield, 1897, p. 890, 891, pl. 66, figs. 36–40; Bassler, 1932, pl. 20, figs. 19, 20.

*Diagnosis.*—Shell having somewhat flattened dorso-lateral slopes and subangular dorsum; umbilici relatively small; transverse and radial ornament distinct.

*Description.*—Shell moderately large (up to 36 mm long), consisting of about three rapidly expanding volutions; coiling rather tight, umbilicus relatively small and deep. Dorsolateral whorl slopes slightly flattened, making the dorsal crest subangular; umbilical shoulders tightly rounded; ventral whorl only slightly concave, with low, broad hump on parietal floor, reflecting adjacent subangular dorsum. Aperture broad and roughly subtriangular. Shell becomes quite thick in mature growth, particularly along posterolateral (inner) whorl slopes. Slit fairly deep, about one-fourth the aperture length, and situated in broad, rounded sinus; selenizone moderately wide, forming a flattened to slightly elevated crest to subangular dorsum. Growth lines evenly and closely spaced, becoming coarsely lamellose in later growth; revolving threads closely spaced, and, although distinct, weaker than growth lines and much stronger dorsally than within umbilicus.

*Measurements.*—Measurements of *B. nashvillensis* are listed in table 51.

*Material.*—Ulrich's (1897) type suite consists of six silicified syntypes; five are numbered USNM 45725, and one is numbered USNM 45724. Three of these syntypes are figured here: USNM 315557 (from suite 45725) (pl. 14, figs. 10–14) is here designated the lectotype; USNM 315558 (from suite 45725) (pl. 14, figs. 6–9), USNM 45724 (pl. 14, figs. 1–5), and the three unfigured specimens left under number USNM 45725 are designated paralectotypes.

Numerous specimens in the USGS silicified collections from the Lexington Limestone of Kentucky are assigned to this species. Those figured here are designated USNM

315566 (pl. 13, figs. 15, 16), 315567 (pl. 13, figs. 17, 18), 315568 (pl. 13, fig. 19), 315569 (pl. 13, figs. 20, 21), 315572 (pl. 15, figs. 1, 2), 315573 (pl. 15, figs. 3–5), and 315574 (pl. 15, figs. 6, 7). Another new silicified specimen from Tennessee, UCGM 44284, is shown on plate 27, figures 21 and 22. In all, about 32 new specimens were identified as *B. nashvillensis*.

*Distribution.*—Ulrich and Scofield's (1897) type specimens are labeled as coming from the Cannon facies of the Bigby-Cannon Limestone (Kirkfieldian-Shermanian) at Nashville and in Dekalb County, Tenn. Specimen UCGM 44284 is from the same unit at a "hill north of Well No. 1, Smith Co., Tennessee."

Specimens of *B. nashvillensis* in the USGS silicified collections from Kentucky came from the Grier Limestone Member (4073-CO, 4959-CO) and the Salvisa (5015-CO, 6915-CO, 6916-CO) and Faulconer (6136-CO) Beds of the Perryville Limestone Member (Shermanian) of the Lexington Limestone.

*Comparison.*—The six type specimens for which this species was named were originally assigned to *Bucania lindsleyi* (Safford) by Safford (1869), but Ulrich and Scofield (1897, p. 890) concluded that they constituted a distinct species. *B. nashvillensis* has a slightly more rapid rate of whorl expansion and is more tightly coiled, resulting in a slightly smaller and deeper umbilicus (pl. 14, figs. 3, 12; pl. 27, fig. 22) compared with *B. lindsleyi* (pl. 18, fig. 3). The dorsum of *B. nashvillensis* is slightly angled medially and has somewhat flattened dorsolateral slopes (pl. 14, figs. 1–5, 6, 9, 11, 13), whereas that of *B. lindsleyi* is broadly rounded (pl. 18, figs. 1, 7). The slitband of *B. nashvillensis* is slightly elevated (pl. 14, figs. 2, 6, 13) instead of channellike (pl. 18, figs. 1, 5, 7), and the lunulae are not as strongly developed as in *B. lindsleyi* (pl. 18, figs. 5, 7). Differences in shell sculpture between the two species cited by Ulrich and Scofield (1897, p. 890) are difficult to evaluate because of generally poor preservation, but one point is certain: the revolving threads of *B. nashvillensis* (pl. 14, figs. 3, 7, 13, 14) are much weaker than those of *B. lindsleyi* (pl. 18, figs. 3, 4, 6, 7). Finally, the shell is thicker in *B. nashvillensis*.

*Discussion.*—Prior to this study, *B. nashvillensis* had been reported only from the Bigby-Cannon Formation of Tennessee. Ulrich and Scofield (1897, p. 891) cited the species from the "Trenton group, Dekalb County, and Nashville, Tennessee." Bassler (1932, p. 106, pl. 20, figs. 19, 20) reported the species from the "Cannon limestone," which is in agreement with the labeling of the type suite. Wilson (1949, p. 118, 125), on the other hand, reported the species from only the Bigby and dove-colored facies of the Bigby-Cannon Limestone. Specimen UCGM 44284 (pl. 27, figs. 21, 22) was in a collection of

gastropods from the Cannon facies in Smith County, Tenn.

Numerous fragmentary specimens from the USGS silicified material from Kentucky are smaller than the large specimens of the type suite (pl. 14, figs. 1–14); however, they resemble these type specimens in their angular whorl forms. The characteristic revolving threads of *Bucania* are not clearly preserved on any of these specimens from the Lexington Limestone of Kentucky, but neither are they preserved in paralectotype USNM 45724 (pl. 14, figs. 1–5). It should be noted that many other bellerophonaceans from some of the silicified collections from Kentucky described herein that are known to have shell markings also lack preserved ornament markings (see, for example, *Bucanopsis carinifera*, pl. 27, figs. 5, 16).

The small specimens from the Grier Limestone Member (pl. 15, figs. 1–7) appear to have the typical umbilical size and whorl form, and show a tendency toward slight dorsal angulation. It must be noted that, as seen in the earlier volutions of the type specimens of *B. nashvillensis* (pl. 14, figs. 5, 6), the dorsomedian angulation was an adult feature; submature specimens have a more evenly rounded dorsum (as in the small Grier specimens). Similarly, the specimens from the Perryville Limestone Member that are assigned to *B. nashvillensis*, such as specimen USNM 315569 (pl. 13, figs. 20, 21), are somewhat larger than the Grier specimens and show greater dorsomedian angulation, as do the lower dorsal fragments of USNM 315566 (pl. 13, figs. 15, 16) and USNM 315568 (pl. 13, fig. 19), which also shows a thickened parietal lip as seen in the type specimens (pl. 14, figs. 3, 5, 7). Although different collections of Kentucky specimens differ in small ways from the type suite, I believe they are all so similar in overall morphology that they are best assigned to *B. nashvillensis*.

#### *Bucania frankfortensis* Ulrich, 1897

Plate 13, figures 22–24; Plate 16, figures 1–4

*Bucania frankfortensis* Ulrich in Ulrich and Scofield, 1897, p. 891, pl. 66, figs. 30–33; Bassler, 1932, pl. 21, figs. 11, 12.

*Diagnosis.*—Shell aperture having distinctly triangular outline; whorls high, relatively narrow, with subangular dorsal crest.

*Description.*—Shell moderately large (up to 40.5 mm long), consisting of about three or four volutions; umbilicus moderately wide and deep; juvenile whorls somewhat depressed, subreniform in shape, and only slightly, if at all, angled dorsally; whorls expand more rapidly anteriorly in later growth so that dorsum becomes increasingly angular; adult dorsal slopes gently convex and steeply inclined, umbilical shoulders rather tightly rounded, and umbilical slopes steep, broadly convex,

TABLE 52.—Measurements (in millimeters) of holotype of *Bucania frankfortensis*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Dorsal width	Posterior width	Ventral width
45716	40.5	25.5	26.8	29.8	14.0	16.9	14.0	11.5

resulting in gently rounded but distinctly triangular apertural outline. Inner aperture lip thickened and folded back to form a posterior shelf to aperture; apertural margins thin around lateral rims to broad, fairly deep anterior sinus; slit unknown; selenizone slightly elevated and rounded. Shell markings known only on adult thickened aperture flanks, consisting of rather regularly spaced, wrinkled, lamellose growth lines; revolving threads very weak.

*Measurements.*—Measurements of the holotype of *B. frankfortensis* are listed in table 52.

*Material.*—The holotype, USNM 45716 (pl. 16, figs. 1-4), is a silicified replica in which the anteromedian portion of the shell has been rebuilt with plaster. The reconstruction appears to be quite faithful to the form of the actual shell. The species was identified here from silicified fragments, mainly of the thickened posterior aperture, from USGS sample 5036-CO.

*Distribution.*—The museum label states that the holotype, USNM 45716, is from the "Trenton (Cynthiana) at Frankfort, Kentucky." Writing on the specimen itself states, "Top of Trenton, Gastropoda beds, Frankfort, Kentucky." The highest gastropodal beds in the interval previously referred to as the Cynthiana Formation in the vicinity of Frankfort, Ky., are those of the Devils Hollow Member of the Lexington Limestone (Shermanian) (Pomeroy, 1968), which in part is characterized by a profusion of gastropods, most conspicuously species of the genus *Lophospira*, this facies being interpreted as very shallow bank deposits (Cressman, 1973, p. 40, 41). *B. frankfortensis* occurs in USGS silicified sample 5036-CO from the Devils Hollow Member of the Lexington Limestone (Shermanian) in the Coletown quadrangle, Ky. Bassler (1932, p. 113, 114, pl. 21, figs. 11, 12) cited this species as being characteristic of the Catheys Formation (Shermanian-Edenian) of the Central Basin of Tennessee.

*Comparison.*—This species most resembles *B. nashvillensis*, which also has an angular dorsum, but the dorsum of *B. frankfortensis* is higher, its dorsal whorl slopes are steeper, and its aperture is much more trian-

gular. The coarse, wrinklelike growth lamellae on the thickened posterior portion of the adult whorl of *B. frankfortensis*, as well as the weakness of the revolving threads, also distinguish the species.

*Discussion.*—By virtue of their similar shell forms, particularly the angular dorsal whorl, *B. frankfortensis* and *B. nashvillensis* are closely related, but distinct, species.

#### *Bucania peracuta* Ulrich, 1897

Plate 16, figures 5-8

*Bucania peracuta* Ulrich in Ulrich and Scofield, 1897, p. 896, pl. 66, figs. 34, 35; Bassler, 1932, pl. 20, fig. 29.

*Diagnosis.*—Shell medium in size, thick; aperture broadly subtriangular, angular dorsally and laterally; umbilici wide; dorsolateral slopes with rugae.

*Description.*—Shell medium in size (up to 29 mm long) and thick, the adult parietal lip being particularly massive. Aperture broadly subtriangular, the width being more than twice the length; whorl dorsum angular, dorsolateral slopes broadly spread and gently convex; umbilical shoulders angular; umbilical slopes deeply cut and slightly concave to nearly flat; base of whorl nearly flat, except for low ridge over previous dorsal angle. Slit unknown, but selenizone rather narrow for such a large shell, being slightly elevated and truncated. Dorsolateral slopes marked by low, but rather sharp and distinct, rugae that angle straight back from umbilical shoulder to selenizone, reflecting a very straight sided, V-shaped apertural sinus; rugae form nodes at umbilical shoulder, but do not pass over it. Growth lines indistinct, and revolving threads unknown.

*Measurements.*—Measurements of the holotype of *B. peracuta* (USNM 45726) are listed in table 53. Figures 5-8 on plate 21 show the difficulties in making these measurements.

*Material.*—Only one specimen of *B. peracuta* is known, the holotype (USNM 45726). This specimen is a large, thick, brown, weathered, silicified fragment.

TABLE 53.—Measurements (in millimeters) of holotype of *Bucania peracuta*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Dorsal width	Posterior width	Ventral width
45726	29.1	20.0	16.3	34.8	15.5	21.0	15.3	—

TABLE 54.—Measurements (in millimeters) of lectotype of *Bucania sublata*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Dorsal width	Posterior width	Ventral width
315561	11.8	9.5	7.1	11.5	6.7	9.4	6.4	5.0

*Distribution.*—The museum label states that the holotype is from the "Trenton (Cannon), Dekalb Co., Tennessee." Bassler (1915, p. 137) cited the species from the Catheys Formation, but this is probably incorrect, because Bassler (1932, p. 106) later confirmed the occurrence as in the Cannon facies of the Bigby-Cannon Limestone (Kirkfieldian-Shermanian) of central Tennessee.

*Comparison.*—The rugae on the dorsolateral slopes of this species are reminiscent of *Cyrtolites*, but *B. peracuta*'s extremely thick shell and slitband show that this resemblance is only superficial. Its rapid rate of expansion and angular dorsum led Ulrich and Scofield (1897, p. 897) to suggest a possible relation to *B. nashvillensis*.

The common possession of rugae and a rather narrow, slightly elevated selenizone show a close relationship between *B. peracuta* and *B. singularis* (pl. 19, fig. 15–18) of the Catheys Formation (Shermanian-Edenian) of Tennessee.

*Discussion.*—*B. peracuta* is similar to members of the *B. lindsleyi* group of species; however, the thick, angular shell of *B. peracuta* sets it apart from the more rounded species. It may represent a branch of the *B. lindsleyi* group, or, as indicated by its wide, angular umbilicus, it may be an independent evolution from the ancestral *B. sulcatina* group.

Although I place *B. peracuta* in the genus *Bucania*, I point out that revolving lines are not confirmed on the holotype. However, the specimen is worn. Likewise, the specimens of the possible descendant species, *B. singularis*, are too poorly preserved to retain any ornament other than the rugae (pl. 19, figs. 15–18). Based on my examination of the known specimens of both species, I believe both species have very fine shell markings that are extremely difficult to discern and photograph.

***Bucania sublata* Ulrich and Scofield, 1897**

Plate 13, figures 1–14

*Bucania sublata* Ulrich and Scofield, 1897, p. 888, 889, pl. 66, figs. 16–19.

*Diagnosis.*—Shell small (up to about 12 mm long), umbilicus moderately wide, whorls very broad, globose; selenizone wide, flush with dorsum, bordered by distinct thin ridges; slit short, sinus shallow or absent.

*Description.*—Shell small, rate of whorl expansion gradual; umbilicus moderately wide, exposing earlier volutions; umbilical shoulders sharply rounded in early

growth, becoming more rounded in adult growth; umbilical slopes nearly flat. Dorsum very broad and somewhat globose; apertural outline acutely subelliptical, becoming less angular with growth; whorl floor has low, broad, median ridge. Selenizone wide, flush with adjacent whorl slopes, and bordered by distinct thin ridges; slit short, and, as shown by growth lines, which run nearly straight over dorsal slopes, sinus either very shallow or possibly lacking. Growth lines weak, evenly spaced, essentially straight; revolving threads even weaker, fine, closely spaced.

*Measurements.*—Measurements of the lectotype of *B. sublata* are listed in table 54.

*Material.*—The type suite consists of three silicified syntypes listed under the museum number USNM 45733. Of these, the specimen on plate 13, figures 1–4, is designated the lectotype for *B. sublata* and assigned the new number USNM 315561. Specimen USNM 315562 (pl. 13, figs. 5–8) and the unfigured third syntype (retained under USNM 45733) are paralectotypes. Specimens from the USGS collections identified as *B. cf. B. sublata* are USNM 315563 (pl. 13, figs. 9, 10), 315564 (pl. 13, fig. 11), and 315565 (pl. 13, figs. 12–14).

*Distribution.*—The type suite was collected from the so-called "Flanagan beds," a name that erroneously was applied to silicified beds at different horizons in the upper Lexington Limestone (Shermanian) and treated as correlatives of a silicified bed, near Burgin, Ky.

Specimens of *B. cf. B. sublata* from the Lexington Limestone were found as fragments in USGS silicified samples from the Grier Limestone Member (4879-CO) (pl. 13, figs. 9, 10), the Faulconer Bed of the Perryville Limestone Member (6136-CO) (pl. 13, fig. 11), and the Devils Hollow Member (5095-CO) (pl. 13, figs. 12–14) (Shermanian).

*Comparison.*—*B. sublata* can be distinguished from related species such as *B. halli* and *B. emmonsii* by its broader, more globose whorls, its slightly smaller umbilicus, its essentially straight growth lines, its very weak revolving lines, and its wide, flush selenizone bordered by distinct, thin ridges.

*Discussion.*—*B. sublata* is a member of the *B. sulcatina* group, as indicated by its large, open umbilici and depressed whorls, and is related to *B. halli* and *B. emmonsii*, which are present in the Cincinnati arch area in slightly older strata. *B. sublata* shows a more advanced condition, because of its more globose dorsal

TABLE 55.—Measurements (in millimeters) of holotype of *Bucania micronema*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Dorsal width	Posterior width	Ventral width	Selenizone width
45720	9.8	7.2	6.0	10.2	4.7	6.5	4.0	3.0	0.7

whorls and its small umbilici, both traits seen in the more advanced *B. lindsleyi* group.

All the specimens identified here as *B. cf. B. sublata* are fragments in which silicification has destroyed all traces of shell ornament. USNM 315563 (pl. 13, figs. 9, 10) compares well in its small shell size, umbilical size, and aperture lip shape to a paralectotype of *B. sublata*, USNM 315562 (pl. 13, figs. 5–8). The other fragments from the USGS collections are somewhat larger, but their whorl breadth and umbilical size suggest that they probably belong to this species.

***Bucania micronema* Ulrich, 1897**

Plate 19, figures 1–6

*Bucania micronema* Ulrich in Ulrich and Scofield, 1897, p. 892, pl. 66, figs. 26–29.

**Diagnosis.**—Shell small (up to about 10 mm long), rapidly expanding, umbilicus of moderate size, with narrowly rounded shoulders; aperture broadly rounded, subtriangular; revolving lines fine (five per millimeter), continuous, slightly wavy; selenizone slightly elevated, flat topped, having distinct lunulae, and bordered by very fine ridges.

**Measurements.**—Measurements of the holotype (USNM 45720) of *B. micronema* are listed in table 55.

**Material.**—The holotype (USNM 45720) is a small silicified replica and is the only known specimen of the species.

**Distribution.**—The holotype is labeled as coming from the so-called “Flanagan Chert,” a name that erroneously recognized silicified beds at different horizons in the upper Lexington Limestone (Shermanian) of central Kentucky as the same bed. The specimen was collected at Danville, Ky.

**Comparison.**—The species is quite similar to *B. lindsleyi* (pl. 18, figs. 1–9), but is much smaller, and its revolving threads are finer, more continuous across growth lines, and slightly wavy (pl. 19, fig. 6).

**Discussion.**—*B. micronema* is known only from the holotype, but it appears to be a valid taxon, as that specimen preserves sufficient detail to demonstrate its distinctiveness. Its relation to *B. lindsleyi* is obvious, and it likely is descended from that species. Its small size may have enabled it to dwell among erect marine algal foliage.

***Bucania rugatina* Ulrich, 1897**

Plate 16, figures 9–15; Plate 17, figures 1–12

*Bucania rugatina* Ulrich in Ulrich and Scofield, 1897, p. 890, pl. 66, figs. 13–15.

**Diagnosis.**—Shell moderate in size (up to 26 mm long), whorls rapidly expanding and tightly enrolled; umbilicus small; selenizone flush with dorsum; growth lines evenly and closely spaced, gently wrinkled to sublamellose; revolving threads distinct, but subordinate to growth lines.

**Description.**—Shell moderate in size, reaching a maximum length of about 26 mm; whorls rapidly expanding and relatively tightly enrolled, resulting in rather small, deep umbilici. Dorsum broad and very convex, umbilical shoulders well rounded. Adult aperture nearly semicircular and somewhat explanate laterally, never much thickened; thin inner parietal lip blankets previous dorsal whorl, resulting in broad ridge at base of aperture; outer parietal lip folds back over coil slightly beyond plane of aperture. Selenizone of moderate width, bordered by fine ridges, flush with dorsolateral slopes. Growth lines evenly and closely spaced, may be developed as weak wrinkles or weak lamellae, the latter becoming stronger in maturity; lines strongly developed onto umbilical slopes. Revolving threads slightly subordinate to growth lines, but still quite distinct as fairly coarse ridges that appear increasingly restricted to single growth increments as growth lines become more lamellose.

**Measurements.**—Measurements of *B. rugatina* are listed in table 56.

**Material.**—Ulrich’s (1897) type suite (USNM 45728) consists of five silicified syntypes. From this suite, USNM 315555 (pl. 16, figs. 9–12) is here made the lectotype; USNM 315556 (pl. 16, figs. 13–15), a paralectotype, is figured, and the other three paralectotypes retain the original museum number, USNM 45728.

From the USGS silicified collections, four specimens have been identified as *B. rugatina*: USNM 315579 (pl. 17, figs. 1–6), 315580 (pl. 17, figs. 7–11), 315581 (pl. 17, fig. 12), and 315597 (not figured).

**Distribution.**—Ulrich’s (1897) type specimens are labeled as coming from the “Trenton (Flanagan), 1–1/2 miles south of Burgin, Kentucky.” According to McFarlan (1943, p. 14), the Flanagan is an obsolete unit in the upper Lexington Limestone (Shermanian). It included

TABLE 56.—Measurements (in millimeters) of *Bucania rugatina*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Dorsal width	Posterior width	Ventral width	Selenizone width
315555	—	~12.6	~10.6	14.6	7.1	11.6	8.5	6.6	—
315556	—	10.9	~6.0	10.8	6.5	9.0	7.0	—	1.4
315580	~26.3	18.0	~16.0	21.6	8.2	15.8	—	~9.4	0.9
315579	~21.3	11.9	~13.2	23.2	~7.1	12.5	~8.3	6.7	—
315597	—	~7.6	—	~10.7	5.0	~5.9	~4.5	~3.3	—

different silicified beds now in the Grier and (or) Perryville Limestone Members of the Lexington Limestone. The species is known from two USGS silicified samples from Kentucky, 6143-CO and 7348-CO, both from the upper tongue of the Clays Ferry Formation (Shermanian), which is overlain by the Tanglewood Limestone Member and underlain by the Millersburg Member of the Lexington Limestone.

*Comparison.*—*B. rugatina* is generally similar to *B. lindsleyi*, but differs in its smaller size, its more explanate aperture, its flush (rather than concave) selenizone, and its more closely spaced, wrinkled growth lines. Ulrich and Scofield (1897, p. 890) claimed that the umbilicus of *B. rugatina* was smaller than that of *B. lindsleyi*. Measurements show that the shell length/umbilical diameter ratio is about 3.1 in *B. rugatina* and 2.7 in *B. lindsleyi*, supporting their claim. A difference is also reflected in the dorsal width/ventral width ratio, which is 1.77 in *B. rugatina* and 1.46 in *B. lindsleyi*. Combined, these two ratios show that *B. rugatina* expands its shell width at a greater rate while coiling more tightly, which supports Ulrich and Scofield's (1897) qualitative observations. *B. rugatina* also might be confused with *B. nashvillensis*, but the former's more globose dorsum, flush selenizone, and distinctive sculpturing should distinguish it.

*Discussion.*—This species obviously is closely related to *B. lindsleyi* and *B. nashvillensis*, and may have evolved from *B. lindsleyi*.

***Bucania singularis* Ulrich, 1897**

Plate 19, figures 15–18

*Bucania singularis* Ulrich in Ulrich and Scofield, 1897, p. 894, pl. 66, fig. 47.

*Diagnosis.*—Shell moderate in size (up to 27 mm long), whorls depressed, broadly convex dorsally, with narrowly rounded umbilical shoulders; dorsolateral slopes with prominent rugae, forming nodes at shoulders; sele-

nizone elevated, flat topped, notably wider over last half-whorl; adult aperture laterally expanded and more or less square in outline.

*Measurements.*—Measurements of the poorly preserved lectotype of *B. singularis* are listed in table 57.

*Material.*—The specimen shown on plate 19, figures 15–18, is here made the lectotype and given the number USNM 315549. The other syntype, which is now a paralectotype, retains the original suite number, USNM 45730 (unfigured). The lectotype retains very little shell material; its umbilici and ventral aperture are covered by matrix, its dorsum is largely covered by an encrusting bryozoan, and the entire specimen is weathered.

*Distribution.*—The museum label with the type specimens states that they came from the Catheys Formation (Shermanian-Edenian) at Nashville, Tenn. No other occurrences are known.

*Comparison.*—Ulrich and Scofield (1897, p. 894) were in doubt about the evolutionary relations of this species, but believed it to be nearest *B. crassa* and *B. lindsleyi*. They did not state their reasons for this conclusion, and I can see no reason for these comparisons.

The broad, depressed whorls of *B. singularis* are reminiscent of the *B. sulcatina* group, as is the squared-off adult aperture. The only other species of *Bucania* that displays the dorsal rugae of the shell is *B. peracuta*, but that species is larger and has a highly angular dorsum, resulting in a more triangular apertural outline.

*Discussion.*—After first examining the poorly preserved type specimens of *B. singularis*, I was uncertain about the validity of the species. However, further examination and comparison with Ulrich and Scofield's (1897, pl. 66, fig. 47) interpretive, but accurate, reconstruction led me to conclude that the specimens do represent a distinct species of *Bucania*. Its more or less square apertural outline, prominent rugae, and distinctly elevated selenizone distinguish it from all other species.

TABLE 57.—Measurements (in millimeters) of *Bucania singularis*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Dorsal width	Posterior width	Ventral width
315549	27.0	20.2	18.3	20.2	17.0	14.2	11.1



TABLE 58.—Measurements (in millimeters) of *Bucania pojetai*

UCGM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Dorsal width	Posterior width	Ventral width	Selenizone width
44285	40.4	26.5	22.0	31.7	17.2	19.4	16.5	12.8	—
44286	42.9	26.5	27.5	29.1	17.0	18.4	15.2	14.0	—
44287	32.5	21.9	17.0	25.5	14.2	17.4	12.6	10.6	—
44288	28.3	—	11.6	22.0	—	17.6	14.0	—	2.1
44288	24.5	19.4	11.9	17.5	11.7	15.2	13.5	—	1.6
44289	28.6	19.8	14.9	19.6	—	—	—	—	2.3

The common possession of distinct rugae on the dorsolateral slopes of this species and *B. peracuta* may indicate a genetic relationship. As stated in the discussion of *B. peracuta*, that species may be part of a separate phylogenetic branch of the genus *Bucania* distinct from the *B. lindsleyi* group. If so, *B. singularis* also appears to be part of the branch, and might indicate by its depressed whorl form the connection to ancestors in the more ancient *B. sulcatina* group.

***Bucania pojetai* new species**

Plate 20, figures 1–8

**Diagnosis.**—Shell moderately large (up to 43 mm long), gradually expanding; umbilici large; whorl shape reniform in submaturity, cordate in maturity; growth lines wrinkled in maturity.

**Description.**—Shell moderately large, rate of whorl expansion gradual. Umbilicus large and circular in appearance, showing relatively loose style of coiling. Submature whorls depressed and reniform in outline, broadly and evenly rounded dorsally, with well-rounded umbilical shoulders and gently concave ventral side covering only the dorsum of the previous whorl; with growth toward maturity, length of aperture increases at greater rate than width, so that dorsum becomes jutting and angular, and apertural outline becomes subtriangular to cordate. Thickness of shell unknown, but parietal lip became moderately thick in adulthood. Slit unknown; selenizone a low rounded ridge showing only faint lunulae. Growth lines preserved as low wrinkles (almost rugose) fairly closely spaced; lines swing back over dorsum very gently, reflecting only a shallow anteromedian apertural sinus; wrinkled growth lines become stronger with growth. No revolving ornament known.

**Measurements.**—Measurements of *B. pojetai* are listed in table 58.

**Material.**—Twelve specimens of this new species are known. Figured specimens are the holotype, UCGM 44285 (pl. 20, figs. 3, 4), and paratypes UCGM 44286 (pl. 20, figs. 1, 2) and 44287 (pl. 20, figs. 5–8). Eight paratypes are placed under one number, UCGM 44288, and the eleventh paratype is cataloged under UCGM 44289. Most of the specimens have some calcitic shell material preserved (see “Discussion”).

**Distribution.**—All known specimens are from a collection made by R. Flower and W. Shideler from the Liepers Formation (Maysvillian) at Rowena Ferry, Russell County, Ky. Note that this locality is in southern Kentucky near the Tennessee border where the Central Basin facies persist and their stratigraphic names are used.

**Comparison.**—*B. pojetai* is quite similar to *B. simulatrix* (pl. 19, figs. 11–14) and *Salpingostoma richmondensis* (pl. 26, figs. 1–8). Problems with separation of the latter two species are covered in discussions in their respective sections. The three species have very similar shell forms, but *S. richmondensis* shows evidence of a long, open slit that was closed off anteriorly, as is characteristic of *Salpingostoma*. As in *B. simulatrix* (pl. 19, figs. 11–14), the slit in *B. pojetai* (pl. 20, figs. 1, 3, 6) appears to have been covered by a selenizone to near the apertural margin. *B. pojetai* differs from *B. simulatrix* in having a broader whorl form, a less elevated selenizone, and wrinklelike growth lines.

**Discussion.**—The marked similarity between the Maysvillian *B. pojetai* and the Richmondian *B. simulatrix* indicates a close evolutionary relationship. *B. pojetai* almost certainly is an ancestor of *B. simulatrix*.

The mode of preservation of *B. pojetai* is quite similar to that of *B. simulatrix* and *S. richmondensis*. Although specimens of *B. pojetai* have remnants of replaced original shell, the only ornament preserved is the wrinklelike (almost rugose) growth lines in one specimen (pl. 20, figs. 5–8). Where the shell is broken away, the deep-brown calcitic shell material can be seen to be quite thin dorsally (pl. 20, figs. 1, 6); however, the parietal lip clearly was progressively thickened in mature growth, as seen by coarse crystalline calcite remnants in the umbilici of adult specimens (pl. 20, figs. 2, 4). *B. simulatrix* has a similar thin, dorsal, poorly preserved, calcitic shell remnant, and its holotype shows a parietal gap (which may have been widened through vertical compaction); the latter probably reflects a similar thickened adult parietal region (pl. 19, fig. 13). It is difficult to determine whether these similar conditions of preservation are due to similar original shell structure and mineralogy or similar diagenetic histories, or both. The shells of known specimens of *B. pojetai* apparently have been so totally recrystallized,

TABLE 59.—*Measurements (in millimeters) of lectotype of Bucania simulatrix*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Dorsal width	Posterior width	Ventral width
315548	45.6	26.8	24.7	31.7	~23.0	17.6	12.9	9.6

or acted upon by surface dissolution, that details of ornamentation are masked. What remains may be a single more stable shell layer.

***Bucania simulatrix* Ulrich, 1897**

Plate 19, figures 11–14

*Bucania simulatrix* Ulrich in Ulrich and Scofield, 1897, p. 892, pl. 63, figs. 48, 49; pl. 67, fig. 45; Cumings, 1908, p. 955, pl. 42, figs. 9, 9a.

**Diagnosis.**—Shell large (up to 45.6 mm long), loosely coiled, with large, open umbilicus; submature whorls subreniform, adult aperture greatly expanded anteriorly with elongate subtriangular outline.

**Description.**—Shell large, consisting of about three volutions, loosely coiled so as to create a wide, open umbilicus. Submature whorls rather narrow and depressed, subreniform in outline; dorsum gently convex, convexity gradually increases at greater rate than width, but in adulthood aperture expands anteriorly at even a greater rate, resulting in an elongate subtriangular outline. Posterolateral lip of adult aperture slightly reflexed; anterior lip curved upward into fairly deep V-shaped sinus; parietal lip apparently thickened centrally. Dorsomedian ridge over expanded portion of whorl on internal molds reflects an elevated, hollow slitband. No surface markings known.

**Measurements.**—Measurements of the lectotype of *B. simulatrix* are given in table 59. Weathering of the specimen and the mode of preservation affected the measurements.

**Material.**—Specimen USNM 315548 (pl. 19, figs. 11–14) is here designated the lectotype. The paralectotype retains the suite number USNM 45729, which was originally used for both syntypes. Numerous other unnumbered specimens in the U.S. National Museum of Natural History and Miami University collections were also examined. Two types of preservation were observed. One group of specimens are generally micritic, compressed and distorted internal molds. The second group, nearly as large and very similar, are internal molds coated by a hard, glossy, resistant layer, most likely representing some portion of the original shell. The type specimens are preserved in this second manner (pl. 19, figs. 11–14). The lectotype shows a gap between the coil and parietal lip of the expanded aperture, representing a thickened area of the shell now dissolved (pl. 19, fig. 13). Some layer of the shell may have been of a different

mineralogy and retained preferentially, thus accounting for the glossy, thin, calcitic coating on such specimens.

**Distribution.**—The species is known only from the Whitewater Formation (Richmondian) in the vicinity of Richmond, Ind.

**Comparison.**—A detailed comparison of this species and *Salpingostoma richmondensis* is presented in the section on the latter species. The primary reason for distinguishing *B. simulatrix* from that species is the apparent continuation of the dorsomedian ridge, which represents the path of the slit, to the outer margin of the aperture lip in *B. simulatrix* (pl. 19, figs. 11–13). *B. simulatrix* differs from *B. pojetai* in having a more narrow whorl form and a more elevated selenizone, and in lacking the wrinklelike growth lines of *B. pojetai*.

**Discussion.**—Present evidence supports Ulrich's claim for distinction of this species from *S. richmondensis*, as the dorsomedian ridge of *B. simulatrix* (pl. 19, figs. 11–14) apparently represents the path of a raised, hollow selenizone. However, better preserved material will be required to confirm differentiation of these species.

***Bucania crassa* Ulrich, 1897**

Plate 19, figures 7–10

*Bucania crassa* Ulrich in Ulrich and Scofield, 1897, p. 893, pl. 67, figs. 46–48; Cumings, 1908, p. 955, pl. 39, figs. 4–46.

**Diagnosis.**—Shell moderately large (up to 36 mm long), dorsal whorl inflated, nearly semicircular, uniformly convex; umbilicus moderately small, with sharply rounded shoulders; shell very thick and massive.

**Description.**—Shell moderately large, thick, massive, rather tightly coiled. Umbilicus deep, moderately small, circular in appearance, with sharply rounded umbilical shoulders and nearly horizontal umbilical slopes. Dorsal whorl inflated, nearly semicircular and evenly convex. Outer aperture lip has broad, V-shaped sinus and becomes slightly upturned in maturity; inner and posterolateral aperture lips massively thickened. Selenizone slightly elevated and moderately wide. Growth lines broadly curved and rather evenly spaced. Revolving threads finer, closely spaced, always intersecting growth lines at right angles.

**Measurements.**—Measurements of the lectotype of *B. crassa* (USNM 315547) are listed in table 60.

**Material.**—Only Ulrich's two syntypes are known; both are calcitic replicas and were cataloged under

TABLE 60.—*Measurements (in millimeters) of Bucania crassa*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Dorsal width	Posterior width	Ventral width
315547	~35.8	23.9	19.7	29.2	11.65	18.0	15.2	12.9

USNM 45714. The specimen figured (pl. 19, figs. 7–10) is the same one illustrated by Ulrich (1897, pl. 67, figs. 46–48), and is here designated the lectotype, USNM 315547. The second specimen, designated the paralectotype, retains the number USNM 45714.

*Distribution*.—The species is known only from Elkhorn Falls, near Richmond, Ind., from the Elkhorn biofacies of the Whitewater Formation (Richmondian), at the top of the Cincinnati Series.

*Comparison*.—There can be no doubt about the distinctiveness of this species. Ulrich (1897) pointed out that its evenly convex, inflated dorsum and its smaller, more abrupt umbilicus readily distinguish it from species such as *B. frankfortensis* and *B. nashvillensis*, which have a more subangular dorsum. He also noted a resemblance between *B. crassa* (pl. 19, fig. 9) and *B. lindsleyi* (pl. 18, figs. 1–9). *B. crassa* is closely related to *B. lindsleyi*, which has both comparable shell markings and a similarly evenly rounded dorsum (pl. 18, figs. 1–9), but *B. crassa* has deeper umbilici and a much thicker, more massive shell.

*Discussion*.—Uppermost Cincinnati rocks represent the last deposition of a regressing Ordovician sea on the Cincinnati arch Region, and are characterized by coarse grainstones made up of broken and worn skeletal fragments. The strata are further characterized in many places by thick-shelled invertebrates and massive bryozoan colonies, all indicating rather high energy environmental conditions. The massive shell of *B. crassa* seems to fit well into this picture.

#### Genus KOKENOSPIRA Bassler, 1915

[pro] *Kokenia* Ulrich and Scofield, 1897, p. 849.

[not] *Kokenia* Holzapfel, 1895.

*Diagnosis*.—Shell phaneromphalous, gradually expanding; selenizone elevated, flat topped; shell surface with numerous uninterrupted revolving threads.

*Description*.—Shell gradually and evenly expanding; umbilicus moderately wide. Selenizone elevated, flat topped; adjacent dorsolateral slopes on either side concave; outer dorsolateral slopes and umbilical shoulders convex; umbilical slopes convex to flat. Shell surface marked by numerous uninterrupted threads; growth lines very weak, in many cases not visible.

*Type species*.—*Bucaniella esthona* Koken (1889, p. 389), by original designation.

*Distribution*.—The type species of the genus is known only from Ordovician float in Pleistocene glacial drift at

Berlin, Germany. The only other known species, *K. costalis*, was described by Ulrich and Scofield (1897, p. 883) from the Prosser Formation (Shermanian-Edenian) near Cannon Falls, Minn., and was reported from the Ordovician of Frobisher Bay, Baffin Land, Canada, by Schuchert (1900). *K. costalis* is reported here for the first time from the Kope Formation (Edenian) at Cincinnati, Ohio.

*Comparison*.—As pointed out by Ulrich and Scofield (1897, p. 882), *Kokenospira* differs from *Tetranota* in two significant ways: first, the aperture is much less expanded laterally than it is in *Tetranota*; and second, the revolving surface lines continue to the aperture, are more numerous, and are more threadlike and less angular than in *Tetranota*.

The type species, *K. esthona* (Koken, 1889), was originally placed in *Bucanella*, but was distinguished from that sinus-bearing genus by its possession of a slit by Ulrich and Scofield (1897).

*Discussion*.—By its shell form, elevated slitband, and dominant revolving threads, *Kokenospira* shows a close relationship to *Tetranota*, the two most likely having evolved from a common ancestral stock. *Bucania* also had a common ancestry with these two genera. All three genera evolved in the Middle Ordovician.

#### *Kokenospira costalis* (Ulrich and Scofield), 1897

Plate 20, figures 9–12

*Kokenia costalis* Ulrich and Scofield, 1897, p. 882, pl. 64, figs. 46–49.

*Diagnosis*.—Shell moderately small (up to 13.5 mm long); slitband elevated, flat topped; six or seven revolving threads on each dorsolateral slope.

*Description*.—Shell moderately small and apparently rather thin, gradually expanding. Umbilicus rather large and open. Selenizone distinctly elevated and flat topped, with fine, sharp bordering threads. Dorsolateral slopes concave immediately adjacent to slitband, but rapidly become convex, continuing to be rounded over umbilical shoulders. Whorls reniform in section, aperture length/width ratio about 0.60–0.65. Growth lines indistinct; each dorsolateral slope with six or seven thin, uninterrupted revolving threads which continue to apertural margin; first revolving thread adjacent to slitband weaker than others on dorsal whorl slope, as are other threads within umbilicus.

*Measurements*.—Measurements of *K. costalis* are listed in table 61.

TABLE 61.—Measurements (in millimeters) of *Kokenospira costalis*

UCGM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter
26519	13.5	12.0	8.0	12.4	12.5

*Material*.—Only one specimen of this species was examined, UCGM 26519, a worn and fragmentary calcitic replica (pl. 20, figs. 9–12) collected by Leigh Van Valen. The holotype is cataloged under USNM 45868.

*Distribution*.—Ulrich and Scofield (1897, p. 883) described the species on the basis of a single specimen from the *Clitambonites* bed, Prosser Formation (Shermanian-Edenian), near Cannon Falls, Minn. Schuchert (1900, p. 164) reported the species from the "Trenton" of Frobisher Bay, Baffin Land, Canada.

The specimen described here comes from the Southgate biofacies of the Kope Formation (Edenian), from a pit on Beekman Street, Cincinnati, Ohio.

*Comparison*.—*K. costalis* differs from *K. esthona* (Koken) in having a less prominent slitband and a more rounded shell form. *K. costalis* can be distinguished from similar species of the genus *Tetranota* by its more numerous revolving threads which remain distinct to the apertural margin.

*Discussion*.—This rare species appears to be quite widespread geographically. The specimen described here (UCGM 26519) (pl. 20, figs. 9–12) compares well with Ulrich and Scofield's (1897) single specimen, which was reported to be about 10 mm long. Measurements of the aperture on the figures of their specimen (their pl. 64, fig. 48) give an aperture length/width ratio of 0.61, closely comparable to the ratio of 0.64 for the Cincinnati specimen. UCGM 26519 clearly shows the centralmost revolving thread to be weaker than the others, but it is difficult to say with certainty whether six or seven threads are present on each side.

#### Subfamily UNDULABUCANIINAE new subfamily

*Diagnosis*.—Whorls subtrapezoidal to rounded in cross section; slit long, narrow, generates selenizone; shell surface marked only by closely spaced, regularly wavy, fine collabral threads, which may or may not intersect.

*Stratigraphic range*.—Middle Ordovician (Kirkfieldian)-Upper Ordovician (Maysvillian).

*Type genus*.—*Undulabucania* n. gen. is the type and only known genus of the subfamily.

*Discussion*.—The subfamily Undulabucaniinae is unique in its possession of a deep slit, a characteristic ornament of closely spaced, wavy threads, and a shell form similar to that of the primitive *Bucania sulcatina* group, with broad-topped, depressed whorls and wide

umbilici. The long slit and wavy shell markings suggest descent from the Tropidodiscidae, and most likely from *Phragmolites*.

#### Genus UNDULABUCANIA new genus

*Diagnosis*.—Shell gradually expanding, with wide, open umbilici; slit very deep; shell ornament of fine, closely spaced, undulating collabral threads, which may or may not intersect.

*Description*.—Shell small to moderate in size (about 15–20 mm long), gradually and evenly expanding; umbilici wide, open. Whorl shape generally subtrapezoidal, but may be much more uniformly rounded. Slit very deep, usually generating channellike selenizone. Surface sculpturing of fine, closely spaced, undulating collabral threads, which when intersecting form a netlike meshwork. No revolving ornament known, except for threads bordering selenizone.

*Type species*.—*Bellerophon gorbyi* Miller, 1892 (p. 694), is here designated the type species of the new genus *Undulabucania*.

*Other species placed in Undulabucania*.—In addition to the type species, *Bellerophon punctifrons* Emmons (1842) and *Bucania punctifrons primaeva* Bradley (1930) are here assigned to *Undulabucania* n. gen.

*Distribution*.—Species of the new genus are known from strata ranging in age from the Kirkfieldian (upper Middle Ordovician) to Maysvillian (middle Upper Ordovician) Stages in Eastern North America.

*Discussion*.—Of the three species included in *Undulabucania*, *U. punctifrons* (Emmons, 1842) and *U. gorbyi* (Miller, 1892) were originally described as members of the genus *Bellerophon*, although Hall (1847) transferred *U. punctifrons* to *Bucania*. The third species, *U. primaeva*, was described from the Kimmswick Limestone (Kirkfieldian-Edenian) near Dutchtown, Ill., as *Bucania punctifrons primaeva* by Bradley (1930, p. 236, pl. 25, figs. 23–24). This taxon is here regarded as a distinct species because of its more narrow, somewhat circular whorl form. All three of the species, but particularly *U. punctifrons* and *U. gorbyi*, have a shell form closely resembling that of species belonging to the *Bucania sulcatina* group. They have thin shells, broad umbilici, gradually enlarging depressed whorls, a wide, yet not expanded, aperture with thin lips, and a long slit. Although the species of *Undulabucania* exhibit all of these traits, they differ in one very significant aspect. By definition, species of the genus *Bucania* have revolving threads that intersect the growth lines at right angles. The species here included in *Undulabucania* lack revolving ornament, except threads bordering the selenizone; they do have the common presence of fine, undulating growth lines that intersect, or nearly do so.

TABLE 62.—Measurements (in millimeters) of holotype of *Undulabucania gorbyi*

UC No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Dorsal width	Posterior width	Ventral width	Selenizone width	Slit length
6138	20.5	14.3	12.4	13.5	10.0	11.7	9.5	8.8	<0.8	15.0

The similarity in all characteristics but shell sculpturing suggests that *Undulabucania* had a common ancestry with the *Bucania sulcatina* group. As discussed previously, it is likely that *Undulabucania* and *Bucania* had a common ancestral connection with the tropidodiscids. That family contains the oldest known slit-bearing bellerophon, *Chalarostrepsis* Knight, 1948, from the Upper Cambrian of Canada. It is assumed that this genus was of the stock that gave rise to *Phragmolites* Conrad (1838) and *Tropidodiscus* Meek and Worthen (1866) in the Ordovician. *Undulabucania* and *Phragmolites* have a great deal in common, such as their wide umbilici, their long slits, and, particularly, their wavy growth lines. However, *Undulabucania* differs from *Phragmolites* in its lack of spiral ornament and its shell form, which closely resembles that of the *Bucania sulcatina* group. Given our present knowledge, it seems possible that *Undulabucania* evolved from a *Phragmolites*-like tropidodiscid.

***Undulabucania gorbyi* (Miller), 1892**

Plate 23, figures 10–15

*Bellerophon gorbyi* Miller, 1892, p. 694, pl. 14, figs. 7–9; Cumings, 1908, p. 953, pl. 39, figs. 1–16.

**Diagnosis.**—Shell having broad, dorsally rounded, subtrapezoidal whorl outline; slit deep and narrow; growth lines fine, wavy, closely spaced but not intersecting.

**Description.**—Shell small to moderate in size (about 20 mm long), increasing in size gradually and evenly. Umbilici fairly wide; dorsum of shell evenly and highly convex; umbilical shoulders narrow but well rounded; umbilical slopes flat to slightly convex, angling rather gently from shoulders to lower dorsolateral slope of previous whorl; ventral whorl deeply concave as it closely covers dorsum of previous whorl. Slit long and narrow, bordered by fine ridge on either side; selenizone slightly depressed, with fine lunulae. Shell ornament of very fine, closely spaced, nearly equidistant, wavy growth lines which never intersect; growth lines bend back over dorsum, reflecting a broad, moderately deep apertural sinus. Only revolving ornament known is ridges bordering selenizone. Aperture lips tend to flare laterally slightly in maturity.

**Measurements.**—Measurements of the holotype of *U. gorbyi* are listed in table 62.

**Material.**—Only one specimen of this species was located, UC 6138, which is the holotype. This well-

preserved calcitic replica was collected by S. S. Gorby, after whom it was named, and is deposited in the Gurley Collection at the Field Museum of Natural History, Chicago, Ill.

**Distribution.**—The holotype was collected from Maysvillian (middle Upper Ordovician) strata in Dearborn County, Ind. No more specific horizon or locality was given by the original author on the museum label. Maysvillian-age strata in southeastern Indiana are now included in the Dillsboro Formation.

**Comparison.**—This species obviously is closely related to *U. punctifrons*, but its whorls are much broader (pl. 23, figs. 11, 12) and its wavy growth lines never intersect, but remain nearly equidistant (pl. 23, fig. 10).

**Discussion.**—Superficially, the shell ornament of *U. gorbyi* appears much like that of *U. punctifrons*. On closer examination, however, the wavy growth lines can be seen to remain separate, although they do come close to touching one another. Nevertheless, the camouflage effect of the ornament would be the same as for *U. punctifrons*, which was probably directly ancestral to this species.

The slit of *U. gorbyi* is very long (15 mm) (pl. 23, figs. 10, 11, 13, 14). As the shell of the holotype is so well preserved, it is doubtful that this impression is false. Lunulae are visible dorsally where the slit was covered by the selenizone, and there the dorsomedian line is barely depressed, whereas anteriorly it is excavated as a deep channel. It should also be noted that the small bump situated about one-third of a whorl back on the right side of the slit (pl. 23, fig. 10) is a small bryozoan colony. This colony may have been situated on the living gastropod so as to take advantage of exhalant currents being emitted from the deep slit.

***Undulabucania punctifrons* (Emmons), 1842**

Plate 23, figures 1–9

*Bellerophon punctifrons* Emmons, 1842, p. 392, fig. 5; Lesley, 1889, p. 87, figs.

*Bucania punctifrons* (Emmons) Hall, 1847, p. 187, pl. 40A, figs. 1a–e; Ulrich and Scofield, 1897, p. 894, pl. 67, figs. 41–44; Raymond, 1902, pl. 19, figs. 9, 10; Weller, 1903, p. 177, pl. 12, figs. 10–12; Grabau and Shimer, 1909, p. 614; Bassler, 1932, pl. 13, figs. 16, 17; Wilson, 1951, p. 27, pl. 2, figs. 21–23.

**Diagnosis.**—Shell having relatively large umbilici; aperture rounded subtrapezoidal; undulating growth lines intersecting to form netlike meshwork.

TABLE 63.—Measurements (in millimeters) of *Undulabucania punctifrons*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Dorsal width	Posterior width	Ventral width	Selenizone width
45727	19.75	14.35	10.35	13.25	10.8	10.4	8.65	6.7	0.7
315546	17.4	12.5	9.0	12.25	10.3	10.0	8.15	6.6	0.6

*Description.*—Shell small to moderate in size (up to 20 mm long), consisting of about three volutions; gradually and evenly expanding throughout growth. Umbilici relatively wide for genus; whorls rounded subtrapezoidal in outline, with evenly and rather deeply convex dorsum and sharply rounded umbilical shoulders, flat and broad umbilical slopes that angle gently inward to shoulder of previous whorl, and concave ventrum covering surface of previous whorl. Aperture shows only very slight flaring as an adult, and has wide, fairly deep anterior sinus; slit quite deep, generating channellike selenizone bordered by thin, sharp ridge on either side. Shell surface covered by evenly undulating, wavy growth lines which intersect to form fine, slightly raised, netlike meshwork; this sculpturing present on juvenile whorls visible in umbilicus. Growth becomes coarsely lamellose in later growth.

*Measurements.*—Measurements of *U. punctifrons* are listed in table 63.

*Material.*—Only Ulrich and Scofield's (1897, pl. 67, figs. 41–44) two hypotypes from the Hermitage Formation at Nashville, Tenn., were examined. One retains the original museum number, USNM 45727 (pl. 23, figs. 1–4). This well-preserved calcitic specimen has a massive bryozoan colony plugging the aperture (probably a post mortem association) and is missing some of the dorsal shell. The other specimen, here numbered USNM 315546 (pl. 23, figs. 5–9), is very similarly preserved and is also missing a small portion of the dorsal shell. Emmon's (1842) original type material could not be located and is assumed to be lost.

*Distribution.*—This species is known from Rocklandian to Edenian rocks throughout Eastern North America. Emmons (1842), Hall (1847), Lesley (1889), and Ulrich and Scofield (1897) reported the species from the Trenton Group in New York, Canada, Pennsylvania, and Tennessee. Wilson (1951, p. 27) reported it from the Rockland, Sherman Falls, and Cobourg beds (Rocklandian-Edenian) of the Ottawa Formation in the Ottawa-St. Lawrence Lowland, Ontario, Canada. Weller (1903) cited the species from the Trenton Group in New Jersey. Bassler (1932, pl. 13, figs. 16, 17) reported the species from the Hermitage Formation (Kirkfieldian) of central Tennessee, which are the horizon and area where the specimens figured here (pl. 23, figs. 1–9) were collected.

*Comparison.*—The shell form of *U. punctifrons* is similar to that of members of the *B. sulcatina* group,

particularly *B. halli*, but its meshlike shell sculpturing easily distinguish it. *U. punctifrons* can be distinguished from *U. gorbyi* by the intersection of its wavy collabral threads, which in *U. gorbyi* remain separated.

*Discussion.*—Hall (1847, pl. 40A, fig. 1e) and Ulrich and Scofield (1897, pl. 67, fig. 44), among other authors, have illustrated the shell markings of *U. punctifrons* as being a regular pitting of the shell surface. As shown here on plate 23, figure 4, this sculpturing is in reality a rather regular netlike meshwork of raised, wavy, intersecting collabral threads. This shell pattern may have served as camouflage for the animal, mingling with the intersecting patterns of light in a shallow subaqueous environment much like a fishnet. Such an adaptation would be an important protective cover from predators.

#### Subfamily PLECTONOTINAE Boucot and Yochelson, 1966

*Diagnosis.*—Shell having raised dorsomedian lobe, giving the whorls a trilobed cross section.

*Stratigraphic range.*—Middle Ordovician-Devonian.

*Genera included.*—*Tetranota* Ulrich and Scofield, 1897; *Plectonotus* Clarke, 1899; *Tritonophon* Opik, 1953.

*Genera considered here.*—*Tetranota*.

*Discussion.*—*Plectonotus* was described by Clarke (1899) as having a slit that generates a selenizone. Knight (1941) redescribed the type material and noted only a V-shaped sinus in the apertural margin. Therefore, Knight and others (1960) placed *Plectonotus* in the Sinuitidae as a subgenus of *Bucanella* Meek (1871). Boucot and Saul (*in* Boucot, Saul, and Finks, 1963) discovered new material from the Devonian of Ghana that confirmed Clarke's original observation of a slit in the genus. In light of this discovery, Horny (1963a) placed *Plectonotus* near *Tetranota* in the subfamily Bucaniinae of the Bellerophontidae. Boucot and Yochelson (1966) proposed the subfamily Plectonotinae of the Bellerophontidae, including only the genus *Plectonotus*. Peel (1974) summarized the information about trilobed bellerophontaceans and analyzed their functional morphology. He accepted the subfamily Plectonotinae and added the genus *Tritonophon*, placing *Nylanderina* Boucot (1967) in synonymy with it. Herein, *Tetranota* is also placed in the Plectonotinae.

The Plectonotinae is transferred to the family Bucaniidae because of their somewhat depressed whorl forms, open umbilici, flaring lateral apertural margins, and spiral ornamentation.

*Tetranota* is the earliest known member of the subfamily and is regarded as ancestral to the later genera. Bretsky (1970a) reported *Plectonotus*? from the Upper Ordovician of the Central Appalachians, but these internal molds may actually belong to the widespread Ordovician genus *Tetranota*. Peel (1974) suggested that *Bucanella* might also have a slit, rather than merely a sinus, but currently known material is too poorly preserved to resolve the matter. If it is found that *Bucanella* is slit bearing, then that genus should also be placed in the Plectonotinae. It would thereby be the oldest member of the subfamily, being Early Ordovician in age.

Genus **TETRANOTA** Ulrich and Scofield, 1897

**Diagnosis.**—Shell with selenizone lying on broad, elevated dorsomedian band, in many cases bordered by pair of revolving threads, with one or two pairs of dorsolateral revolving angular ridges; aperture lip chiefly expanded laterally.

**Description.**—Shell variable in size, thin. Umbilici moderate to large in size, deep. Whorls broad and depressed, aperture wider than long throughout growth. In maturity, aperture lips tend to flare, chiefly in lateral directions. Parietal lip without thickened callosity. Selenizone on broad, elevated, gently convex to nearly flat topped dorsomedian band, which generally has revolving threads along its edges; lunulae faint in most cases. Outward from dorsal band, shell briefly concave to dorsolateral pair of angular revolving ridges; in some cases a second outer pair of dorsolateral ridges also present; pairs of dorsolateral ridges best developed in youth, gradually becoming indistinguishable in many mature shells. Apertural sinus broad and moderately deep, terminating in wide, short slit. Growth lines fine, closely spaced.

**Type species.**—*Bucania bidorsata* Hall, 1847, by original designation.

**Other North American Ordovician species.**—*T. sexcarinata* Ulrich and Scofield, 1897; *T. macra* Ulrich and Scofield, 1897; *T. obseleta* Ulrich and Scofield, 1897, *T. wisconsinensis* (Whitfield, 1878), *T. charon* (Billings, 1860); *T. rugosa* (Emmons).

**Distribution.**—In Eastern North America, the genus is widely known from strata of latest Chazy or early Blackriveran to Maysvillian age. Walcott (1884) also reported the type species from the upper Pogonip Group (Whiterockian?) of Nevada.

In Europe, the genus is known only from the British Isles. Reed (1921, p. 41) described a possible species from the Lower-Middle Ordovician Arenigian Series of England, and three "varieties" of a species from the Stinchar Limestone (Llanvirnian-Llandeilian), the Balclatchie Group (Caradocian), and the Drummock Group

(Ashgillian) of Girvan. These occurrences are discussed further below.

**Discussion.**—Of the species now included in the genus *Tetranota*, *T. bidorsata* (Hall, 1847) was originally assigned to *Bucania*, and *T. charon* (Billings, 1860), *T. rugosa* (Emmons), and *T. wisconsinensis* (Whitfield, 1878) were first placed in *Bellerophon*. Koken (1889, p. 389) incorrectly placed *T. bidorsata* with unrelated Silurian-Devonian European species in the sinuate genus *Bucanella* (for discussion, see Ulrich and Scofield, 1897, p. 876).

Ulrich and Scofield (1897, p. 875) proposed the genus *Tetranota* for those Ordovician species that are phanerocephalous and slit-bearing and have four revolving ridges on the shell, two bordering an elevated slit and two dorsolaterally. The lines bordering the slitband are often not well preserved; when they are (pl. 21, figs. 2-9, 14), they appear to be quite threadlike. The dorsolateral lines are not threadlike, but rather are like angled ridges or carinas. In this respect, these dorsolateral revolving ridges are more similar to the revolving ornament of *Kokenospira* than to the ornament of genera such as *Bucania* or *Bucanopsis*. In its gradually expanding, depressed whorls, and in its possession of revolving ornament, *Tetranota* shows relationship to *Bucania* and *Kokenospira*. Besides the difference in the character of the revolving ornament, *Tetranota* also differs from *Bucania* in expanding at maturity chiefly only in the lateral directions, rather than anteriorly. In addition to the similarity in the character of the revolving lines, *Kokenospira costalis* (pl. 20, figs. 9-12) also bears an elevated, nearly flat topped, dorsomedian band similar to that of *Tetranota*. Therefore, *Kokenospira* and *Tetranota* may be closely related bucaniid genera, even though they are placed in separate subfamilies.

The earliest occurrences of *Tetranota* in North America are those of *T. bidorsata* reported by Walcott (1884) from the Upper? Pogonip Group (Whiterockian?) of Nevada, and by Raymond (1908) from Chazy strata in New York; Butts (1926) reported *T. cf. T. obseleta* from the Little Oak Limestone north of Pelham, Ala. (see herein, pl. 22, figs. 16-18). Ross and others (1982) dated the Little Oak as upper Whiterockian in age. Reed (1921, p. 43) reported *T. hippapus* (Salter) from the Lower-lower Middle Ordovician Arenigian Series of England, but noted (p. 44) that the two known specimens are poorly preserved. Reed also described three "varieties" of *T. carrickensis* Reed, the earliest being from the Stinchar Limestone, which Bergstrom (1971, p. 114) correlated with the upper Lenoir Limestone of eastern Tennessee. As shown by Ross and others (1982), in some places the upper Lenoir and Little Oak Limestones are time equivalent, suggesting age correlation between the confirmed occurrences of *Tetranota* in Great Britain and



TABLE 64.—Measurements (in millimeters) of *Tetranota bidorsata*

Museum No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Dorsal width	Posterior width	Ventral width	Selenizone width	Width of lateral ridges
AMNH F1										
29592	~20.0	~16.5	—	—	—	—	—	—	—	—
787	—	—	—	—	—	—	—	—	2.2	~7.2
29594	18.0	~14.0	14.5	16.7	11.6	~14.0	~9.3	~8.5	~2.8	~8.9
29593	~21.0	—	~13.1	24.1	12.0	15.2	13.3	—	~4.0	—
USNM										
17301	20.5	14.9	9.3	23.6	6.4	~13.0	—	8.2	3.0	—
47545	22.0	—	12.2	34.9	9.8	16.3	14.5	—	3.0	—
UCGM										
44291a	—	—	—	—	—	—	—	—	1.8	8.1
44291b	—	—	—	—	—	—	—	—	2.1	8.4
44292	~16.1	~13.0	~8.5	~18.0	8.5	—	11.4	—	2.0	9.0
44293	—	—	—	—	—	—	—	—	1.9	~10.0
44294	—	—	—	~12.1	—	—	—	—	1.4	6.5

North America. Comparisons between the specimens I examined and Reed's illustrations are difficult, but British species of *Tetranota* do not appear significantly different from the American species. Examination of Reed's specimens probably will show the species names he proposed to be synonymous with American species names.

As pointed out by Ulrich and Scofield (1897, p. 877), some species of *Tetranota* are quite long ranging relative to most other bellerophontaceans. For example, *T. bidorsata* occurs in rocks ranging in age from Whiterockian through Edenian. As far as preservation and present collections allow, specimens of *T. bidorsata* from widely different stratigraphic levels and geographic localities appear essentially morphologically identical (compare pl. 22, figs. 1 and 5). Scheltema (1977, p. 105) pointed out that there may be a relationship between larvae dispersal potential, geographic range, and longevity of species. Geographically widespread and stratigraphically wide ranging species are generally eurytopic and have a greater genetic diversity. Following this line of reasoning, most bellerophontacean species, which are usually quite short ranging and local, may have been stenotopic, being too narrowly specialized to survive long periods in a constantly fluctuating epicontinental environment. *T. bidorsata* is a likely exception to this scenario, because of its broad geographic and stratigraphic distribution.

***Tetranota bidorsata* (Hall), 1847**

Plate 21, figures 1-14; Plate 22, figures 1-10

*Bucania bidorsata* Hall, 1847, p. 186, pl. 40, figs. 8a-g; 1862, p. 39, fig. 6; Chamberlin, 1883, p. 158, fig.; Walcott, 1884, pl. 1, figs. 13a-c; Lesley, 1889, p. 96, figs.

*Tetranota bidorsata* (Hall), Ulrich and Scofield, 1897, p. 877, pl. 65, figs. 10-18; Weller, 1903, p. 176, pl. 12, figs. 18, 19; Raymond, 1908, p. 197, pl. 50, fig. 5; Grabau and Shimer, 1909, p. 612, figs. 819a-d; Knight, 1941, p. 347, pl. 8, fig. 4; Shimer and Shrock, 1944,

p. 441, pl. 177, fig. 119; Steele and Sinclair, 1971, p. 19, pl. 10, figs. 4, 15; ?Wilson, 1951, p. 30, pl. 4, figs. 1, 2.

**Diagnosis.**—Shell having prominently elevated, broad dorsomedian band with distinct bordering threads and carrying slightly concave selenizone; dorsolateral slopes with centrolateral grooves between median band and single pair of distinct lateral revolving ridges.

**Description.**—Shell small to moderate in size, maximum known shell length about 22 mm. Whorls depressed, subreniform in outline, more than twice as wide as long, this ratio increasing in maturity, when aperture flares laterally somewhat. Umbilici wide and deep; shoulders squared off and angular in specimens that retain shell, tightly rounded in internal molds. Dorsum with prominently elevated, broad median band that carries slightly concave selenizone having fine but distinct lunulae, bordered by two angular revolving threads; median line visible down axis of selenizone of some specimens. Median band appears as broad, flat topped to rounded ridge in molds. Outward from the dorsomedian band is pair of centrolateral concave grooves, followed by pair of angular, slightly elevated ridges; lateral ridges distinct in small- to moderate-sized shells, but as known from molds only, tend to disappear in maturity, the dorsal slopes flattening and flaring laterally; outer dorsal slope nearly flat to the angular umbilical shoulder. Growth lines very fine, closely spaced, and quite distinct, being nearly straight, though angled slightly toward posterior on outer slopes, then increasing in curvature from dorsolateral ridges to median band; fine collabral threads pass over dorsolateral ridges uninterrupted.

**Measurements.**—Measurements of *T. bidorsata* are listed in table 64.

**Material.**—Hall's (1847) type suite was examined. Specimen AMNH F1 29592 (pl. 21, figs. 12, 13) (Hall, 1847, pl. 40, figs. 8c, d) was designated the lectotype by

Knight (1941, p. 347, pl. 8, fig. 4). That specimen retains part of the shell, but all the paralectotypes, AMNH F1 29593 (pl. 22, fig. 1), AMNH F1 29594 (pl. 22, figs. 2-4), AMNH F1 29595, and AMNH F1 787 (pl. 21, fig. 14), are black, micritic internal molds. Walcott's (1884, pl. 1, fig. 13) specimen from Nevada (USNM 17301) is also largely an internal mold, but it retains some shell on the left anterodorsal slope (pl. 22, figs. 5-10).

Ulrich and Scofield (1897, pl. 65, fig. 24) illustrated a specimen they identified as *T. sp. indet.* from Edenian strata at Cincinnati. They favored an identification as *T. obsoleta* rather than *T. bidorsata* because of the "obsolescence of the laterodorsal ridges." This specimen, USNM 47545 (pl. 21, figs. 9-11), is here identified as *T. bidorsata*, and is discussed further below. Some small, partially crushed specimens of the species, UCGM 44308 and 8695, were found in other collections from Edenian strata in the Cincinnati area.

Five well-preserved specimens retaining the shell, UCGM 44291a, 44291b, 44292, 44293, and 44294 (pl. 21, figs. 1-8), were collected by John Pojeta, Jr., William Harrison, and me from a mollusk bed in Edenian strata east of Cincinnati (locality OH-1, Bear Creek Quarry). To my knowledge, these are the best preserved specimens of *T. bidorsata* available, and they clarify features poorly shown in the lectotype.

**Distribution.**—Ulrich and Scofield (1897, p. 878) listed *T. bidorsata* from Blackriveran to Edenian strata throughout Eastern North America, including New York and adjacent Canada, West Virginia, Kentucky, Tennessee, Ohio, and Minnesota. Weller (1903) reported the species from numerous horizons in the "Trenton limestone" of New Jersey. Raymond (1908, p. 197) tentatively identified specimens from Chazy (Whiterockian) strata on Valcour Island, N.Y., as *T. bidorsata*. Walcott (1884) reported the species from the upper Pogonip Group (Whiterockian?) in the White Pine District of Nevada. Wilson (1951) and Steele and Sinclair (1971) reported the species from Blackriveran strata in eastern Canada.

The new specimens shown here are five well-preserved calcitic replicas from the Kope Formation (Edenian) at Bear Creek Quarry (locality OH-1), located in the bluffs on the northern side of the Ohio River, on the northeastern corner of the junction of U.S. Route 52 and Bear Creek Road, between Neville and Chilo, Ohio. The specimens came from a lenticular mollusk bed about 10 ft above the Point Pleasant Tongue of the Clays Ferry Formation (Shermanian), and were associated with abundant specimens of *Sinuities granistriatus*, as well as sparse specimens of *C. (Cyrtolites) claysferryensis*, small lophospirids, and orthoconic nautiloids.

**Comparison.**—*T. bidorsata* can be distinguished from *T. wisconsinensis* (pl. 38, figs. 13-16) by its prominent

dorsolateral revolving ridges (pl. 21, figs. 1-14; pl. 22, figs. 1-10). Otherwise, the two species are quite similar. *T. sexcarinata* is somewhat more globose than *T. bidorsata* and has a second pair of lateral ridges.

**Discussion.**—*T. bidorsata* is unusually long ranging stratigraphically and widespread geographically for a bellerophonacean. This may be a result of the similar appearance of internal molds of a group of closely related species. Most known specimens are internal molds. Comparison of steinkerns from New York (pl. 22, figs. 1-4), Ohio (pl. 21, figs. 9-11), and Nevada (pl. 22, figs. 5-10) shows that all have the same depressed, laterally spreading whorls, the same broad, elevated dorsomedian band, and the same low, rounded lateral ridges. The last two of these specimens retain some remnant of the shell, and both show fine, closely spaced growth lines. Besides the lectotype of the species (pl. 21, figs. 12, 13), the only specimens preserving a significant portion of the shell are five new specimens collected from the Edenian portion of the Kope Formation in southern Ohio (pl. 21, figs. 1-8). These specimens are mostly deeply embedded in fairly compact mudstone, but they nevertheless show, for the first time, the true form of the shell and nature of the ornament. They show that the lateral revolving lines are not cords, but angular ridges over which the growth lines pass essentially uninterrupted. They also confirm the presence of a dark median line along the selenizone (pl. 21, figs. 2, 3), which is also visible in the lectotype (pl. 21, fig. 13). The origin of this median line is unknown.

Specimen USNM 47545 (pl. 21, figs. 9-11), an Edenian-age internal mold, was identified as *T. obsoleta*? by Ulrich and Scofield (1897, pl. 65, fig. 24) because of the "obsolescence of the laterodorsal ridges"; however, as shown here (pl. 21, figs. 9-11), there are faint low ridges over the dorsal slopes of the specimen, and the form of the shell, the flaring of the adult aperture, and the large umbilicus clearly indicate that the specimen belongs to *T. bidorsata*.

#### ***Tetranota obsoleta* Ulrich and Scofield, 1897**

Plate 20, figures 13-15; Plate 22, figures 16-21

*Tetranota obsoleta* Ulrich and Scofield, 1897, p. 880, pl. 65, figs. 19-23; Grabau and Shimer, 1909, p. 613, figs. 819i-k; Bassler, 1919, p. 310, pl. 55, figs. 22-24; Butts, 1926, pl. 26, figs. 12, 13, Shimer and Shrock, 1944, p. 441, pl. 177, figs. 20, 21.

**Diagnosis.**—Shell relatively tightly coiled, umbilici relatively small; dorsum evenly rounded, nearly semicircular, with low, broad median band and single pair of weak dorsolateral ridges which disappear by adulthood.

**Description.**—Shell small (up to about 14 mm long), thin, rather tightly coiled; umbilici small and deep for genus. Aperture subelliptical to nearly semicircular; umbilical slopes flat, slightly sloped to nearly horizontal; umbilical shoulders tightly rounded; dorsum evenly

TABLE 65.—Measurements (in millimeters) of *Tetranota obsoleta*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Posterior width	Selenizone width
46014	13.8	11.0	7.8	16.2	4.4	7.2	2.4
71496	11.7	10.2	5.3	11.3	4.3	—	1.5
315541	9.5	—	4.2	9.9	4.0	—	1.2

rounded. No distinct parietal lip over previous whorl surface at base of aperture. Dorsomedian band slightly elevated, slightly concave, bordered by distinct revolving threads; band gradually widens with growth. Low, angular dorsolateral ridges present on juvenile whorls, but disappear toward maturity. No lunulae or growth lines well preserved.

*Measurements.*—Measurements of *T. obsoleta* are listed in table 65.

*Material.*—Three specimens were examined; all are silicified. Specimen USNM 46014 (pl. 22, figs. 19–21) is here designated the lectotype. Specimen USNM 71496 was previously figured by Butts (1926; herein pl. 22, figs. 16–18) as *T. cf. T. obsoleta*, and is here accepted as a valid member of the species. Specimen USNM 315541 (pl. 20, figs. 13–15) is a fragment of a little more than a half-whorl here referred to *T. cf. T. obsoleta*.

*Distribution.*—Ulrich and Scofield (1897, p. 880) cited *T. obsoleta* from Blackriveran- and Shermanian-age strata in Minnesota and Wisconsin, from Blackriveran-age strata in Mercer County, Ky., and from Edenian-age strata in the vicinity of Cincinnati, Ohio. Bassler (1919, p. 310, 311) reported it from the Edenian-age portion of the Martinsburg Shale in Maryland. Butts (1926, pl. 26, figs. 12, 13) found the species in the Little Oak Limestone north of Pelham, Ala., which Ross and others (1982) dated as late Whiterockian in age.

One specimen of *T. cf. T. obsoleta*, USNM 315541, was found in USGS silicified collection 6131-CO from the upper Curdsville Member of the Lexington Limestone (Kirkfieldian) of central Kentucky.

*Comparison.*—Specimens of this species examined here are smaller than average specimens of *T. bidorsata*, *T. sexcarinata*, and *T. wisconsinensis*, but Ulrich and Scofield (1897, p. 880) cited specimens up to 30 mm long. *T. obsoleta* differs from *T. bidorsata* and *T. sexcarinata* in lacking lateral revolving ridges in adulthood, and having only a weak pair as a juvenile. *T. wisconsinensis*, which is known only from dolomitic steinkerns, also

seems to lack dorsolateral revolving ridges in adulthood, but the species is easily distinguished by its smaller umbilicus and by the form of its adult whorl, which is more similar to that of *T. bidorsata* in its lateral flaring and its flattened anterior slope.

*Discussion.*—*T. obsoleta* is regarded as a species the genus *Tetranota* because of the presence of a pair of dorsolateral ridges on the juvenile whorls of the lectotype (pl. 22, figs. 19–21), and on the small specimen, USNM 315541 (pl. 20, figs. 13, 14). Like *T. bidorsata* and *T. sexcarinata*, *T. obsoleta* is widely distributed geographically and stratigraphically.

#### *Tetranota sexcarinata* Ulrich and Scofield, 1897

Plate 22, figures 11–15

*Tetranota sexcarinata* Ulrich and Scofield, 1897, p. 878, 879, pl. 65, figs. 3–9; Grabau and Shimer, 1909, p. 613, figs. 819e–h, 1; Shimer and Shrock, 1944, p. 441, pl. 177, figs. 9–11; Wilson, 1951, p. 31, pl. 4, figs. 10, 11.

*Diagnosis.*—Shell relatively large (up to 23.6 mm long), dorsum broad; two pairs of dorsolateral ridges on either side of elevated dorsomedian selenizone.

*Description.*—Shell relatively large and inflated for genus, broader over dorsum than other species; umbilici wide, open. Dorsomedian band wide, distinctly elevated, only slightly concave; bordering ridges somewhat indistinct. Two pairs of angular dorsolateral ridges present, with broad grooves between each; area between outer dorsolateral ridge and angular umbilical shoulder narrower and only slightly concave to flat. Lunulae of selenizone poorly known, but appear to have been straight. Growth lines are raised threads, rather widely spaced for genus, and distinct on umbilical slopes as well as dorsally, where they increase in their backward deflection across each dorsolateral ridge; these lines reflect broad sinus, narrowing to rather deeply set, squared-off slit.

*Measurements.*—Measurements of *T. sexcarinata* are listed in table 66.

TABLE 66.—Measurements (in millimeters) of *Tetranota sexcarinata*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Ventral width	Selenizone width	1st ridge width	2d ridge width
46018	23.6	22.6	13.3	25.3	12.7	16.9	3.9	11.7	18.7
47712	18.8	15.0	7.7	7.9	8.9	8.5	2.6	7.2	11.3

TABLE 67.—Measurements (in millimeters) of *Tetranota wisconsinensis*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Ventral width	Selenizone width
158279	21.4	14.75	12.4	23.95	7.4	8.15	3.5

*Material*.—No new specimens of *T. sexcarinata* are described here. All of Ulrich and Scofield's (1897) type specimens (USNM 46016–46018) are from the Minnesota-Illinois area. USNM 46018 is here designated the lectotype (pl. 22, figs. 14, 15). This specimen probably is a recrystallized calcitic replica. The only other specimen figured here (USNM 47712) (pl. 22, figs. 11–13) is an internal mold from Tennessee, which clearly shows the outer pair of lateral ridges.

*Distribution*.—The lectotype, USNM 46018, is from the *Fusispira* bed of the Prosser Formation (Shermanian) at Wykoff, Minn. The paralectotypes are from the Platteville Formation (Blackriveran): USNM 46017 is from the *Vanuxemia* bed at Minneapolis, Minn., and USNM 46016 is from Dixon, Ill. USNM 47712 is from the Lebanon Formation (Blackriveran) at Laverne, Tenn. Wilson (1951, p. 31) reported the species from numerous localities in the Ottawa-St. Lawrence Lowland of eastern Canada, in beds ranging from Blackriveran to at least Edenian in age. In summary, *T. sexcarinata* has been reported from Blackriveran- to Edenian-age strata throughout Eastern North America.

*Comparison*.—*T. sexcarinata* is similar to *T. bidorsata* (Hall), but differs in being larger and broader, in having six rather than four revolving lines of ornament, and in having slightly coarser and more widely spaced growth lines.

*Discussion*.—With the discovery of the new specimens of *T. bidorsata* from the Kope Formation of Ohio (pl. 21, figs. 1–8), it is possible for the first time to make clear side-by-side comparisons of this species and *T. sexcarinata* (pl. 22, figs. 14, 15). Although the differences stated above are clear, there can be little doubt that the two species are closely related. It is interesting that they share a very similar stratigraphic distribution, being known over most of Eastern North America from Blackriveran to Edenian strata. The main differences in their distribution is that *T. bidorsata* apparently is more common and also has been reported from Western North America.

#### *Tetranota wisconsinensis* (Whitfield, 1878)

Plate 38, figures 13–16

*Bellerophon wisconsinensis* Whitfield, 1878, p. 78; 1882, p. 223, pl. 26, figs. 15, 16.

*Tetranota wisconsinensis* (Whitfield), Ulrich and Scofield, 1897, p. 881, pl. 65, figs. 26–29; Shrock and Raasch, 1937, p. 558, 559, pl. 8, figs. 1–9.

*Diagnosis*.—Shell rather large (up to 21.4 mm long), whorls broad and depressed; adult aperture lip expanded, mainly laterally; dorsolateral ridges present in juveniles, lacking in adults.

*Description*.—Shell large, tightly coiled, consisting of 2.5 to 3 whorls in adults. Whorls broad and depressed. Dorsomedian band wide and distinctly elevated; selenizone is groove between two prominent, rather thick cords. Dorsal slopes broad, showing low dorsolateral ridges in juvenile whorls, these gradually disappearing during ontogeny; umbilical shoulders tightly rounded; umbilical slopes cut steeply inward; umbilical slopes cut steeply inward; umbilici moderately small and deep. At maturity, aperture expands laterally and anterior slope flattens somewhat; expanded aperture has broad sinus which ends in wide slit having nearly parallel sides, and an arch-shaped termination. Ornamentation unknown.

*Measurements*.—Measurements of *T. wisconsinensis* are listed in table 67.

*Material*.—The holotype could not be located, but Shrock and Raasch's (1937, pl. 8, fig. 1) hypotype (USNM 158279) was examined and is shown here on plate 38, figures 13–15.

Small collections of unnumbered specimens of the species were also examined at the University of Cincinnati and Miami University Geology Museums. One specimen, MU 251T, is shown here because of its excellent preservation of the slit (pl. 38, fig. 16). All known specimens of the species are dolomitized steinkerns.

*Distribution*.—Ulrich and Scofield (1897, p. 881, 882) reported the species from the Blackriveran strata of Minnesota and Wisconsin; Bassler (1915, p. 1271) specified these occurrences as being from the Platteville Formation. Shrock and Raasch (1937, p. 558, 559) also cited the species as occurring in the Platteville Formation, at McCray quarry, Kentland, Ind. Although the Platteville traditionally has been considered Blackriveran in age, Sweet and Bergstrom (1976, text-fig. 3) indicated that it is Rocklandian in age. Ross and others (1982) showed the Platteville as late Blackriveran in age.

*Comparison*.—*T. wisconsinensis* is distinguished from *T. obseleta* by its laterally expanded adult aperture and its more prominent dorsal band, but shares with that species the loss of the dorsolateral ridges in maturity.

The depressed whorls, prominent dorsal band, and laterally expanded adult aperture ally *T. wisconsinensis* with *T. bidorsata*, but *T. wisconsinensis* lacks the adult dorsolateral ridges generally so prominent in (even in

steinkerns of) *T. bidorsata*. For example, compare plate 38, figures 13-15, and plate 22, figures 5-10. *T. wisconsinensis* could eventually be placed in synonymy with *T. bidorsata*, if specimens retaining the shell are found to retain dorsolateral ridges in adulthood.

*Discussion.*—Although *T. wisconsinensis* is from just outside the present area of study, and is actually from an adjacent faunal province, the species is considered here because of its morphological similarity to *T. bidorsata*. These two species are without doubt closely related, and both might have evolved from an earlier, simpler stock represented by *T. obsoleta*. If new material confirms a pattern of continuing accentuation of the dorsal ridges in *Tetranota*, then *T. sexcarinata* could be considered a more advanced species and *Tetranota* could be considered to have developed from an early bucaniid such as *Eobucania* Kobayashi, which had revolving lines only along the borders of the selenizone. However, the tendency toward reduction of the dorsolateral ridges during ontogeny in *T. obsoleta* and *T. wisconsinensis*, and to some extent in gerontic specimens of *T. bidorsata*, suggests an opposite evolutionary trend. This problem can be resolved only when more specimens of all North American species of *Tetranota* are available.

#### Subfamily SALPINGOSTOMATINAE Koken, 1925

*Diagnosis.*—Shell having wide umbilici; submature whorls depressed and gradually expanding, aperture greatly expanded at maturity; slit long and open on adult whorl, being closed off anteriorly; selenizone generated over submature whorls.

*Stratigraphic range.*—Middle Ordovician-Middle Silurian.

*Genera included.*—The only genus included in this subfamily at present is *Salpingostoma* Roemer, 1876, which is considered below.

*Discussion.*—Koken (1925) erected the subfamily Salpingostomatinae, which then included only the type genus and was placed in the family Bellerophontidae McCoy. Knight and others (1960, p. 1180) made this taxon into the tribe Salpingostomatides of the subfamily Bucaniinae, family Bellerophontidae; they included the genera *Salpingostoma* and *Tremanotus*, and defined the group on the basis of the presence of an exhalant orifice consisting of one or more tremata. Horny (1962), on the other hand, elevated the subfamily to family rank and included in it the genera *Salpingostoma*, *Tremanotus*, and *Boiotremus* Horny from the Upper Silurian and Lower Devonian of Bohemia. *Boiotremus* included species previously assigned to *Tremanotus*, but only those that developed tremata throughout ontogeny rather than merely during adulthood. *Boiotremus* probably evolved directly from the Lower Silurian genus *Tremanotus*. The evolution may have been paedomorphic in nature, that is,

involving maturation at the juvenile stage of development. Sprinkle and Bell (1978, p. 82) have pointed out that “organisms entering new niches or colonizing new environments different from or marginal to their ancestral range often show large and rapid evolutionary changes in their morphology, life history, and mode of reproduction.” Horny (1963a, p. 65, fig. 6) showed that *Tremanotus* occurs in a largely clastic sequence of strata and occupied (p. 67) “a hard bottom of tuffaceous and organic debris” in shallow seas near volcanic islands; *Boiotremus*, in contrast, occurs in an immediately overlying carbonate sequence of bituminous limestones in the Upper Silurian and biohermal facies in the Lower Devonian. This regional change in sedimentologic conditions may have encouraged the proliferation of taxa that develop tremata at early growth stages.

Peel (1972) believed that *Salpingostoma* was only homeomorphic with *Tremanotus* and *Boiotremus*. He pointed out that while *Salpingostoma* had a slit throughout its ontogeny, the other two genera were merely sinuate, and that their tremata were formed by repeated expansion of the aperture and concomitant closing off of all but the deepest portion of the sinus. He therefore rejected Horny’s (1962) familial grouping, transferring *Salpingostoma* back to the subfamily Bucaniinae (as in Knight and others, 1960), and erected the new subfamily Tremanotinae of the family Sinuitidae for the other two closely related genera.

Peel’s (1972) emendation seems valid, because the basic difference in the development of the shells of *Salpingostoma* and *Tremanotus-Boiotremus* would seem to indicate quite different origins. The separation of the Salpingostomatinae into a separate subfamily of the Bucaniidae expresses the close resemblance of *Salpingostoma* to some species of *Bucania* in most characteristics save the morphology of the elongated closed-off slit.

#### Genus SALPINGOSTOMA Roemer, 1876

*Diagnosis.*—Adult shell having expanded, trumpet-like aperture and long, open slit extending from dorsum to slightly inside outer lip, where it is closed off.

*Description.*—Shell generally large, involute, with wide, open umbilici revealing numerous earlier volutions; submature whorls in many cases vertically depressed, subreniform, and submature aperture at plane level with ventral umbilical shoulder; at maturity, aperture expanding abruptly to trumpetlike form, becoming tangentially oriented toward coil; submature whorls with selenizone; mature expanded whorl with long, open slit extending from dorsum to near outer sinuate apertural margin, where it is closed off; shell surface in many cases marked by transverse and radial ornament.

*Type species.*—*Bellerophon megalostoma* Eichwald, 1840, by monotypy.

*Other North American species.*—Ordovician species of *Salpingostoma* in North America are *S. billingsi* Wilson; *S. buelli* (Whitfield); *S. kentuckyense* Ulrich and Scofield; *S. canadense* (Billings); *S. expansa* (Hall); *S. fraternus* (Billings); *S. imbricata* Ulrich and Scofield; *S. (?) lata* Foerste; *S. richmondensis* Ulrich and Scofield; and *S. sculptilis* Ulrich and Scofield. Silurian species in North America (Canada) listed by Peel (1972, p. 420) are *S. boreale* Whiteaves; *S. dilatus* (Sowerby); *S. inornatum* Northrop; and *S. orientalis* Twenhofel.

*Distribution.*—Middle Ordovician (Blackriveran)-Middle Silurian (Niagaran) of North America. In Europe, the genus supposedly appears lower in the Middle Ordovician (Koken, 1925) and continues at least to the end of the Ordovician.

*Discussion.*—The genus *Salpingostoma* was proposed by Roemer (1876) for *Bellerophon megalostoma* Eichwald, 1840, from the Ordovician of Estonia. Koken (1925) later listed 15 species from the Ordovician of the Baltic area. However, Koken's generic assignments and species should be reevaluated, as he recognized cephalopodlike chambers in one supposed species, *S. locator* (Eichwald) (Koken, 1925, p. 26).

Adult specimens of *Salpingostoma* are easily recognized by their expanded trumpetlike aperture and long, open slit. The slit is recognizable on internal molds as a long dorsal ridge that ends rather abruptly just inside the aperture lip (pl. 24, figs. 1–3; pl. 26, figs. 1–3, 6). However, in immaturity, before the above-mentioned morphological features are developed, the genus is not nearly so distinctive. Ulrich and Scofield (1897, p. 897) believed that juvenile specimens "correspond in nearly every respect with the whole adult shell of the most typical species of *Bucania*." They proposed that there was a progressive morphological development from one genus to another in a series—*Bucania* to *Salpingostoma* to *Tremanotus*. They stated (p. 900): "In the first the aperture is never greatly expanded, in the second it flares abruptly at maturity, while in the third the expanded mouth is developed at more or less frequent intervals." They further suggested that the resemblance of the external sculpturing of these three genera demonstrates their close evolutionary relationship. I believe that the depressed whorl forms, broad umbilici, and long slits that characterize submature specimens of species of *Salpingostoma* (pl. 24, figs. 6–8, 13–16) and adults of the *Bucania sulcatina* group (pl. 12, figs. 1–9) show that the former is directly descended from the latter.

Koken (1925) disagreed with Ulrich and Scofield's (1897) interpretations concerning not only their progressive evolutionary sequence, but even their generic identification of the American species. Koken apparently

believed that the American species assigned to the genus *Salpingostoma* by Ulrich and Scofield should instead be placed in his *Bucania cornu* group, which he asserted to have had a derivation different from that of the true *Salpingostoma* group. Koken claimed that the style of ornament of *S. buelli* (Whitfield) from the Middle Ordovician of Minnesota was more like that of a *Bucania* and that its slit was situated too far anterior. He further pointed to *S. sculptilis* Ulrich and Scofield as clearly being derived from a *Bucania*, as shown by its ornament, slit, and selenizone. Koken noted Ulrich and Scofield's (1897) claims that *Salpingostoma* should include shells whose inner volutions resemble the adult shell of *Bucania sulcatina* (Emmons), and that it is only in the fully mature specimens that the peculiarities of the genus are apparent. Koken stated that these claims demonstrated that the American species differed from the type species of the genus. Koken did not believe that juvenile specimens of the type species resembled *Bucania*, or that the type species was distinct throughout growth. In Koken's generic description he claimed that in many specimens, particularly juveniles, the shell is characteristically wrinkled, the wrinkling being independent of the threadlike growth lines, and also distinct from the wrinkled spiral lines of *Bucania*. Some of his figures of species of *Salpingostoma* (Koken, 1925, pls. 19–21) show this transverse wrinkling, but others do not. It should be noted that some of Reed's (1921, pl. 12, figs. 1, 2) species from the Ordovician of Great Britain also show rather strong transverse wrinkling. However, the American species illustrated by Ulrich and Scofield (1897, pls. 67, 82) do not. Koken (1925, p. 27, 28) concluded that *Salpingostoma* and *Bucania* are completely unrelated, but that several species of *Bucania* in the submature state are misleadingly similar to *Salpingostoma*. He further concluded that *Tremanotus* and *Salpingostoma* are not directly related because of the differences in the production of the expanded aperture in the two genera, being abrupt and occurring only once (at maturity) in *Salpingostoma*, but occurring periodically in *Tremanotus*.

Although American species of *Salpingostoma* lack the marked transverse wrinkling of the shell present in many of the European species, this does not seem to be adequate justification for generic differentiation. The common features shown by both the American and European species—expanded aperture, long, closed-off slit, shell markings—are numerous and indicate a close evolutionary relationship.

#### *Salpingostoma buelli* (Whitfield, 1878)

Plate 24, figures 1–9

*Bucania buelli* Whitfield, 1878, p. 76; Chamberlin, 1883, p. 158, fig. 33f.

TABLE 68.—Measurements (in millimeters) of *Salpingostoma buelli*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Dorsal width	Posterior width	Ventral width
265957	20.5	22.0	7.4	13.9	8.0	11.85	8.85	5.85
45980	46.3	22.0	35.4	34.3	21.3	15.50	13.20	—
47590	48.5	—	38.4	36.0	—	—	—	11.09

*Bucania* (*Tremanotus*?) *buelli* Whitfield, 1882, p. 224, pl. 6, figs. 12–14.

*Salpingostoma buelli* (Whitfield), Whiteaves, 1897, p. 189; Ulrich and Scofield, 1897, p. 900, pl. 67, figs. 34–37; Grabau and Shimer, 1909, p. 614, figs. 823a–c; Shimer and Shrock, 1944, p. 443, pl. 177, figs. 14–16; Knight and others, 1960, figs. 96–6a, b.

**Diagnosis.**—Moderately large *Salpingostoma* (up to 48.5 mm long), having expanded adult aperture extended anteriorly into a long, slightly recurved apron; shell surface entirely sculptured by curving, transverse growth lines and thin, nodular revolving threads, the latter increasing in strength on expanded aperture, with a smaller set being intercalated between, giving an alternating pattern; adult shell length/umbilical diameter ratio 2.17.

**Measurements.**—Measurements of *S. buelli* are listed in table 68.

**Material.**—Two dolomitized specimens from a set of five of Ulrich and Scofield's (1897) hypotypes, suite number USNM 45980, are illustrated here. USNM 265957 (pl. 24, figs. 6–8) is a submature internal mold; USNM 265960 (pl. 24, figs. 1–5) is an adult specimen that preserves part of the shell around the expanded apertural margin, the remainder of the specimen being a composite mold retaining an impression of the shell ornament pattern. These specimens are from the Platteville Formation (Blackriveran) at Beloit, Wis. USNM 45790 (pl. 24, fig. 9) is a dark-gray calcitic (partly carbonaceous?) replica that is embedded in gray, finely crystalline biosparite from the Platteville Formation of Minnesota.

**Distribution.**—Ulrich and Scofield (1897, p. 901) reported *S. buelli* from the "Stones River Group" of Minnesota and the "Black River Group" of Wisconsin, which strata are now recognized as the Platteville and Decorah Formations (Blackriveran-Rocklandian) (Weiss, 1957; Sweet and Bergstrom, 1976; Ross and others, 1982). Weiss (1957, fig. 1) reported *Salpingostoma* sp. (probably *S. buelli* from the Cummingsville Member of the Galena Formation (Kirkfieldian-Shermanian) of Minnesota. Bassler (1915) cited the species from Wisconsin, Minnesota, Illinois, and Manitoba.

**Comparison.**—See this heading under *S. kentuckyense* Ulrich and Scofield.

**Discussion.**—This species is not represented in the fauna of the Cincinnati arch region, but is considered

here for comparison with *S. kentuckyense* Ulrich and Scofield, which was originally designated a subspecies of *S. buelli*.

Specimen USNM 265957 (pl. 24, figs. 6–8) apparently is a specimen on the verge of maturity, just before the aperture began its abrupt expansion, because the shell height of this specimen is equal to that of an expanded adult specimen (USNM 265960, pl. 24, figs. 1–5). Note that this submature specimen of *S. buelli* is nearly identical to a submature specimen of the stratigraphically younger *S. richmondensis* Ulrich and Scofield (pl. 24, figs. 13–16), although the relative proportions are slightly different. In all submature specimens of the genus examined for this study, the plane of the aperture is at a level with the ventral umbilical shoulder. This nearly radial orientation of the apertural plane of juveniles may indicate a much less mobile life style than that led by the adults, which had a tangential aperture. This interpretation is supported by Linsley's (1978a) observations of modern conispiral gastropods, which have shells with radial apertures and are generally very sluggish or even sedentary. Also note the depressed form of the juvenile whorls of *S. buelli* (pl. 24, fig. 8), which would seem to make the shell rather awkward to balance in a highly active organism. As pointed out in the discussion of *S. kentuckyense*, the whorls of the submature coil are quite thin shelled, and this may have alleviated this awkwardness to some degree.

Specimen USNM 265960 (pl. 24, figs. 1–5) is an adult of *S. buelli*. The shell around the apertural margin shows how the lip was expanded far to the anterior as an apron. On the portion of the specimen where the shell is lacking, there is a prominent dorsomedian ridge over the anterior slope. This ridge is the reflection of the long, open slit of the shell. Lateral to this ridge, the mold becomes composite and the external sculpturing is preserved (pl. 24, figs. 1–3). The sculpture consists of growth lines that curved back toward the slit, and thin, parallel revolving threads. Specimen USNM 47590 (pl. 24, fig. 9) was photographed without whitening for better definition. This specimen shows the shape of the aperture, with its anterior sinus and wide anterior marginal apron.

*Salpingostoma kentuckyense* Ulrich and Scofield, 1897

Plate 24, figures 10–12; Plate 25, figures 1–14; Plate 26, figures 11, 12



TABLE 69.—*Measurements (in millimeters) of Salpingostoma kentuckyense*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical length	Umbilical height	Dorsal width	Ventral width
265961	43.5	28.7	32.40	31.0	—	—	—	—
265964	42.4	23.3	30.70	30.2	19.1	13.9	18.80	11.65
265965	41.2	22.5	29.75	31.5	15.0	13.6	18.25	10.90
265966	—	—	30.10	31.3	—	—	—	—
265979	—	—	32.80	32.8	—	—	—	11.45
265980	45.2	—	35.05	35.0	16.5	14.5	17.25	13.05
265980	—	—	49.75	45.0	—	—	—	—
265980	45.3	22.5	36.60	33.0	17.3	15.0	19.80	12.50
265980	—	—	32.85	33.7	—	—	—	—
265980	—	—	31.60	33.4	—	—	—	12.80
265980	—	—	40.30	40.5	—	—	—	14.85
265980	—	—	26.20	27.7	—	—	—	10.70
265980	—	—	28.00	27.8	—	—	—	—
265980	—	—	25.55	27.4	—	—	—	—
265980	—	—	34.30	38.2	—	—	—	—
265980	—	—	32.30	31.6	—	—	—	—
265980	—	—	29.80	32.4	—	—	—	12.20
265980	—	—	39.40	36.0	—	—	—	13.85
265981	—	—	33.90	32.5	—	—	—	—
265981	—	—	41.30	39.3	—	—	—	—

*Salpingostoma buelli* var. *kentuckyense* Ulrich and Scofield, 1897, p. 901.

**Diagnosis.**—Shell moderately large (up to 45.5 mm long), expanded apertural rim thickened and massive, not strongly flexed anteriorly; shell markings restricted to external rim of expanded aperture, consisting of coarse spiral ribs and growth lines; adult shell length/umbilical diameter ratio 2.70.

**Description.**—Shell moderately large, relatively thin on submature portion, becoming thick and massive on mature expanded aperture; volutions numerous, visible in wide, open umbilici; sutures deeply impressed; submature whorls depressed, subreniform, with dorsum broadly convex, umbilical shoulders narrowly rounded, venter slightly concave; whorl size increases quite gradually until maturity, when aperture abruptly expands and thickens; shell length/umbilical diameter ratio in adults averages 2.70; expanded aperture may slope anteriorly to margin, or may reflex slightly to form short apron; anteromedian sinus quite shallow; dorsomedian slit extends from dorsum down the anterior slope, where it is closed far posterior to the anterior apertural margin; selenizone distinct, narrow, appears as rounded cord; posterior expanded aperture with broad reentrant around previous whorl; outer parietal rim of expanded aperture, where coil rests, in many specimens bears coarse, chevronlike wrinkles angling outward and down-

ward; submature shell surface smooth; mature expanded shell surface marked by coarse radiating ribs and fine to lamellose growth lines.

**Measurements.**—Measurements of *S. kentuckyense* are listed in table 69 and shown graphically in figure 31.

**Material.**—Ulrich and Scofield (1897) designated eight "cotypes" now listed under the number USNM 45981. All eight are fragmentary, highly weathered silicified casts from the Curdsville Limestone Member of the Lexington Limestone. Two specimens from this set of syntypes are figured here; USNM 265961 (pl. 24, figs. 11, 12), here designated the lectotype for the species, and USNM 265962, a paralectotype (pl. 24, fig. 10). The other six specimens retain the number USNM 45981 and are designated paralectotypes.

The USGS silicified collections from Kentucky yielded numerous new specimens that are far better preserved than the type suite. Sample 6034-CO, from the Tyrone Limestone, includes USNM 265964 (pl. 25, figs. 1–8), USNM 265965 (pl. 25, figs. 9–13), USNM 265966 (pl. 26, figs. 11, 12), USNM 265979 (pl. 25, fig. 14), and USNM 265980; the last is used for a set of about 40 specimens and fragments. All of the specimens from sample 6034-CO are firmly silicified. All other new specimens are from USGS samples 6131-CO, 7784-CO, and 7785-CO, all are coarsely silicified fragments of columellas and aperture rims, and all are from the Curdsville Limestone Member of the Lexington Limestone.

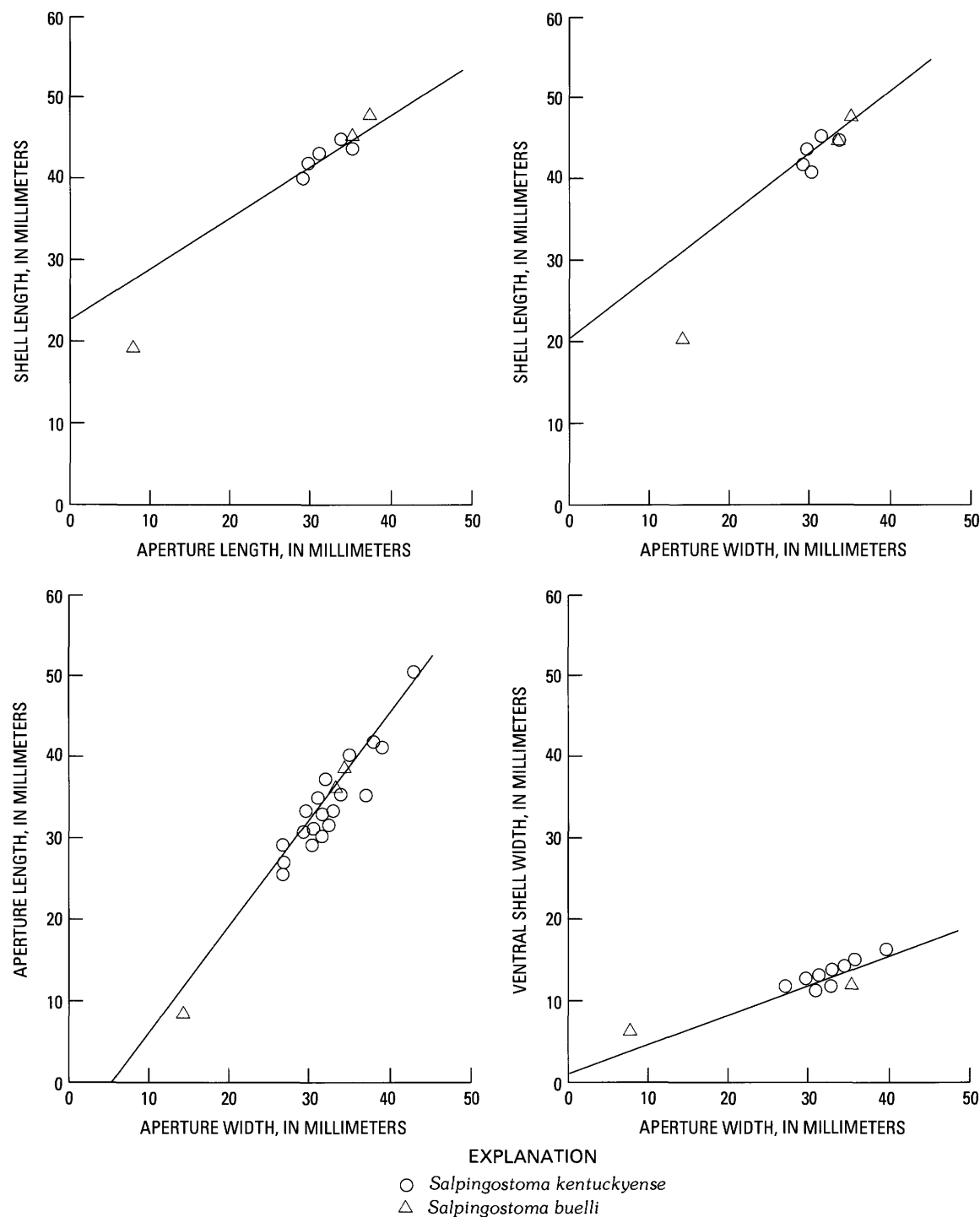


FIGURE 31.—Bivariate plots of measurements made on specimens of *Salpingostoma kentuckyense* and *S. buelli*.

*Distribution.*—*S. kentuckyense* is known from the Tyrone Limestone of the High Bridge Group (Rocklandian) and the Curdsville Limestone Member of the Lexington Limestone (Kirkfieldian). The species was found in the Tyrone Limestone (6034-CO) in the Little Hickman quadrangle, Jessamine County, Ky., at 1–2 ft (7784-CO) and 11–12 ft (7785-CO) above the base of the

Curdsville Limestone Member in the same quadrangle and county, and also at 23 ft above the base of that unit (6131-CO) in the Danville quadrangle, Boyle County, Ky.

*Comparison.*—Ulrich and Scofield (1897, p. 902) briefly described *S. buelli* var. *kentuckyense* from silicified fragments from the “Black River Limestone of Kentucky” and stated that it differed from *S. buelli* “in

having a thicker shell, coarser surface markings, and smaller inner volutions when compared with the expanded aperture which is fully as large as *S. buelli*." Like *S. expansa*, the apertural rim of *S. kentuckyense* is not so abruptly turned outward as in *S. buelli*; *S. kentuckyense* is smaller than *S. expansa*, and it is rounded over the dorsum rather than subangular. Two of Ulrich and Scofield's (1897) type specimens are shown herein (pl. 24, figs. 10–12); Ulrich and Scofield (1897) did not illustrate the species. The new and much better preserved USGS silicified material confirms many of Ulrich and Scofield's (1897) interpretations and has revealed more detail, enabling recognition of the Kentucky specimens as a distinct species.

The mature expanded aperture of the Kentucky specimens is greatly thickened and much more massive than that of *S. buelli* (pl. 25, figs. 10–12). In the Kentucky specimens, this expanded aperture is sculptured with rather thick radiating ribs and often lamellose growth lines (pl. 24, figs. 1–8, 9–11); the submature portion of the shell seems to lack ornament. On the other hand, *S. buelli* has relatively fine transverse and spiral threads which seem to cover the entire shell (pl. 24, figs. 1–3).

Ulrich and Scofield (1897) stated that the Kentucky specimens had a smaller coil in proportion to the size of the expanded aperture. The umbilical diameter/shell length ratio in *S. buelli* (USNM 265960) is 2.17, compared with an average ratio for three specimens of *S. kentuckyense* of 2.70, thus demonstrating that the latter species has a relatively smaller coil. Although the average aperture length/aperture width ratios of the two species do not differ significantly, the form of the extended anterior margin does differ. *S. buelli* has a steeper anterior slope, the anterior lip then flattening outward into a relatively broad apron. Many specimens of *S. kentuckyense* show no tendency to form an anterior apron (pl. 25, figs. 4, 5), but a few specimens do reflex the apertural margin to form a relatively small apron (pl. 25, fig. 11). *S. buelli* and *S. kentuckyense* were contemporaries during the Rocklandian and Kirkfieldian Stages. There can be little doubt that the two are closely related, but subtle differences in morphology, as well as different paleogeographic distributions, suggest that they are geographic variants and distinct species.

Another species that should be considered closely related to *S. buelli* and *S. kentuckyense* is *S. billingsi* Wilson (1951, p. 28) from the Blackriveran and Rocklandian strata of the Ottawa-St. Lawrence Lowland, Canada. According to Wilson, "the species differs from both *S. buelli* (Whitfield) and *S. expansum* (Hall) in its smaller size, more rapidly increasing and more tightly coiled whorls, and in its less abrupt aperture." *S. billingsi* is very similar in size to *S. kentuckyense*, and it also has a thickened expanded aperture with lamellose

growth increments (Wilson, 1951, pl. 3, figs. 1–3). The only obvious differences between the two species are that *S. billingsi* bears *S. buelli*-like sculpturing on the entire shell and apparently has a more highly raised anteromedian sinus. *S. buelli*, *S. kentuckyense*, and *S. billingsi* seem to form a closely related group. *S. billingsi* appeared first, in the Blackriveran, and may have given rise to the other two.

*Discussion.*—The expanded aperture of *S. kentuckyense* is much thicker than the submature portion of the shell. As a result, the great majority of the specimens in Ulrich and Scofield's (1897) type suite and in the USGS silicified collections are only the apertural rims of the shells (pl. 24, fig. 10; pl. 25, fig. 14; pl. 26, fig. 11). All the more complete specimens of the species (pl. 25, figs. 11–13) are missing the anterior slope of the expanded aperture, presumably because of the structural weakness resulting from the long, open slit. Ulrich and Scofield (1897, p. 898) pointed out that the anterior closing of the slit may have been a "necessity of overcoming the liability of fracture to which the aperture would have been subject had the slit been allowed to continue to the outer margin."

The only known specimen that preserves any portion of the slit, USNM 265964 (pl. 25, figs. 1–8), shows only the uppermost part. In that specimen, the slit was closed well back from the apertural edge. Specimen USNM 265965 (pl. 25, figs. 9, 10) shows the slit in the process of being closed anteriorly, with only a crack remaining dorsally and being entirely closed ventrally. As known from the apertural rims only, adults of all sizes had the slit closed anteriorly. When most of these specimens are held up to light, the median closed-off slit area is slightly translucent, showing that it is distinctly thinner than the lateral portions of the rim. The shell along this antero-medial line originally was secreted thinner than the adjacent shell rim. It seems that as the expanding aperture grew anteriorly along its outer edge, the slit must have been lengthened anteriorly by resorption of the thin shell along the median line. When the animal reached a certain age in later ontogeny, it essentially halted further outward growth and thickened only the aperture rim, apparently also filling in the already closed off anterior part of the slit with interior shell layers (pl. 25, figs. 9, 10).

*Salpingostoma richmondensis* Ulrich, 1897

Plate 24, figures 13–16; Plate 26, figures 1–8

*Salpingostoma richmondensis* Ulrich in Ulrich and Scofield, 1897, p. 903, pl. 67, figs. 39, 40; Cumings, 1908, p. 974, pl. 39, figs. 7, 7a; Grabau and Shimer, 1909, p. 614, figs. 823d–3; Shimer and Shrock, 1944, p. 443, pl. 177, figs. 17, 18; Foerste, 1924, p. 206, pl. 34, fig. 8.

TABLE 70.—Measurements (in millimeters) of *Salpingostoma richmondensis*

Museum No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Dorsal width	Posterior width	Ventral width
USNM								
45983	43.3	25.0	37.0	33.6	13.4	16.8	—	11.9
UCGM								
28660	27.3	20.3	13.50	22.2	13.7	17.50	14.1	10.5
44281	47.6	28.6	32.50	32.2	19.9	18.15	15.0	12.0
44280	24.6	19.2	10.10	19.2	13.6	16.50	13.2	10.5
38549	26.9	19.9	10.85	20.7	14.2	17.00	14.0	10.5
38549	49.6	25.3	34.75	28.8	23.6	19.85	16.7	13.6

*Diagnosis.*—Shell moderately large (up to 50 mm long); submature whorls depressed, reniform, width about twice length; coiling loose; at maturity, aperture expands abruptly, extending anteriorly at much greater rate than laterally, so that aperture becomes longer than wide, anterior slope steep, lateral margins slightly explanate.

*Description.*—Shell moderately large for genus, with about three loosely coiled volutions and wide-open umbilici; submature whorls depressed, reniform, width about twice length (length/width ratio 0.55), broadly convex dorsally, umbilical shoulders narrowly rounded, venter concave where contiguous with preceding whorl; at about 15–20 mm shell length, aperture expands abruptly, mainly anteriorly, so that in fully mature specimens aperture length slightly exceeds width (length/width ratio 1.11); expanded aperture widest posteriorly, reaching back to about even with posterior umbilical shoulder, lateral and posterolateral apertural margins flare slightly but do not recurve upward; anterior slope of expanded aperture steeply convex to or nearly to margin, generally flaring very little, anterior margin raised above level of lateral margins in broad, shallow sinus; slit open from dorsum to just inside anterior apertural margin, the anteromedian closure being marked by shallow linear indentation; selenizone apparently developed on submature whorls; no shell markings known.

*Measurements.*—Measurements of *S. richmondensis* are listed in table 70.

*Material.*—The holotype (USNM 45983), which preserves some shell around the margin of the expanded aperture (pl. 26, figs. 1–5), and hypotypes UCGM 44281 (pl. 26, figs. 6–8), UCGM 44280 (pl. 24, figs. 13–16), and UCGM 28660 and UCGM 38549 (the latter two measured but not figured) are all internal molds. Numerous other internal molds in the collections of the U.S. National Museum of Natural History and the geology museums of the University of Cincinnati and Miami University were examined.

*Distribution.*—The species is known only from the Richmondian (upper Upper Ordovician) of southeastern

Indiana and southwestern Ohio. Most collections examined are from the Whitewater Formation (Richmondian), near Richmond, Ind., or Camden, Ohio. Other collections are labeled only “Richmond.” All of Cumings’ (1908, p. 975) specimens are from the Whitewater Formation near Richmond, Ind., being most abundant near the top of the unit. Cumings (1908, p. 662, 663) noted the species as common in “lumpy limestones” associated with abundant *Rhynchotrema dentatum*, several species of gastropods, and *Strophomena sulcata*. He cited *S. richmondensis* as occurring in a typical Whitewater biofacies of brachiopods and bryozoans.

*Comparison.*—As noted by Ulrich and Scofield (1897, p. 904), many specimens of this species in old collections are labeled *Bucania expansa* Hall, a species from the Middle Ordovician of New York that is now placed in *Salpingostoma*. The two species are easily distinguished morphologically. *S. richmondensis* has one less volution than *S. expansa* for the same size of shell. In addition, *S. expansa* has a subtriangular whorl shape, which is in sharp contrast to the broader reniform whorl shape of *S. richmondensis*.

It is much more difficult to distinguish between *S. richmondensis* and *Bucania simulatrix* Ulrich. The two species are homeomorphic, and thus have very similar shell forms. Both species are known mainly or completely from internal molds, and both are found in the Richmondian Whitewater Formation in the vicinity of Richmond, Ind. Preliminary examination gave me the impression that the two species are synonymous, but on close scrutiny I became certain they are distinct. Many museum collections that are labeled as containing one species or the other commonly include both species. In well-preserved specimens, the slit of *B. simulatrix* can be observed to extend to the anterior apertural margin, readily distinguishing that species from *S. richmondensis*.

Comparison of the lectotype of *B. simulatrix* (USNM 315548 pl. 19, figs. 11–14) with the holotype of *S. richmondensis* (USNM 45983, pl. 26, figs. 1–5) shows the distinctiveness of the two species. Figure 32 shows the

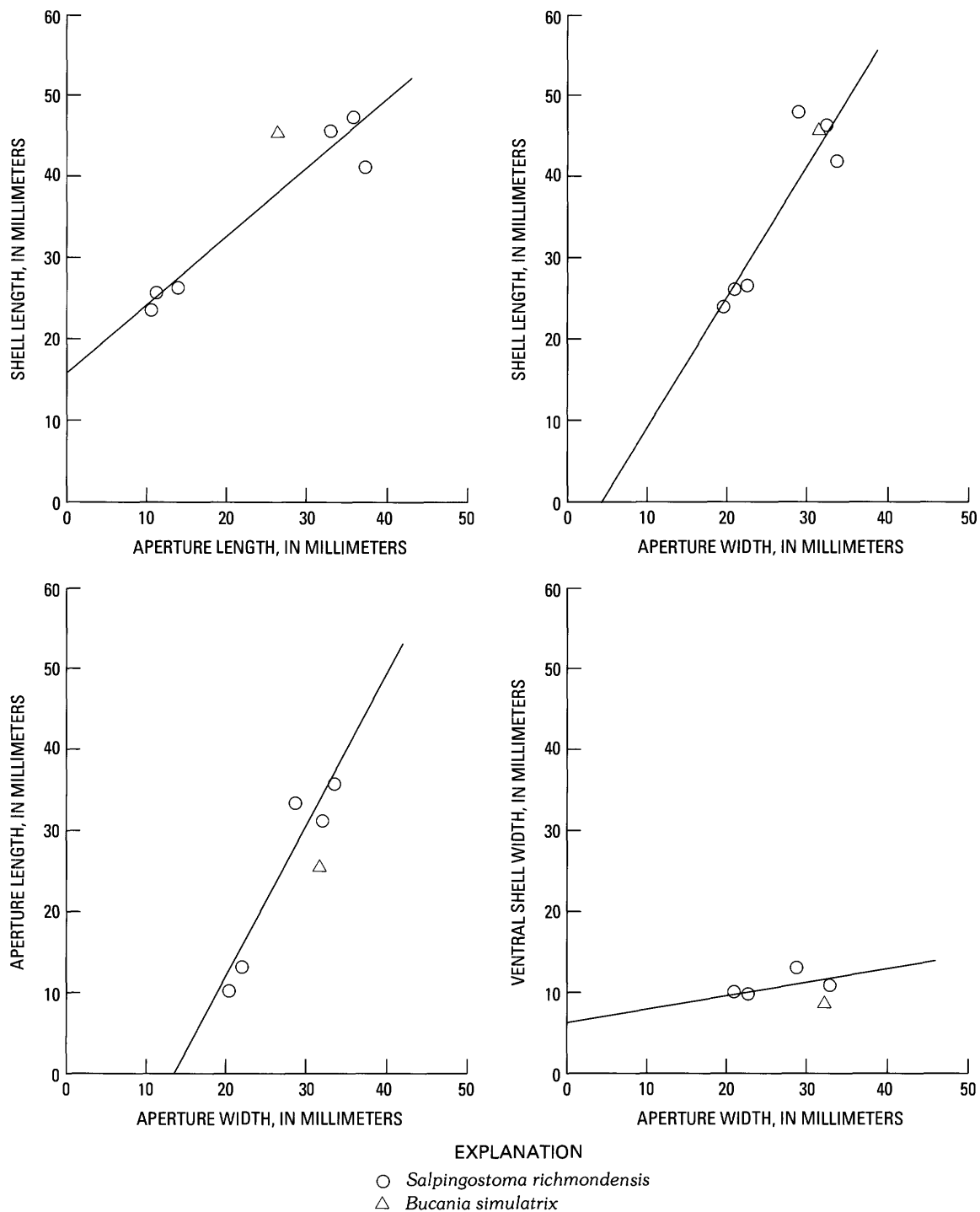


FIGURE 32.—Bivariate plots of measurements made on specimens of *Salpingostoma richmondensis* and *Bucania simulatrix*.

lateral expansion rates of six (three immature and three mature) specimens of *S. richmondensis* and the lectotype of *B. simulatrix*, using width measurements taken at every quarter revolution on the last whorl. These measurements reveal that the last whorl of *B. simulatrix*

is a good deal narrower than that of *S. richmondensis*. Moreover, in *B. simulatrix* the anterior width gradually and constantly increases throughout ontogeny. Conversely, *S. richmondensis* grows gradually until maturity, then expands abruptly, reaching the same width as

*B. simulatrix*, but over a shorter length and after a much briefer period of increased expansion.

Figure 32 shows scattergrams for the six specimens of *S. richmondensis* listed in table 70, as well as for the lectotype of *B. simulatrix*. The regression line was calculated only for the measurements of *S. richmondensis*. *B. simulatrix* stands slightly away from the other points in three of the four graphs, agreeing best on the plot of shell length versus aperture width.

Although there are no known complete specimens of *S. richmondensis* retaining the shell, there can be little doubt about its generic placement. In the anteromedian area of the holotype, where some shell is preserved, there is a shallow linear indentation (pl. 26, fig. 1), just as in *S. kentuckyense* (pl. 25, fig. 9), which reflect the thinness of the shell there. This thin strip of shell apparently was easily resorbed in the lengthening of the slit as the anterior margin of the aperture was extended. Posterior to this indentation is a low, weathered median ridge (pl. 26, figs. 1–3) reflecting the long, open slit on the internal mold. This ridge is better preserved on another internal mold, UCGM 44281 (pl. 26, figs. 6, 7). Furthermore, the anteromedian apertural margin is raised above the level of the lateral margins (pl. 26, fig. 8), but only slightly, and there apparently is only a broad, shallow sinus.

Although the general shell form of *B. simulatrix* (pl. 19, figs. 11–14) is very similar to that of *S. richmondensis* (pl. 26, figs. 1–5), the anteromedian expanded aperture of *B. simulatrix* shows a deeply cut, V-shaped sinus in the anteromedian lip which reaches to about the level of the dorsal umbilical shoulder on the coil (pl. 19, figs. 11, 14). Posterior to this deep sinus is a long median ridge in the internal mold (pl. 19, figs. 11, 12) as was seen in *S. richmondensis*; however, in *B. simulatrix* the ridge reaches all the way to the tip of the sinus. It is doubtful that this ridge reflects a long, open slit; it more likely represents a selenizone on an elevated dorsal carina which formed an internal channel along the interior median crest of the shell.

**Discussion.**—Ulrich and Scofield (1897) observed revolving ribs and transverse growth lines preserved on the dorsum of a single specimen of *S. richmondensis*, but no ornament was seen on any specimens examined during this study. Therefore, these features have not been included in the description given here. I could not locate any such specimen among Ulrich's collections at the U.S. National Museum of Natural History.

The species most similar to *S. richmondensis* is the Middle Ordovician *S. expansa* from New York, and that species might be ancestral to *S. richmondensis*. However, this similarity may be superficial, and the result of similar preservation of both species as internal molds. Such preservation suggests that these species were

fairly thin shelled compared with *S. buelli*, *S. kentuckyense*, and *S. billingsi*, which have thickened apertures. In further support of this contention is the fact that molds of *S. richmondensis* commonly are strongly compressed. A similar situation exists with some species of *Sinuities* (for example, *S. cancellatus*) in the Cincinnati rocks of the study area, and it is known that these species were quite thin shelled.

As previously noted, Cumings (1908, p. 662, 663) cited *S. richmondensis* as characteristic of the *Rhynchotrema dentatum* beds near the top of the Whitewater Formation, where it occurred in "lumpy limestone" beds with several species of gastropods, and *R. dentatum* and *Strophomena sulcata*. Although most internal molds of *S. richmondensis* are composed of fine carbonate mudstone or wackestone, the matrix in which most specimens occur is packstone to grainstone. Putting this information together, it seems that *S. richmondensis* probably inhabited a quiet environment in a typical molluscan-brachiopod community. Shells commonly were transported into adjacent higher energy environments (probably during storms) and deposited in adjacent banks of shell debris, being associated there with a more typical bryozoan-brachiopod assemblage. This reasoning is in keeping with the regressive nature of the Whitewater Formation, which records the last stage of Ordovician deposition in the northwestern part of the area. Scattered low, shelly banks and intervening quieter lagoons would fit this picture. Moreover, this interpretation agrees with Peel's (1977b) conclusion that explanate bellerophontaceans are adapted for life on fine substrates.

I collected very fragmentary specimens of *S. richmondensis* at Thistlewaite Falls along the Whitewater River at Richmond, Ind. The specimens occurred in nodular limestone beds composed of the fragmented skeletal debris of brachiopods, bryozoans, and mollusks. The fragmented, worn skeletal debris was neither sorted nor oriented, but gave the impression of debris transported and deposited by storms.

#### Family BELLEROPHONTIDAE McCoy, 1851

**Diagnosis.**—Shell rounded, in many cases inflated; apertural margins in many cases flaring or even somewhat explanate, parietal lip generally reflexed; anteromedian slit generating distinct selenizone; umbilicus narrow or closed.

**Stratigraphic range.**—Middle Ordovician–Lower Triassic.

**Discussion.**—This family encompasses most late Paleozoic bellerophonts. Golikov and Starobogatov (1975) preferred to recognize as families the taxa herein treated as subfamilies. The problem is how to best represent the phylogenetic relationships between these taxa in the

systematic hierarchy. It is believed here that the common morphological features of the taxa represent a phylogenetic grade of shell development that is best treated under one family name. Four subfamilies are recognized within the family Bellerophontidae—Bellerophontinae McCoy, 1851; Bucanopsinae new subfamily; Knightitinae Knight, 1956; and Cymbularinae Horny, 1962.

As discussed later, in the section on the family Carinaropsidae, *Bucanopsis* and *Sphenosphaera* are quite distinct from *Carinaropsis* and are not included in that family; herein, they are placed in the new subfamily Bucanopsinae of the Bellerophontidae. The strong revolving ornament of *Bucanopsis* indicates a common ancestry with the subfamily Bucaniinae of the family Bucaniidae. *Sphenosphaera* has a shell form very similar to that of *Bucanopsis*, and both bear a keel along the median whorl floor. *Sphenosphaera* also bears a striking resemblance to *Bellerophon* in general shell form. *Sphenosphaera* was separated from *Bellerophon* because of subtle differences in the form of the parietal lip and the presence of a median whorl floor keel (Knight, 1945a, p. 334). It is likely that the Bellerophontinae evolved from the Bucanopsinae, through *Sphenosphaera*. It may be that the Knightitinae also evolved from the Bucanopsinae through *Bucanopsis* or closely related forms. This view is supported by the common possession of strong radial ornament by *Bucanopsis* and genera of the Knightitinae, and by the presence of a whorl floor keel in at least one species of *Knightites*, as reported by Rollins (1967), who also regarded *Bucanopsis* as the ancestor of the Knightitinae.

The Cymbularinae was proposed by Horny (1962) for globose shells having a distinct V-shaped sinus preceding the slit. Its ancestry is unclear, and its placement within the Bellerophontidae is debatable. If the genus *Coelocyclus* is a valid member of the Cymbularinae, as Horny thought, then the Cymbularinae may have evolved from the Bucaniinae of the Bucaniidae. Bucaniinae is the subfamily to which *Coelocyclus* was assigned by Knight and others (1960).

#### Subfamily BELLEROPHONTINAE McCoy, 1851

*Diagnosis*.—Shell convolute or nearly so, umbilici small or absent; whorls in most cases broadly rounded, somewhat globose; slit fairly short, generating selenizone; shell surface having only growth lines.

*Stratigraphic range*.—Middle Ordovician-Lower Triassic.

*Genera included*.—*B. (Bellerophon)* Montfort, 1808; *B. (Aglaoglypta)* Knight, 1942; *B. (Pharkidonotus)* Girty, 1912; *Liljevallospira* Knight, 1945a; *?Ptychobellerophon* Delpey, 1941; *?Bubovicus* Horny, 1962. Horny (1962) assigned two rather unusual genera to the Belle-

rophontinae, *Bubovicus* Horny and *Kodymites* Horny. Both genera could be placed in the Bellerophontidae, but they do not conform to the morphobases used for defining the subfamily Bellerophontinae. *Kodymites* has umbilici filled with the inductural deposits, and may represent a new subfamily, as suggested by Horny (1962). *Bubovicus* is here left in the Bellerophontinae for the time being, but its high, narrow whorls and moderately small, open umbilicus are somewhat atypical of the subfamily. Because of some spiral ornamentation, Horny (1963a, p. 121) suggested a possible relationship to *Kokenospira*, but concluded that the development of the selenizone and the general shape of the growth lines are typical of the Bellerophontinae. Thus far, only one species of *Bubovicus* has been described, and more data are needed before its higher level placement can be decided with confidence.

*Discussion*.—With Horny's (1962) removal of the Cymbulariinae from the subfamily (three or four genera), the Bellerophontinae is now a very homogeneous grouping of genera. Because of the close morphologic similarity between these genera and *Sphenosphaera*, there is little doubt that the Bellerophontinae evolved from the Bucanopsinae through *Sphenosphaera*, or a genus much like it.

#### Genus BELLEROPHON Montfort, 1808

*Diagnosis*.—Shells having broadly rounded whorls, but some having subdued dorsal crest; umbilici small or closed; median whorl floor ridge absent.

*Type species*.—*Bellerophon vasulites* Montfort, 1808, by original designation.

*Distribution*.—Middle Ordovician-Lower Triassic. Cosmopolitan.

*Discussion*.—Throughout most of the 19th century, the genus *Bellerophon* encompassed nearly all described bellerophontaceans. Late in that century, subtle differences in different groups of species within the genus were recognized and new genera were described and proposed.

Knight (1945a, p. 334) proposed the genus *Sphenosphaera* to include American Ordovician species assigned to *Bellerophon* by Ulrich and Scofield (1897), and related species. The primary taxobasis distinguishing *Sphenosphaera* was the presence of a median whorl floor ridge. Rollins (1967) has contested the collective assignment of American Ordovician species to *Sphenosphaera*, pointing out that some of these species lack a whorl floor ridge, and in many others the whorl floor is not known. He believed that all such species should be returned to *B. (Bellerophon)*. It should be noted that the whorl floor ridge dies out at the parietal callosity in *Sphenosphaera*, and does not extend outside the aperture, so any filling of the aperture prevents being able to see this structure.



TABLE 71.—Measurements (in millimeters) of *Bellerophon* (*Bellerophon*) subglobulus

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Dorsal width	Posterior width	Ventral width	Selenizone width
45709	19.4	13.8	14.6	16.0	11.8	—	—	0.85
387022	11.8	8.6	8.4	10.5	7.5	5.3	3.6	0.60

In the fauna discussed here, three species are confirmed as members of *B. (Bellerophon)* (lacking a whorl floor ridge), five species are confirmed as members of *Sphenosphaera* (possessing a whorl floor ridge), and three species are of uncertain generic assignment (specimens not exposing the whorl floor). The generic placement of the group of uncertain species was based on other comparative morphological features. Two of these species, *S. recurvus* (Ulrich) (pl. 33, figs. 1–4) and *S. subangularis* (Ulrich) (pl. 33, figs. 10–15), have comparatively angled, nonglobose shells and nearly closed umbilici, and seem to be related to *S. clausus* Ulrich. The third species of uncertain affinity, *Bellerophon subglobulus* Ulrich (pl. 33, figs. 7–9), is poorly preserved and its proper generic assignment is difficult to determine, particularly because it is the earliest known species of the two genera in the Cincinnati arch faunas (Blackriveran-Rocklandian in age). It is similar to *S. troosti* in the size of its umbilici and its thin, ridgelike selenizone, but because of the globosity of its shell and the lack of evidence of a whorl floor keel, the species is tentatively assigned to *B. (Bellerophon)*.

With confirmation of the assignment of *B. (B.) bilineatus*, *B. (B.) nana*, and *B. (B.) subpatula* to the subgenus *Bellerophon* (*Bellerophon*), the range of the genus is once again extended back to the Middle Ordovician. This is at variance with Knight and others (1960), who claimed a Silurian origin for *B. (Bellerophon)*.

**Subgenus BELLEROPHON (BELLEROPHON) Montfort, 1808**

**Diagnosis.**—Shell rounded or commonly globose; selenizone distinct, in some cases on dorsal crest; aperture lips flaring slightly near small umbilici; inductura thin to slightly thickened but in all cases smooth, and extending only short distance out of plane of aperture; ornament predominantly collabral.

**Type species.**—Same as for genus.

**Distribution.**—Same as for genus.

**Discussion.**—Three subgenera are currently recognized within the genus *Bellerophon*. *B. (Aglao glypta)* is like *B. (Bellerophon)* but is ornamented with quincunally arranged pustules (Knight and others, 1960). *B. (Pharkidonotus)* differs from the other two subgenera in having strongly thickened inductural deposits that in many cases are padlike in shape, an ornament of collabral undulations, a crested selenizone, and no umbilicus

(Knight and others, 1960). The subgenera *B. (Aglao glypta)* and *B. (Pharkidonotus)* are Middle and Late Paleozoic in age. *B. (Bellerophon)* is the oldest of the three subgenera (appearing in the Middle Ordovician), and most likely was ancestral to the other two more specialized subgenera.

***Bellerophon* (*Bellerophon*) subglobulus Ulrich, 1897**

Plate 33, figures 7–9

*Bellerophon subglobulus* Ulrich in Ulrich and Scofield, 1897, p. 917, pl. 64, figs. 17, 18.

**Diagnosis.**—Shell moderately small (up to 19.4 mm long), subglobose; umbilici small, circular; selenizone thin, elevated, ridgelike, with lunulae.

**Description.**—Shell moderately small, subglobose in form; dorsal slopes uniformly well rounded; umbilici small, circular, with slightly reflexed parietal lip passing just beneath them. Aperture rounded; whorl floor not visible because of filling by matrix. Growth lines broadly rounded over dorsum, sharp, evenly and closely spaced. Selenizone thin, elevated, ridgelike, with lunulae.

**Measurements.**—The measurements of *B. (B.) subglobulus* given in table 71 are only approximations, because of the poor preservation of the known specimens.

**Material.**—Only two specimens were located, both cataloged under USNM 45709. The lectotype designated herein (pl. 33, figs. 7–9) retains that number, and the unfigured paralectotype is assigned the number USNM 387022.

**Distribution.**—Ulrich and Scofield (1897) stated only that the specimens came from the “Black River limestone, Mercer County, Kentucky.” The species probably occurs in the High Bridge Group (Blackriveran-Rocklandian) of central Kentucky.

**Comparison.**—Although poorly preserved, the type specimens of *B. (Bellerophon) subglobulus* can be distinguished from *Sphenosphaera troosti* by their lack of distinct continuous whorl floor ridges and by their more globose form, their more broadly curved and threadlike growth lines, their narrower, ridgelike selenizone, and, probably, their smaller parietal callosity. *S. clausus* shows the same differences and also has a channellike selenizone and lacks umbilici. *B. (Bellerophon) bilineatus* has larger umbilici and a channellike selenizone.

TABLE 72.—Measurements (in millimeters) of *Bellerophon* (*Bellerophon*) *bilineatus*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Dorsal width	Posterior width	Ventral width	Selenizone width
45697	12.9	10.9	5.0	14.0	8.6	6.5	5.4	0.9
45697	—	8.7	—	13.6	7.3	5.9	4.9	0.9
315612	—	14.6	—	20.2	—	—	—	—

***Bellerophon* (*Bellerophon*) *bilineatus* Ulrich, 1897**

Plate 28, figures 1–9

*Bellerophon bilineatus* Ulrich in Ulrich and Scofield, 1897, p. 917, pl. 64, figs. 19–21.

**Diagnosis.**—Shell moderately small (up to 13 mm long); umbilici relatively large; whorl floor keel very low or absent; selenizone concave, bordered, and lunulate.

**Description.**—Shell moderately small, expanding rather slowly. Whorl slopes cutting downward sharply, forming rounded dorsolateral shoulder and giving shell a squarer appearance than in other species. Umbilici relatively large for genus. Parietal lip not much thickened centrally; posterolateral lips folded back just beneath umbilici. Low, rounded whorl floor keel present in some specimens. Selenizone nearly flush with dorsal whorl slopes, slightly concave, bordered by distinct revolving thread on either side, lunulae well developed. Growth lines fine, threadlike, very closely and evenly spaced, gently curved.

**Measurements.**—Measurements on *B. (B.) bilineatus* are listed in table 72.

**Material.**—Both the holotype (USNM 45697) (pl. 28, figs. 1–5) and the unfigured paratype (USNM 387023) are silicified and fragmentary. One possible new specimen of *B. (B.) cf. bilineatus* was identified from USGS silicified sample 6136-CO (USNM 315612) (pl. 28, figs. 6–9).

**Distribution.**—The type specimens are listed as coming from the “upper portion of the Trenton Group, near Danville, Kentucky” (Ulrich and Scofield, 1897), this corresponding to the upper Lexington Limestone (Shermanian) of modern usage. The possible new specimen is from the Faulconer Bed of the Perryville Limestone Member of the Lexington Limestone (Shermanian) in central Kentucky.

**Comparison.**—This species is most similar to *Sphenosphaera troosti* and *S. burginensis*, but is distinguished by its larger umbilicus, its squarer whorl form, its lack of

a distinct whorl floor keel, and its concave, lunulate selenizone bordered by revolving threads.

**Discussion.**—As pointed out by Rollins (1967, p. 118), the holotype of this species apparently lacks a true whorl floor ridge, and therefore does not fit the definition of the genus *Sphenosphaera*. In every other characteristic, the holotype seems closely related to contemporaneous species of that genus, but by definition it must be assigned to *Bellerophon* (*Bellerophon*). The relatively large umbilicus of the species is a primitive morphological feature.

***Bellerophon* (*Bellerophon*) *nana* (Ulrich), 1897**

Plate 18, figures 13–17

*Bucania nana* Ulrich in Ulrich and Scofield, 1897, p. 895, pl. 66, figs. 41–44.

*Sphenosphaera nana* (Ulrich), Rollins, 1967, p. 119, pl. 4, figs. 2, 3.

**Diagnosis.**—Shell small (up to 9.5 mm long), whorls rounded but relatively narrow; selenizone channellike and bordered by thin ridges; growth lines broadly curved.

**Description.**—Shell small; whorls rounded dorsally and laterally, but relatively narrow rather than globose; umbilici of moderate size for genus; apertural outline subreniform, lips not known to flare laterally. Sinus moderately shallow; selenizone concave, channellike, with distinct lunulae and bordering threads. Growth lines broadly curved over dorsum, threadlike, closely and quite evenly spaced.

**Measurements.**—Measurements of the lectotype and a paralectotype of *B. (Bellerophon) nana* are listed in table 73.

**Material.**—The lectotype, USNM 315553 (pl. 18, figs. 13, 14), and a paralectotype, USNM 315554 (pl. 18, figs. 15–17), are figured from Ulrich's (Ulrich and Scofield, 1897) syntypic suite of 11 small silicified specimens. The remaining nine paralectotypes remain cataloged under USNM 45722. No new material is known.

TABLE 73.—Measurements (in millimeters) of *Bellerophon* (*Bellerophon*) *nana*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Dorsal width	Posterior width	Ventral width
315553	6.4	4.8	4.0	5.5	4.5	3.5	3.0
315554	9.5	7.0	5.0	8.0	5.0	3.8	3.2

TABLE 74.—Measurements (in millimeters) of *Bellerophon* (*Bellerophon*) *subpatula*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Dorsal width	Posterior width	Ventral width
315552	7.1	4.5	4.0	7.0	4.7	3.3	2.8

*Distribution*.—The museum label with the type material says the collection is from the “Flanagan beds of the Trenton, one and a half miles south of Burgin, Kentucky.” The Flanagan is an outdated stratigraphic name for silicified beds in the upper Lexington Limestone that are at different levels; however, the geographic locality makes it probable that the specimens are from the Perryville Limestone Member of the Lexington Limestone (Shermanian).

*Comparison*.—This species can be differentiated from *B. (B.) bilineatus* by its smaller umbilici and narrower whorl form.

*Discussion*.—Ulrich and Scofield (1897, p. 896) assigned this species and its supposed subspecies *B. nana subpatula* to the genus *Bucania* because they believed *Bellerophon nana* to have faint revolving threads. However, they qualified the assignment to *Bucania* by noting that they were not satisfied that either was a “true *Bucania*,” as their umbilici were too small and their sculpturing was “not what it should be.”

Rollins (1967, p. 119) suggested that both subspecies might be juveniles of *Sphenosphaera troosti* or *S. clausus*, because of similarities in the character of the collabral ornament and the presence of strong threads bordering the selenizone; he decided to call the species *Sphenosphaera nana*.

It appears that this species is distinct, particularly by virtue of its rounded but narrow whorls. It shows no evidence of a whorl floor ridge (pl. 18, figs. 14, 17), and therefore it is recognized here as a species of *B. (Bellerophon)*.

***Bellerophon* (*Bellerophon*) *subpatula* (Ulrich), 1897**

Plate 18, figures 10–12

*Bucania nana* var. *subpatula* Ulrich in Ulrich and Scofield, 1897, p. 896, pl. 66, figs. 45, 46.

*Diagnosis*.—Shell small (up to 7.1 mm long); whorls broadly rounded over dorsum; umbilici moderately small; selenizone narrow, slightly concave, with fine bordering threads; growth lines fine, threadlike, only slightly curved over dorsum, reflecting a very shallow apertural sinus.

*Measurements*.—Measurements of the lectotype of *B. (Bellerophon) subpatula* are listed in table 74.

*Material*.—The lectotype, USNM 315552 (pl. 18, figs. 10–12), is here designated from the syntypic suite,

USNM 45723, which consists of three small silicified specimens. No new material is known.

*Distribution*.—The museum label with the type suite reads “Trenton, 1.5 miles south of Burgin, Kentucky.” The specimens most likely are from the upper Lexington Limestone (Shermanian).

*Comparison*.—This species can be distinguished from *B. (B.) nana* by its wider aperture and whorl form, its slightly smaller umbilici, its narrower and less concave selenizone, and its nearly straight growth lines.

*Discussion*.—See the discussion under *B. (B.) nana* for the history of *B. (B.) subpatula*. The species is included in *B. (Bellerophon)* because the lectotype shows no evidence of bearing a whorl floor ridge (pl. 18, fig. 11).

**Subfamily BUCANOPSINAE new subfamily**

*Diagnosis*.—Shell anomphalous or very nearly so; median keel or ridge on whorl floor; selenizone generally slightly elevated.

*Stratigraphic range*.—Middle Ordovician–Silurian.

*Genera included*.—*Bucanopsis* Ulrich in Ulrich and Scofield, 1897, the type genus, and *Sphenosphaera* Knight, 1945a.

*Discussion*.—The revolving ornament of *Bucanopsis* suggests that the genus may be ancestral to the Knightitinae. Rollin’s (1967) observation of the presence of a median whorl floor ridge in a species of *Knightites* further supports this idea.

The Bucanopsinae is thought to be ancestral to the Bellerophontinae. Knight (1945a) proposed the genus *Sphenosphaera* for Ordovician species previously assigned to *Bellerophon*. The two genera are almost indistinguishable except for the presence of a prominent whorl floor keel in *Sphenosphaera*. The median whorl floor keel in the tropidodiscids, the earliest appearing family of the slit-bearing Bellerophontacea, is simply the result of the wrapping of a subsequent whorl coiling over the carinate dorsum of the previous whorl. However, in the Bucanopsinae, this whorl floor keel persists even in forms lacking a dorsomedian prominence. The whorl floor keel may have served an unknown function. A function would explain the continued presence of a whorl floor keel when no dorsomedian prominence is present. On the other hand, the whorl floor keel of the bucanopsids may be a vestigial structure.

Knight and others (1960, p. 1180) placed *Bucanopsis* and *Sphenosphaera* in the Carinaropsinae because of their rapidly expanding shells and their possession of

whorl floor keels. However, these two genera do not have the parietal lip developed into a platform that extends well into the apertural opening; nor do they show true reduction of the coil. It is believed here that *Carinaropsis* and its relatives, which do show these features, are a distinct, specialized group, and that group is placed in a separate family within the bellerophontacean taxonomic scheme. However, it is quite likely that the Carinaropsidae and Bucanopsinae had a common ancestry, or that the Carinaropsidae evolved from a bucanopsid such as *Sphenosphaera*.

Genus BUCANOPSIS Ulrich and Scofield, 1897

*Diagnosis.*—Shell rapidly expanding, selenizone elevated; parietal lip broad, shelflike, with sharp median keel developed over ventral whorl floor; ornament of fine, straight, parallel revolving threads and fine growth lines.

*Description.*—Shell small to moderate in size, rapidly expanding; umbilici of moderate size. Selenizone generally elevated on dorsomedian ridge. Aperture broadly expanded; parietal lip reflexed over coil and spread laterally to form ventral shelf posterior to aperture opening; whorl floor and parietal shelf with median keel caused by covering of dorsomedian elevation by thin parietal lip. Shell surface marked by fine, unwrinkled, uninterrupted revolving threads which run parallel to direction of coiling. In some cases, faint growth lines are of sufficient strength to give weak reticulate pattern to shell.

*Type species.*—*Bucanopsis carinifera* Ulrich and Scofield, 1897, by original designation.

*Distribution.*—In the Ordovician of North America, *Bucanopsis* is known from the species *B. carinifera* and *B. diabloensis* n. sp., which are found in the Lexington Limestone of Kentucky and the Bigby-Cannon Limestone of Tennessee, both formations being Kirkfieldian-Shermanian in age.

Reed (1921, p. 58–62) reported four species of *Bucanopsis* from Caradocian, Ashgillian, and Wenlockian age (Middle Ordovician–Upper Silurian) strata of Great Britain. Horny (1963a, p. 113–116) described four species of *Bucanopsis* from Llandeilian, Caradocian, and Ashgillian strata of Bohemia. Three species of *Bellerophon* named by Lindstrom (1884) from the Middle Silurian of Scotland have been referred to *Bucanopsis* by Rollins (1967, p. 116, 117). Therefore, *Bucanopsis* is known from the Middle Ordovician to Upper Silurian in North America and Europe.

*Discussion.*—Ulrich and Scofield (1897, p. 922–924) proposed the genus *Bucanopsis* for species resembling *Bellerophon* but having straight, nonwrinkled revolving lines which run parallel with the direction of coiling. They discussed the history of these species in some

detail, and only a brief synopsis is presented here. Paleontologists prior to 1880 classified species placed by Ulrich and Scofield (1897) in *Bucanopsis* in the genus *Bellerophon*. Waagen (1880) separated such species from *Bellerophon* on the basis of their spiral sculpture, and placed them in *Bucania* Hall. Koken (1889, p. 379) adopted this approach. Ulrich and Scofield (1897) believed the shell form of species they placed in *Bucanopsis* was more similar to that of *Bellerophon* than *Bucania*, and emphasized differences between *Bucania* and *Bucanopsis* in the character of the revolving ornament. Species of *Bucania* are characterized by oblique revolving lines that are wrinkled and generally interrupted regularly by growth lines; in contrast, the revolving threads of species of *Bucanopsis* are straight and parallel to the direction of coiling, and are never wrinkled or broken by stronger growth lines. Knight (1945a, p. 335) proposed the genus *Retispira* and placed therein all Devonian- through Permian-age species previously placed in *Bucanopsis*; he stated that *Retispira* differs from *Bucanopsis* “by its simple, inductural inner lip and its lack of the sharp ridge on the floor of the interior of the whorl.” Knight and others (1960) treated *Retispira* as a subgenus of *Knightites* in the Bellerophontidae, and placed *Bucanopsis* in the Carinaropsinae, stating that the presence of a whorl floor keel and expanded aperture allied *Bucanopsis* with *Sphenosphaera* and *Carinaropsis* (also see Knight, 1945a, p. 334, 335).

As noted by Rollins (1968, p. 112), it is here recognized that the whorl floor keel of *Bucanopsis* is quite different from those of *Sphenosphaera* and *Carinaropsis*. *Bucanopsis* is partly characterized by a selenizone carried on a highly prominent dorsal carina, as exemplified by the type species *Bucanopsis carinifera* (pl. 27, figs. 1, 16). The whorl floor keel in that species is the result of the covering of this dorsal carina by the parietal lip of the subsequent whorl. This is also shown by the presence of the keel ventrally over the entire parietal lip (pl. 27, figs. 4, 11, 14, 20). Species of *Sphenosphaera* and *Carinaropsis*, on the other hand, do not generally have a prominent dorsal carina (although there are exceptions), but they still develop a whorl floor keel. Furthermore, the whorl floor keel in these genera does not continue ventrally over the extended parietal lip (pls. 28–38).

*Bucanopsis* may represent a more primitive condition. *Sphenosphaera* and *Carinaropsis* may represent intermediate and advanced forms, respectively, that evolved from *Bucanopsis*. *Sphenosphaera* and *Carinaropsis* apparently have lost distinct revolving ornament, except for the threads commonly bordering their selenizones. However, faint revolving threads have been found here in a single silicified specimen of *Carinaropsis cymbula* (Hall) (pl. 38, fig. 8). The selenizones of *Sphenosphaera* and *Carinaropsis* are generally either flat or on low

ridges, but both genera retain a sharp whorl floor keel. This may be because it has assumed some functional significance, such as a muscle attachment site.

Rollins (1967, p. 131, 132) suggested that *Bucanopsis* was ancestral to the subfamily Knightitinae because of similarities in their ornament patterns, their parietal lips, and the presence of a low parietal keel in at least one species of *Knightites*.

***Bucanopsis carinifera* Ulrich, 1897**

Plate 27, figures 1-16

*Bucanopsis carinifera* Ulrich in Ulrich and Scofield, 1897, p. 925, pl. 62, figs. 56-61; Grabau and Shimer, 1909, p. 622, fig. 836; Shimer and Shrock, 1944, p. 443, pl. 178, figs. 24, 25.

**Diagnosis.**—Shell small (up to nearly 11 mm long), with moderate-sized umbilici; aperture cordate in outline, width nearly twice length; sides of whorls somewhat square; high dorsomedian carina becoming increasingly flat topped in maturity.

**Description.**—Shell small, compact, rapidly expanding, and tightly coiled, so that parietal lip is reflexed and coils about umbilical shoulder. Whorls broad and somewhat square at shoulders in dorsal view. Selenizone clearly visible only in adulthood when prominent dorsal carina gradually becomes less angular and more flat topped. Dorsal slopes briefly concave adjacent to carina, then becoming gently convex; umbilical shoulders narrowly rounded, the change of slope being abrupt and giving an angular impression; umbilici moderate in size and deep. Aperture broadly cordate, width nearly twice length; parietal lip folds back over coil to form rather broad ventral shelf posterior to aperture opening; parietal lip thickens laterally from median whorl floor carina that results from covering of dorsal carina by thin parietal lip; whorl floor carina extends length of reflexed parietal lip. Shell sculpturing of numerous thin revolving threads which run parallel to direction of coiling and seem restricted to dorsal slopes of whorls. In some specimens, transverse growth lines, which reflect broadly curved apertural sinus, become strong enough in maturity to create reticulate pattern on shell.

**Measurements.**—Measurements of *B. carinifera* are listed in table 75 and shown graphically in figure 33.

**Material.**—All specimens known are silicified replicas. The lectotype was designated by Knight (1943, p. 60, pl. 14, figs. 3a, b), and was cataloged under the same number as the other original syntypes. It is here numbered USNM 315583 (pl. 27, figs. 1, 2). The paralectotypes remain cataloged under USNM 45734, except for two figured here, USNM 315584 (pl. 27, fig. 3) and USNM 315585 (pl. 27, fig. 4). New Kentucky specimens in the USGS silicified collections are from USGS samples 4073-CO (USNM 315592), 4883-CO, 4928-CO (including USNM 315586), 4959-CO (including USNM 315593),

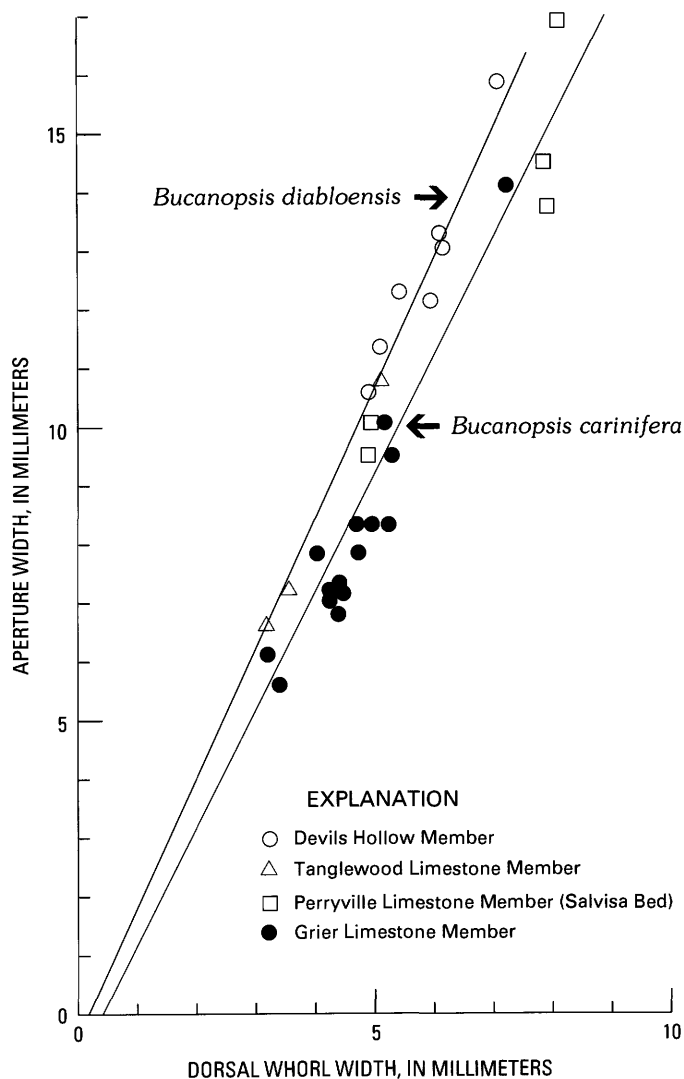


FIGURE 33.—Bivariate plots of measurements made on specimens of *Bucanopsis carinifera* and *B. diabloensis* new species.

5015-CO (including USNM 315587, 315588, 315594), 5096-CO, 5099-CO, 6136-CO (including USNM 315589), 6915-CO (including USNM 315598), 6916-CO, and 7796-CO (including USNM 315595). One specimen from Tennessee is numbered UCGM 44283.

**Distribution.**—The type specimens are labeled as having been collected from the "Trenton (Flanagan), near Danville, Kentucky." The Flanagan chert is an outdated term formerly used for different silicified horizons in the upper Lexington Limestone (Shermanian). Ulrich and Scofield (1897, p. 925) also reported the species from Maysvillian strata in the Cincinnati, Ohio, area, but no specimens from Cincinnati beds were located during this study, and such an occurrence cannot be confirmed.

The species was found in the USGS silicified collections from Kentucky in the Grier Limestone Member (4073-

TABLE 75.—*Measurements (in millimeters) of Bucanopsis carinifera*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Umbilical diameter	Dorsal width	Posterior width	Selenizone width
315583	—	9.2	—	13.5	4.5	7.6	5.4	0.9
45734	~8.7	~6.0	~6.0	8.1	3.2	—	—	0.9
45734	9.0	7.0	6.9	9.6	3.4	—	—	—
45734	9.4	7.1	7.0	8.7	3.5	—	—	—
45734	5.7	4.5	4.5	6.2	2.3	—	—	—
45734	5.9	5.0	4.5	5.8	2.2	—	—	—
45734	7.0	5.7	—	7.9	3.0	—	—	—
45734	—	3.9	—	5.2	2.1	—	—	—
315592	8.8	6.0	7.5	8.3	—	5.1	—	—
315592	7.0	5.2	6.5	7.4	—	—	—	—
315592	7.7	5.3	6.6	7.3	—	4.4	—	—
315592	8.0	5.6	6.5	7.2	—	4.4	—	—
315592	4.3	3.5	3.0	4.2	—	—	—	—
315592	6.4	4.8	5.5	7.0	—	—	—	—
315592	3.7	3.0	2.9	3.8	—	—	—	—
315592	7.3	4.5	5.8	7.8	—	4.0	—	—
315592	8.2	6.0	7.5	9.5	—	5.3	—	—
315592	5.7	4.0	4.3	6.1	—	3.2	—	—
315592	5.5	4.2	4.5	5.5	—	—	—	—
315592	8.2	6.0	6.3	8.3	—	4.7	—	—
315592	8.3	6.0	—	8.3	—	4.9	—	—
315592	—	—	—	6.8	—	4.4	—	—
315592	7.9	6.0	6.2	7.8	—	4.7	—	—
315592	7.2	5.9	5.4	7.1	—	4.3	—	—
315592	7.8	5.3	5.2	7.2	—	4.3	—	—
315592	5.3	4.2	4.3	5.6	—	3.4	—	—
315586	—	—	—	14.0	—	7.3	—	—
315593	—	—	—	10.0	—	5.2	—	—
315589	10.8	8.0	8.3	10.0	—	6.1	5.5	—
315594	—	—	—	13.6	—	8.0	—	—
315594	—	—	—	17.0	—	8.0	—	—
315594	—	—	—	14.4	—	7.9	—	—
315594	—	—	—	10.0	—	4.9	—	—
315594	—	—	—	9.5	—	4.9	—	—
315594	—	—	—	7.8	—	5.0	—	—
315594	—	—	—	10.4	—	6.3	—	—
315594	—	—	—	17.9	—	9.8	—	—
315594	—	—	—	12.2	—	6.4	—	—
315595	—	—	—	10.7	—	5.2	—	—
315595	—	—	—	6.6	—	3.2	—	—
315595	—	—	—	7.2	—	3.6	—	—

CO, 4883-CO, 4928-CO, 4959-CO, 5096-CO, 5099-CO), the Salvisa (5015-CO, 6915-CO, 6916-CO) and Faulconer (6136-CO) Beds of the Perryville Limestone Member, and the lower tongue of the Tanglewood Member (7796-CO) of the Lexington Limestone (Shermanian). Specimens are most abundant in the Grier Limestone Member, particularly in sample 4073-CO, which contains about 50 specimens.

One specimen (UCGM 44283) (pl. 27, figs. 5–7) was found in a collection from the Cannon facies of the Bigby-Cannon Limestone (Kirkfieldian-Shermanian) in Smith County, Tenn., which is the first report of the species in that State.

*Comparison.*—*Bucanopsis carinifera* could be confused with species of *Sphenosphaera*, if the revolving threads are not preserved. However, even when these

are not present, the whorl outline of *B. carinifera* is not as evenly rounded as that of most species of *Sphenosphaera*, the former having a more abrupt change in angle at the umbilical shoulder. Also, the dorsomedian carina of *B. carinifera* is more prominent, and its whorl floor-keel runs ventrally over the entire length of the parietal lip, which forms a broader shelf posterior to the aperture opening.

*Discussion.*—The specimens of *B. carinifera* show well the problems encountered when working with silicified material. Because all specimens examined here were silicified, it is difficult to completely assess the impact of silicification on the shell. The lectotype, USNM 315583 (pl. 27, figs. 1, 2), preserves the revolving threads better than any other specimen seen here, and also shows how the carina widens into a flat-topped, elevated

selenizone in adulthood. Note the fineness of these revolving threads and how they are not visible when the lighting is parallel to them (pl. 27, fig. 2). Most specimens do not preserve these threads at all (pl. 27, figs. 3–10). Some specimens show them very weakly (pl. 27, figs. 13, 15, 16). Some specimens show up to three different shell layers which peel away like layers of an onion (pl. 27, fig. 13). Such circumstances of preservation make it impossible to rely on the presence of the revolving threads to distinguish the species, or even the genus, although this characteristic is a primary generic taxobasis. *B. carinifera* is found in a variety of facies in the Lexington Limestone and apparently was a broadly adapted species.

***Bucanopsis diabloensis* new species**

Plate 27, figures 17–20

**Diagnosis.**—Shell small (up to 15.8 mm long), rapidly expanding; aperture broad, nearly semicircular posteriorly; coil relatively small, rounded, narrow.

**Description.**—Shell small, compactly coiled, and rapidly expanding, so that coil is relatively small in comparison to broad aperture; dorsum has distinct median carina and well-rounded slopes; umbilical shoulders well rounded, and umbilici of moderate size and depth. Aperture broad, apparently subelliptical in outline, and broadly rounded, nearly semicircular in its posterior portion; parietal lip somewhat reflexed, folding back over ventral coil to form wide shelf posterior and posterolateral to aperture opening; whorl floor has distinct, sharp median carina which continues over parietal shelf. Shell ornament unknown.

**Measurements.**—Because available specimens are not well preserved (generally only the coil and posterior aperture are preserved), only two measurements are consistently reliable. These are listed in table 76.

**Material.**—All known specimens are from the USGS silicified collections from Kentucky. Selected from USGS sample 5095-CO, USNM 315590 (pl. 27, figs. 17–20) is designated the holotype. Eleven specimens cataloged under 315591 are also from USGS 5095-CO and are designated paralectotypes, as are two specimens cataloged under USNM 315599 from USGS sample 5087-CO.

**Distribution.**—*B. diabloensis* is known only from the Devils Hollow Member of the Lexington Limestone (Shermanian) of central Kentucky (USGS samples 5087-CO and 5095-CO).

**Comparison.**—*B. diabloensis* is distinguished from *B. carinifera*, which is also found in the upper Lexington Limestone, by its more rapidly expanding shell, its relatively smaller, more rounded, narrower coil, and its more broadly rounded parietal shelf (pl. 27, figs. 17–20).

TABLE 76.—Measurements (in millimeters) of *Bucanopsis diabloensis*

USNM No.	Aperture width	Dorsal width
315590	15.8	7.15
315591	13.2	6.2
315591	12.2	5.45
315591	10.5	5.0
315591	13.0	6.2
315591	11.3	5.15
315591	12.1	6.0
315599	11.5	5.65

**Discussion.**—None of the available specimens of *B. diabloensis* preserve any surface ornament; however, as stated previously, very few specimens of *B. carinifera*, which is also known only from silicified material, have the revolving threads preserved. Although, *B. diabloensis* could be placed in the genus *Sphenosphaera*, I have placed the species in the genus *Bucanopsis* because of its similarity to *B. carinifera*, specifically, the tight coiling, the size of the umbilici, the dorsomedian carina, and the especially broad parietal shelf over which the whorl floor carina continues.

The difference between *B. carinifera* and *B. diabloensis* in the rate of whorl expansion is displayed in a crossplot of aperture width versus dorsal whorl width (fig. 33). In successive samples from the Grier Limestone, Perryville Limestone, and Tanglewood Limestone Members, the aperture width/dorsal whorl width ratios for *B. carinifera* are 1.75, 1.82, and 2.04, respectively; the equivalent ratio for *B. diabloensis* from the Devils Hollow Member is 2.14. *B. diabloensis* was apparently an offshoot (or a culmination) of a phyletic trend in *B. carinifera* of increasing rate of whorl expansion.

**Genus SPHENOSPHERA Knight, 1945a**

**Diagnosis.**—Shell moderately rapidly expanding, aperture flaring posteriorly and laterally; whorl floor with distinct median ridge, ridge not present on parietal shelf; ornament collabral.

**Description.**—Shell small to moderate in size, rather rapidly expanding, rounded but generally not globose in form; umbilici small or closed. Aperture broader than long; margins flared laterally and posteriorly, producing flat to slightly excavated posterolateral shelves; parietal lip reflexed over venter of previous whorl; whorl floor with narrowly rounded to well-rounded median ridge, ridge not extending over onto ventral parietal lip. Slit shallow to moderately deep, housed in broad sinus; selenizone distinct, either a rounded to flat-topped ridge or a concave channel, in many cases with distinct lunulae and a thin revolving thread bordering on each side. Shell surface marked only by fine, generally closely spaced growth lines.



*Type species.*—*Bellerophon clausus* Ulrich, 1897, by original designation (Knight, 1945a).

*Distribution.*—*Sphenosphaera* is known from Middle Ordovician (Blackriveran?-Rocklandian) to Upper Ordovician (Richmondian) strata in Eastern and Central North America (Rollins, 1967).

*Comparisons.*—*Sphenosphaera* differs from *Bellerophon* Montfort in its generally less globose whorl form, its more flared apertural margins, which form prominent posterolateral shelves (pl. 30, figs. 9, 10), and, particularly, its distinct, rounded median ridge on the whorl floor (pl. 30, figs. 2, 9, 17).

*Carinaropsis* Hall has a median whorl floor ridge, but it is sharp rather than rounded (pl. 38, figs. 9, 11). It also differs from *Sphenosphaera* in having a reduced coil, a much greater rate of whorl expansion, and a parietal platform extending well into the apertural cavity (pl. 38, figs. 3-5).

*Bucanopsis* Ulrich also has a sharp median whorl floor ridge as in *Carinaropsis*, but its ridge continues over the ventral parietal shelf. *Bucanopsis* is further distinguished by revolving shell markings. Rollins (1967) noted that some species of *Knightites* bear a low, rounded whorl floor ridge, but that genus is also characterized by revolving shell ornament. In the fauna under consideration, species of *Bucania* having small umbilici can closely resemble *Sphenosphaera* in their general shell form. *Bucaniids* can be readily distinguished, however, by their revolving ornament and their lack of median whorl floor keel.

*Discussion.*—Knight (1945a, p. 334) defined the genus *Sphenosphaera* for the Ordovician species assigned to *Bellerophon* by Ulrich and Scofield (1897) and other related species. He believed that the median whorl floor ridge and the posterolaterally flaring apertural margins allied these species more closely to the Ordovician genera *Carinaropsis* and *Bucanopsis*. Knight and others (1960, p. 1180) placed these three genera together in the subfamily Carinaropsinae Ulrich and Scofield, 1897.

Rollins (1967, p. 117-121) recognized only three species of *Sphenosphaera*: *S. clausus*, *S. troosti*, and, tentatively, *S. mohri*. He claimed that the median floor ridge which largely defines the genus is not present, or at least is not known to be present (owing to lack of preservation), in other Ordovician species, which he returned to *B. (Bellerophon)*. In this study, the presence of a median whorl floor ridge is illustrated in *S. clausus* (pl. 30, figs. 2, 9, 17; pl. 31, fig. 3; pl. 32, fig. 4) and *S. troosti* (pl. 29, figs. 4, 9, 13, 15), and is confirmed in *S. mohri* (pl. 41, figs. 1, 3).

The presence of a whorl floor ridge is also shown here in two additional species. The type specimens of *Bellerophon troosti burginensis* Ulrich (= *Sphenosphaera burginensis*, herein) do not expose the whorl floor, but

fragmentary silicified specimens of the species from USGS sample 4883-CO show a distinct, narrowly rounded whorl floor ridge. The situation is the same with *Sphenosphaera capax* (Ulrich), as new silicified material from USGS sample 6412-CO (pl. 34, figs. 10-13) of that species reveals a distinct, rounded whorl floor ridge. Therefore, both species are assigned to the genus *Sphenosphaera*.

Three Ordovician species named by Ulrich (see Ulrich and Scofield, 1897) are assigned to *B. (Bellerophon)* here, as was done by Rollins (1967), because of the apparent absence of a median whorl floor keel. These are *B. (B.) bilineatus* Ulrich, *B. (B.) nana* (Ulrich), and *B. (B.) subpatula* (Ulrich.) *B. (B.) subglobulus* Ulrich is also placed in *Bellerophon* for reasons noted in the section on that genus.

Two other species in the fauna under discussion unquestionably belong to either *B. (Bellerophon)* or *Sphenosphaera* and herein are tentatively assigned to the *Sphenosphaera*. The known specimens of *S. recurvus* (Ulrich) (pl. 33, figs. 1-6) and *S. subangularis* Ulrich (pl. 33, figs. 10-15) do not expose the whorl floor; however, because of greater similarity of shell morphology with species of *Sphenosphaera*, they were believed better placed in that genus (see discussion in section on *B. (Bellerophon)*).

The whorl floor keel ends within the aperture at the parietal callosity in *Sphenosphaera*, as it also does in *Carinaropsis*; however, the keel extends onto the parietal lip in *Bucanopsis*, *Phragmolites*, and *Tropidodiscus*, where it is the result of the blanketing of a dorsal carina by the parietal lip. The whorl floor keel in *Sphenosphaera* and *Carinaropsis* may be a vestigial structure, and might have been retained in the more advanced genera as a muscle attachment site.

Contrary to Knight and others (1960), who placed *Sphenosphaera* in the Carinaropsinae, the genus is here allied with *Bellerophon* in the Bellerophontinae. There is almost certainly a relationship between *Sphenosphaera* and *Carinaropsis*, the two either arising from the same stock, or more likely the latter being a specialized evolution from the former. The reduction of the coil and the marked growth of a platform into the apertural cavity distinguish the Carinaropsinae. *Sphenosphaera* could easily be considered a subgenus of *Bellerophon*, the only major distinguishing feature being the whorl floor ridge. This whorl floor ridge is rounded, rather than sharp as in *Carinaropsis*, and Rollins (1967) noted low, rounded whorl floor ridges in some members of the Knightitinae, so that the significance of that characteristic as a supragenetic taxobasis is rather dubious.

Here, two previously named species are placed in synonymy: *Bellerophon rogersensis* Foerste (1914c) with

*S. clausus* (Ulrich, 1897), and *Bellerophon cincinnatensis* Miller and Faber (1894) with *S. mohri* (Miller), 1874.

***Sphenosphaera clausus* (Ulrich), 1897**

Plate 30, figures 1–23; Plate 31, figures 1–13;

Plate 32, figures 1–15

*Bellerophon clausus* Ulrich in Ulrich and Scofield, 1897, p. 916, pl. 64, figs. 7–10; Bassler, 1932, pl. 20, figs. 17, 18; Knight and others, 1960, figs. 98, 2a–c.

*Bellerophon rogersensis* Foerste, 1914c, p. 141, pl. 2, figs. 4a–c.

**Diagnosis.**—Shell moderate in size (up to 26.5 mm long), umbilici closed; parietal lip thickened in central area, reflexed posterolaterally forming excavated shelves; selenizone elevated, with distinct bordering threads and lunulae.

**Description.**—Shell moderate in size and in rate of expansion; umbilici completely closed by reflexed parietal lip; dorsal whorl slopes broadly convex, angle of slope becoming more obtuse with growth. Selenizone on elevated, flat-topped median carina, bordered by fine revolving threads on either side, lunulae distinct. Apertural outline subtriangular, flared posteriorly to form concave posterolateral shelves; median parietal area thickened; median whorl floor ridge well rounded, not extending onto parietal callosity. Growth lines as thin threads, closely spaced and regular, becoming less so in maturity, broadly curved over dorsal slopes, reflecting broad, shallow sinus; slit shallow.

**Measurements.**—Measurements of *S. clausus* are listed in table 77.

**Material.**—The holotype, USNM 45701 (pl. 30, figs. 1–6), is a brown, silicified specimen from the Bigby-Cannon Limestone of Tennessee. An Ulrich and Scofield (1897, pl. 64, fig. 9) paratype from Kentucky (USNM 45700, pl. 30, figs. 7, 8) was the only calcitic specimen examined here.

The species is common in the new silicified samples from Kentucky. It was recognized in the Grier Limestone Member of the Lexington Limestone (4879-CO, 4880-CO, 4928-CO, 5067-CO, 5094-CO, 5096-CO, 5107-CO), the Salvisa Bed of the Perryville Limestone Member of the Lexington Limestone (5015-CO, 6915-CO, 6916-CO), the Tanglewood Limestone (7783-CO, 7787-CO, 7796-CO), Devils Hollow (5087-CO, 5095-CO), and Millersburg (7344-CO, 7353-CO) Members of the Lexington Limestone, and the Clays Ferry Formation (6128-CO, 6142-CO, 6143-CO, 7343-CO, 7345-CO, 7348-CO, 7349-CO, 7350-CO, 7450-CO, 7458-CO, 7812-CO).

Two weathered slabs (UCGM 44301 and 44302) from the Cannon Facies of the Bigby-Cannon Limestone of Smith County, Tenn., show well-preserved silicified specimens associated with other mollusk debris and tabulate corals (pl. 31, figs. 11–13).

**Distribution.**—The species is known from both the Cannon and Bigby facies of the Bigby-Cannon Limestone in central Tennessee (Bassler, 1932; Wilson, 1949). In Kentucky, it is known throughout the Lexington Limestone above the Logana Member (see “Material” above) and from the Clays Ferry Formation, mainly where this unit intertongues with the Lexington Limestone. *S. clausus* apparently is restricted to strata of Kirkfieldian-Shermanian age.

*S. clausus* was the most abundant species in the USGS silicified collections from the middle and upper Lexington Limestone of central Kentucky (see section on paleoecology).

**Comparison.**—*S. clausus* is very similar in form to *S. troosti* (d’Orbigny), but the former’s umbilici are entirely closed, its selenizone is more clearly defined by bordering threads and distinct lunulae, and its parietal lip has a more thickened central callosity which is bordered by shallow concavities on the posteriorly flared aperture shelves. The closed umbilicus and the much thickened parietal area also distinguish *S. clausus* from other congeneric species in the Cincinnati arch fauna.

**Discussion.**—*S. clausus* is by far the most common species of the genus *Sphenosphaera* in the Cincinnati arch fauna. It undoubtedly is closely related to *S. troosti*, and working with poorly preserved material it is difficult if not impossible to distinguish the two species. It is believed here that the closure of the umbilicus is an advanced characteristic, and therefore that *S. clausus* is derived from *S. troosti* or some earlier umbilicate species. Late Ordovician species having closed umbilici, such as *S. recurvus*, *S. subangularis*, and *S. mohri*, most likely were descended from *S. clausus*. The extremely well marked selenizone of *S. clausus* is also thought to be an advanced feature.

*S. clausus*, more than any other species of *Sphenosphaera*, shows similarity to *Carinaropsis cymbula* (pls. 37, figs. 1–11), and it is likely that the *Carinaropsis* evolved from *Sphenosphaera*. Like *C. cymbula*, *S. clausus* has a well-defined selenizone; more importantly, the two species have similar inner apertural regions. Both species have a median whorl floor ridge, an enlarged parietal area, and posterolateral excavations on the parietal shelf. However, the whorl floor ridge is broadly rounded in *S. clausus* (pl. 30, figs. 2, 9, 14, 17), rather than narrow and sharp as in *Carinaropsis* (pl. 38, figs. 9, 11). The parietal area of *S. clausus* is thickened and slightly extended (pl. 30, figs. 9, 10), but it does not protrude well into the apertural cavity as it does in *Carinaropsis* (pl. 38, figs. 1, 2, 4, 5). The posterolateral excavation of the parietal shelf in both species is the result of the median parietal thickening and the flaring and draping of the apertural margins. These excavations probably served similar functions in the two species, but

TABLE 77.—Measurements (in millimeters) of *Sphenosphaera clausus*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Dorsal width	Posterior width	Ventral width	Selenizone width
45701	~22.0	15.3	16.5	~21.9	12.75	10.3	8.2	1.0
45700	~18.0	12.1	~11.6	~17.6	~10.0	9.6	7.0	1.1
315618	~16.0	13.0	7.5	18.95	9.8	9.1	6.7	0.6
315640	—	7.8	—	11.7	6.7	5.0	3.4	0.6
315640	—	—	—	12.5	—	6.1	4.8	—
315640	—	11.6	—	19.0	—	10.0	7.7	—
315640	—	10.1	—	18.0	9.5	7.1	6.3	—
315645	12.6	9.3	9.0	13.7	7.0	—	—	0.6
315645	—	7.2	—	10.6	6.1	4.5	3.1	0.7
315645	12.3	8.6	9.7	11.7	—	—	4.2	—
315645	—	—	—	11.4	—	5.2	4.3	—
315645	—	—	—	13.8	—	—	4.6	—
315645	—	—	—	—	7.2	—	4.4	0.7
315645	—	—	—	10.9	5.9	—	3.6	—
315645	—	—	—	9.1	5.3	—	—	—
315645	—	—	—	8.5	4.9	—	—	0.5
315645	—	—	—	9.9	6.4	—	—	0.7
315647	—	7.2	—	10.7	5.7	5.0	3.7	0.6
315647	—	—	—	9.7	—	—	—	0.6
315647	—	11.8	—	19.0	11.1	8.0	6.7	1.3
315647	—	9.4	—	14.6	9.1	6.9	5.5	0.8
315647	—	—	—	18.8	—	—	6.4	—
315647	—	—	—	16.4	—	—	5.8	—
315647	—	12.8	—	19.6	—	9.6	7.7	—
315647	—	—	—	16.2	7.1	6.6	5.0	—
315647	—	—	—	19.5	—	9.2	7.3	—
315647	—	—	—	23.5	—	—	10.7	—
315647	12.8	9.3	9.4	13.7	7.9	7.0	4.9	—
315649	—	14.6	—	20.2	—	—	—	—
315648	—	—	—	17.0	—	—	—	—
315648	—	—	—	17.0	11.2	—	—	—
315648	—	11.0	—	15.7	10.1	9.2	6.7	1.1
315622	10.6	8.1	7.3	12.4	7.7	6.4	5.1	0.5
315623	—	—	—	20.9	—	—	7.8	1.0

they do not seem to have been effective channels for currents, as they are not linear; nor do they open to the shell interior. The concavities probably housed the posterior foot when the animal clamped down against the substrate.

*Bellerophon rogersensis* Foerste (1914c) was described from compressed internal molds and a single shell fragment collected from the Clays Ferry Formation just above the Millersburg Member of Lexington Limestone in central Kentucky. It was reported from a "gastropod horizon" that also contained specimens of *Tetranota*, *Liospira*, and *Lophospira* and was bounded above and below by strata containing brachiopod-bryozoan-trilobite assemblages. Foerste (1914c, p. 141) compared the species to *Sphenosphaera recurvus*, both having a relatively elongate aperture. I believe that compressed internal molds give this mistaken impression (pl. 32, figs. 13–15), and that the specimens described by Foerste belong to *S. clausus*, which is also reported from the Clays Ferry Formation here (pl. 30, figs. 17–21). The general shell form and the wavy parietal lip that curls back and closes (or nearly closes) the umbilicus support

this conclusion. Further support is given by Foerste's single shell fragment, which shows a slightly elevated selenizone that is concave and bordered by thin threads, as in *S. clausus*. Thus, *Bellerophon rogersensis* Foerste (1914c) is placed in synonymy with *Sphenosphaera clausus* (Ulrich), 1897. The specimen figured by Foerste (1914c, pl. 2, figs. 4a-c) and figured herein on plate 32, figures 13–15 (USNM 315601) is designated the lectotype of *Bellerophon rogersensis* Foerste.

#### *Sphenosphaera troosti* (d'Orbigny), 1840

Plate 29, figures 1–22

*Bellerophon troosti* d'Orbigny, 1840, p. 206; Safford, 1869, p. 289, pl. 3G, figs. 4a-d; Ulrich and Scofield, 1897, p. 915, pl. 64, figs. 1–5; Grabau and Shimer, 1909, p. 618, figs. 829a-c; Bassler, 1909, p. 183, figs. 20, 9, 10; Bassler, 1932, pl. 20, figs. 14–16; McFarlan, 1931, pl. 4, fig. 8; Shimer and Shrock, 1944, p. 443, pl. 178, figs. 12–14; Wilson, 1948, pl. 10, figs. 7–9; Wilson, 1949, pl. 10, figs. 7–9.

*Diagnosis*.—Shell moderately small (up to 19.5 mm long); whorls broad, somewhat inflated; umbilici narrowly open, small; selenizone a rounded dorsomedian ridge, lunulae faint.

TABLE 77.—*Measurements (in millimeters) of Sphenosphaera clausus—Continued*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Dorsal width	Posterior width	Ventral width	Selenizone width
315651	18.0	—	—	20.8	—	—	—	—
315624	18.55	13.5	14.75	21.05	12.75	8.2	7.1	1.3
315652	26.5	—	19.1	26.0	—	—	—	1.2
315652	23.5	—	18.4	28.0	14.8	11.7	—	—
315652	21.0	14.8	16.7	26.0	12.2	9.7	7.0	—
315652	—	—	—	20.8	11.0	—	6.2	1.2
315652	—	—	—	20.2	9.1	7.3	6.2	1.0
315653	—	10.4	—	19.0	9.4	8.2	6.0	—
315626	23.0	17.7	10.7	22.7	—	—	—	—
315627	—	12.0	—	21.0	10.7	8.8	6.5	1.5
315628	—	14.0	—	24.5	13.0	10.0	7.8	—
315654	18.5	14.8	15.8	22.5	10.7	9.4	7.8	1.4
315654	20.2	14.1	16.0	23.0	12.1	10.6	7.7	1.1
315654	22.5	14.7	17.8	24.0	—	—	—	—
315654	—	—	—	23.1	13.7	9.5	8.0	—
315654	—	—	—	24.5	—	—	—	—
315654	—	—	—	24.6	—	—	—	—
315654	13.8	9.4	8.2	16.1	8.9	6.5	5.5	—
315654	13.6	9.4	9.8	15.5	—	7.0	5.6	0.9
315654	16.5	11.1	12.9	17.1	9.3	7.7	6.8	1.2
315654	—	13.6	—	22.9	11.0	9.1	8.4	1.5
315654	—	12.5	—	19.0	9.7	8.2	7.5	1.3
315654	—	12.1	—	17.3	9.4	8.0	6.4	1.25
315654	—	12.8	—	18.5	9.9	7.5	6.5	1.1
315654	—	12.5	—	20.2	9.6	—	7.2	1.2
315654	—	—	—	22.2	—	—	8.1	—
315654	—	12.3	—	22.8	—	—	—	—
315654	—	—	—	17.0	10.2	8.1	6.4	1.3
315654	—	12.7	—	19.0	—	—	—	—
315654	—	10.4	—	16.9	9.6	7.3	6.5	1.1
315654	—	10.5	—	15.8	—	—	—	1.2
315654	—	—	—	17.0	—	—	—	1.4
315654	12.1	9.4	9.0	13.6	7.6	—	—	0.8
315654	—	8.9	—	13.3	7.7	6.5	5.3	0.9

*Description.*—Shell moderately small; whorls somewhat inflated, dorsal slopes broadly convex, width greatest at base, outline subtriangular. Umbilici open, small, in some specimens partly covered by reflexed parietal lip. Apertural margin flared posteriorly and laterally, forming shelves with slight excavations; parietal thickening moderate; whorl floor ridge low, well rounded. Selenizone a prominent, rounded, dorsomedian ridge, with lunulae faint or lacking. Growth lines fine, closely spaced, becoming coarser and even slightly wrinkled on lateral whorl slopes in maturity; growth lines curve gently, showing broad, shallow sinus.

*Measurements.*—Measurements of *S. troosti* are listed in table 78.

*Material.*—Two collections of previously figured material were examined. USNM 45710 consists of 6 silicified specimens from the Cannon facies of the Bigby-Cannon Limestone at Nashville, Tenn., and USNM 45711 consists of 17 silicified specimens labeled "Flanagan Chert" from near Danville, Ky. Ulrich and Scofield (1897, p. 916) stated that these collections were made by J.M. Safford and by E.O. Ulrich, respectively. The

Tennessee specimens are probably the hypotypes on which Safford based his figures of the species; from this collection, USNM 315602 (pl. 29, figs. 1–4) is here designated the neotype of the species and USNM 315665 (pl. 29, figs. 5–9) and the four specimens retaining the number USNM 45710 are designated paraneotypes. The hypotypes USNM 315603 (pl. 29, figs. 10–13) and USNM 315604 (pl. 29, figs. 14–16) were selected from Ulrich's Kentucky collection (USNM 45711) for illustration. New specimens from the USGS silicified collections were recognized in samples from the Grier Limestone Member (4073-CO, 4959-CO, 5067-CO) of the Lexington Limestone.

*Distribution.*—In Tennessee, *S. troosti* is known from the Cannon and dove-colored facies of the Bigby-Cannon Limestone (Bassler, 1932; Wilson, 1949). In Kentucky, the species occurs in the Grier Limestone Member of the Lexington Limestone; McFarlan (1931, pl. 20) reported the species from the Faulconer Bed of the Perryville Limestone Member of the Lexington Limestone. The hypotype collection made by E.O. Ulrich is from the "Flanagan Chert" of the upper Lexington Limestone, an

TABLE 78.—Measurements (in millimeters) of *Sphenosphaera troosti*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Dorsal width	Posterior width	Ventral width	Selenizone width
315602	19.5	14.75	8.0	22.5	11.7	9.3	7.5	1.1
315665	17.8	13.9	7.5	20.8	10.7	7.8	6.9	1.0
315603	—	12.8	—	19.6	10.4	7.8	6.9	1.25
315604	9.5	7.65	4.1	9.8	5.85	4.6	3.9	0.5
45711	—	—	—	18.2	10.15	7.8	6.6	1.1
45711	14.0	11.0	6.0	16.5	8.75	6.2	5.7	0.8
45711	14.1	10.8	6.1	15.9	8.50	7.8	6.1	0.8
45711	—	9.0	—	14.4	7.20	5.3	4.7	0.7
45711	—	7.5	—	9.8	5.85	4.6	3.9	0.5
45711	7.2	5.3	3.1	7.3	4.35	3.7	2.7	0.5
315613	—	9.5	—	17.0	8.6	7.1	5.4	—

outdated term known to represent various silicified horizons.

Some poor fragments of small specimens of *Sphenosphaera* sp. indet. were found in USGS silicified samples 5022-CO and 6131-CO from the Curdsville Limestone Member of the Lexington Limestone. These specimens have an angular dorsum and small, open umbilici; therefore, they may be related to *S. troosti*.

*Comparison.*—The most distinctive features of *S. troosti*, which serve to distinguish it from contemporaneous species, are its small but distinctly open umbilicus and its prominent, rounded, ridgelike selenizone.

*Discussion.*—Although similar to *S. clausus*, *S. troosti* is easily recognized when sufficiently well preserved material is available. *S. troosti* is regarded as closely related to *S. clausus*.

It is interesting that Wilson (1949) listed *S. clausus* from the Bigby-Cannon Limestone. The two species overlapped in the normal marine shelf environment (Cannon), but *S. troosti* also inhabited quiet nearshore lagoons and mudflats (dove-colored facies), whereas *S. clausus* also dwelt in a high-energy shoaling environment (Bigby facies). The more tightly coiled, nonumbilicate shell of *S. clausus* may have been streamlined for life in higher energy environments. The two species were not found to co-occur in the USGS Kentucky samples.

***Sphenosphaera burginensis* (Ulrich), 1897**

Plate 28, figures 10–23

*Bellerophon troosti burginensis* Ulrich in Ulrich and Scofield, 1897, p. 916, pl. 64, fig. 6.

*Diagnosis.*—Shell moderate in size (up to 21.5 mm long); whorls relatively narrow; umbilici narrowly open; posterolateral apertural margins horizontal; selenizone thin, elevated, concave, with bordering threads and lunulae.

*Description.*—Shell moderate in size; expanding rather slowly so that whorls are relatively narrow; whorl slopes evenly convex. Umbilici moderate in size. Posterolateral apertural margins reflexed horizontally, not curling over umbilicus, passing straight beneath it. Whorl floor ridge narrow, sharply rounded. Selenizone elevated on thin dorsomedian carina, concave, bordered by thin revolving threads; lunulae present. Growth lines thin, threadlike, evenly and closely spaced, curving back rather strongly toward selenizone, reflecting moderately deep sinus.

*Measurements.*—Measurements of *S. burginensis* are listed in table 79.

*Material.*—The holotype, USNM 45712 (pl. 28, figs. 10–12), is a brown, worn, silicified specimen. The single paratype, USNM 47595 (pl. 28, figs. 13–15), also is silicified. *S. burginensis* was found in the new USGS silicified collections (pl. 28, figs. 16–23) from the Grier Limestone (4883-CO, 5094-CO, 5096-CO) and Perryville Limestone Members (*S. cf. burginensis*) (6915-CO) of the Lexington Limestone.

*Distribution.*—The type specimens cited above are labeled as coming from the “Flanagan Chert” near Burgin, Ky.; this is an archaic name used for silicified beds at different horizons in the upper Lexington Limestone.

TABLE 79.—Measurements (in millimeters) of *Sphenosphaera burginensis*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Dorsal width	Posterior width	Ventral width	Selenizone width
45712	21.5	15.3	16.45	22.4	11.5	9.8	—	1.1
47595	19.15	13.8	14.5	21.0	9.9	7.6	—	1.2
315615	14.3	11.0	10.2	15.0	8.7	6.2	4.4	—
315641	—	—	—	13.2	—	5.0	3.5	—
315616	17.4	9.8	11.8	15.5	8.25	6.0	5.3	0.75

TABLE 80.—Measurements (in millimeters) of *Sphenosphaera recurvus*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Dorsal width	Posterior width	Ventral width	Selenizone width
45705	16.8	11.6	12.7	—	9.4	7.8	5.6	1.2

New material comes from the Grier Limestone and Perryville Limestone Members of the Lexington Limestone (Shermanian).

*Comparison.*—This species can be separated from all others by its narrow whorl form, resulting from a slower whorl expansion rate and less flaring of the apertural margins. Like *S. troosti*, it has a small, open umbilicus.

*Discussion.*—*S. burginensis* was originally described as a “variety” of *S. troosti* by Ulrich (Ulrich and Scofield, 1897) with some reservations. Considering the subtle differences used to define species of *Sphenosphaera*, *S. burginensis*, with its distinctly narrower whorl profile, is distinct enough to warrant an independent specific designation.

***Sphenosphaera recurvus* (Ulrich), 1897**

Plate 33, figures 1–6

*Bellerophon recurvus* Ulrich in Ulrich and Scofield, 1897, p. 920, pl. 64, figs. 11–13.

*Diagnosis.*—Shell moderately small (16.8 mm long), rather narrow; umbilici closed; selenizone elevated, rounded; growth lines strongly curved back.

*Description.*—Shell moderately small in size, rather narrow in dorsal view, gradually expanding. Umbilici completely closed by thin parietal lip curled back over ventral coil. Aperture seemingly elongate, probably subtriangular, not expanded laterally. Selenizone elevated, truncated but rounded, with no lunulae visible. Growth lines wrinkled-sublamellose, broadly curved, becoming strongly curved backward dorsally to reflect relatively deep sinus, not evenly spaced.

*Measurements.*—Measurements of *S. recurvus* are listed in table 80.

*Material.*—Ulrich (Ulrich and Scofield, 1897) reported that a few specimens of this species were known. Only one was located for this study, the holotype (USNM 45705), a calcitic specimen having a broken aperture and a well-preserved shell surface (pl. 33, figs. 1–4).

*Distribution.*—The holotype is labeled as coming from the Corryville biofacies, which is now the Grant Lake Limestone or Bull Fork Formation (Maysvillian), in the Mt. Auburn area of Cincinnati, Ohio.

A few highly recrystallized, fragmentary specimens from the Maysvillian Leipers Limestone, Rowena Ferry, Russell County, Ky., are here identified as *S. aff. S. recurvus*. The specimens have closed umbilici and rather narrow coils, and seem to have wrinkled growth lines.

The specimen figured here (pl. 33, figs. 5, 6; UCGM 44282) shows moderate lateral expansion of the aperture, a feature that is not preserved in the holotype of the species.

*Comparison.*—*S. recurvus* resembles *S. clausus*, but is narrower in form, with a more elongate aperture. Also, *S. recurvus* has a rounded selenizone with no bordering threads or lunulae, sublamellose rather than threadlike growth lines, a deeper apertural sinus, and a lesser parietal callosity. *S. subangularis* is even higher and narrower than *S. recurvus*, and has thin threadlike, closely and evenly spaced growth lines.

*Discussion.*—This species was placed in *B. (Bellerophon)* Montfort by Rollins (1967), because no specimen was sufficiently well preserved to prove the presence of a median whorl floor ridge. The species is here tentatively placed in *Sphenosphaera* Knight, as Knight (1945a) intended, and is regarded as descended from *S. clausus*. The wrinkled sublamellose growth lines of this species are unique among related species in the fauna under consideration.

***Sphenosphaera subangularis* (Ulrich), 1897**

Plate 33, figures 10–15

*Bellerophon subangularis* Ulrich in Ulrich and Scofield, 1897, p. 920, pl. 64, figs. 14–16.

*Diagnosis.*—Shell moderate in size (up to 21 mm long), with high, angular dorsum; umbilici closed; aperture longer than wide.

*Description.*—Shell moderate in size; whorl expansion rather rapid; umbilici closed by thin reflexed parietal lip. Median parietal callosity poorly developed. Whorls very high, increasingly so in maturity, the dorsal slopes being gently convex and forming an acute angle with one another. Apertural outline subtriangular, lateral expansion apparently slight so that aperture is longer than wide. Selenizone low and rounded in early growth, becoming more prominent in maturity; no lunulae or bordering threads known. Growth lines fine, threadlike, evenly and closely spaced, broadly curved.

*Measurements.*—Measurements of *S. subangularis* are listed in table 81.

*Material.*—Two worn calcitic specimens were cataloged as “holotype(s)” under USNM 45708. The specimen here left cataloged under that number (pl. 33, figs. 11–15) is designated the lectotype. The second specimen (pl. 33,

TABLE 81.—Measurements (in millimeters) of *Sphenosphaera subangularis*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Dorsal width	Posterior width	Ventral width	Selenizone width
45708	~21.0	15.4	~16.5	~16.2	10.1	8.6	6.8	0.9
315666	~13.0	9.8	—	—	—	—	—	0.7

fig. 10) is designated the paralectotype, and is here cataloged under USNM 315666.

*Distribution*.—The type specimens are labeled as coming from the “Richmond Group [Richmondian], Richmond, Indiana.”

*Comparison*.—The extremely high dorsum of this species separates it from *S. clausus* and *S. recurvus*, which are otherwise closest to it morphologically.

*Discussion*.—No known specimen reveals the whorl floor, so it is not known if a whorl floor ridge is present or absent. However, because the species appears to be descended from *S. clausus*, it is placed in *Sphenosphaera*. *S. recurvus* is morphologically, and thus probably phylogenetically, intermediate between *S. clausus* and *S. subangularis*.

#### *Sphenosphaera capax* (Ulrich), 1897

Plate 34, figures 1–13

*Bellerophon capax* Ulrich in Ulrich and Scofield, 1897, p. 921, pl. 63, figs. 50, 51; pl. 64, figs. 40–43.

*Diagnosis*.—Shell large, whorls rapidly expanding; whorls somewhat inflated; whorl floor keel large, broadly rounded.

*Description*.—Shell large, whorls rather rapidly expanding throughout growth, abruptly expanded laterally in maturity. Apertural outline nearly semicircular, broadening to more semielliptical in maturity. In relation to this, whorls somewhat inflated, becoming less so in maturity. Umbilici moderate in size, in many specimens partly covered by reflexed parietal lip. Selenizone a low, rounded ridge, no lunulae known. Whorl floor keel large, broadly rounded; little or no parietal callosity; parietal lip thin, folded back and over coil and reflexed posterolaterally. Shell moderately thin, expanded adult aperture somewhat thicker. Growth lines poorly known, appar-

ently fine, gently curved, becoming more sharply curved dorsally, reflecting rather deep, narrow sinus.

*Measurements*.—The measurements of *S. capax*, listed in table 82, were made on poorly preserved specimens.

*Material*.—Eight poorly preserved calcitic specimens are cataloged as “cotypes” under USNM 45698, and a ninth “cotype” is cataloged under USNM 45699. The lectotype was chosen from this group and numbered USNM 315606, (pl. 34, figs. 1–3). All others from this group are paralectotypes; three are figured here (pl. 34, figs. 4–9)—USNM 315607 and 315608, both formerly in the USNM 45698 suite, and USNM 45699. A small number of fragmentary specimens in USGS silicified collections 6411-CO, 6412-CO, and 6414-CO, including USNM 387016 (pl. 34, fig. 10) and USNM 387017 (pl. 34, figs. 11–13), are here placed in *S. capax*.

*Distribution*.—Ulrich and Scofield (1897, p. 922) cited the species as occurring in the “lower part of the Loraine group and upper part of the Utica group...in the vicinity of Cincinnati, Ohio,” the old stratigraphic names being equivalent to strata of late Edenian and early Maysvillian age. The type suite is from the Maysvillian-age Fairmount biofacies of the Fairview Formation at Covington, Ky. The new silicified material is from the Gilbert Member of the Ashlock Formation (late Maysvillian) in central Kentucky.

*Comparison*.—*S. capax* is quite similar in general shell form to *S. mohri* (Miller), but can be distinguished by its open umbilicus, its much less prominent selenizone, and its more prominent whorl floor ridge. *S. capax* is also easily distinguished from *S. recurvus* by its open umbilicus, as well as by its more inflated and more greatly expanded and inflated whorl form. Additional comments about *S. capax* are included in the discussion of *S. mohri*.

TABLE 82.—Measurements (in millimeters) of *Sphenosphaera capax*

USNM No.	Shell length	Shell height	Aperture length	Aperture width	Dorsal width	Posterior width	Ventral width	Selenizone width
315606	33.0	18.0	26.4	33.2	15.95	13.5	11.0	—
315607	38.2	26.3	28.0	35.6	21.3	17.4	14.0	1.3
315608	—	—	24.8	38.3	—	—	—	—
45699	37.3	—	27.5	45.7	—	—	—	—



TABLE 83.—Measurements (in millimeters) of *Sphenosphaera mohri*

Museum No.	Shell length	Shell height	Aperture length	Aperture width	Dorsal width	Posterior width	Ventral width	Selenizone width UC
UC								
8796	36.4	16.8	30.4	—	13.2	11.3	8.0	1.65
8793a	—	—	—	~32.1	16.0	10.3	—	1.9
USNM								
315629	30.0	18.9	22.4	37.25	16.4	13.0	9.8	1.5
315630	—	—	—	41.1	18.4	14.4	12.8	—
315631	—	19.0	—	37.0	17.5	14.3	11.7	1.6
315632	—	7.5	—	11.6	5.7	4.5	—	0.5
315633	—	12.0	—	21.0	9.4	7.85	6.0	1.0
315656	—	18.6	—	39.3	15.4	13.3	10.7	—
315656	—	—	—	46.3	18.7	14.3	12.2	—
315656	—	15.8	—	33.4	14.2	—	—	1.4
315656	—	—	—	30.8	13.9	11.1	—	—
315656	—	15.5	—	29.0	13.1	8.0	6.8	—
315656	—	19.1	—	32.3	15.2	12.2	11.0	—
315656	—	17.5	—	—	14.0	11.7	9.3	—
315656	—	—	—	30.2	—	12.4	—	—
315656	—	—	—	22.4	13.5	—	—	—
315656	—	—	—	30.0	14.5	9.3	7.4	—
315656	—	14.0	—	26.7	12.0	10.2	7.2	—
315656	—	13.9	—	25.3	11.5	8.0	6.4	—
315656	—	—	—	34.0	15.1	13.7	11.0	—
315656	—	—	—	27.5	13.3	11.0	8.2	—
315656	—	—	—	27.7	—	12.5	9.5	—
315656	—	13.2	—	20.7	10.7	9.25	6.7	—
315656	—	—	—	20.0	9.2	7.2	5.2	—
315656	—	—	—	23.4	10.4	8.1	6.3	—
315656	—	—	—	17.9	9.75	7.55	5.5	—
315656	—	9.5	—	15.3	8.6	7.0	5.0	0.6
315656	—	6.1	—	10.4	5.1	4.4	3.4	—
315656	—	—	—	9.75	5.2	4.15	—	—

*Sphenosphaera mohri* (Miller), 1874

Plate 35, figures 1–16; Plate 36, figures 1–15;  
Plate 41, figures 1–5

*Bellerophon mohri* Miller, 1874, p. 306, fig. 30; 1889, p. 397, fig. 653;  
Ulrich and Scofield, 1897, p. 920, pl. 64, figs. 44, 45; Cumings,  
1908, p. 954, pl. 39, figs. 2, 2a; Foerste, 1924, p. 208, pl. 34, fig. 9.  
*Bellerophon cincinnatiensis* Miller and Faber, 1894, p. 29, pl. 1, figs.  
23, 24.

*Bellerophon parksi* Foerste, 1924, p. 208, pl. 35, figs. 4a–d.

**Diagnosis.**—Shell large (up to 36.4 mm long), umbilici closed; whorls rapidly expanding, somewhat inflated; aperture broad, nearly semicircular; selenizone a prominent ridge.

**Description.**—Shell large; whorls somewhat inflated, expanding rapidly throughout growth, abruptly expanding laterally in adulthood; umbilici closed. Aperture broad, anterior and lateral margins thin and nearly semicircular in outline; posterolateral margins form rounded corners; inner lip nearly straight and parallel to axis of coiling, thickening inward toward well-developed median parietal callosity, and reflexed over coil to close umbilicus. Whorl floor ridge prominent, narrowly rounded to rounded. Selenizone elevated, nearly flat

topped, becoming more prominent through growth; lunulae faint. Sinus moderately narrow and deep; slit apparently rather wide and deep. Growth lines distinct fine threads, very closely spaced throughout growth, broadly curved over whorl slopes, turning abruptly backward only in immediate proximity of selenizone.

**Measurements.**—Measurements of *S. mohri* are listed in table 83.

**Material.**—The syntypes of *S. mohri*, three calcitic specimens, are in the Faber Collection at the Field Museum of Natural History, Chicago, Ill. UC 8793a is designated the lectotype (pl. 35, figs. 1–4), and UC 8793b and UC 8793c, both crushed and distorted by compression, are paralectotypes (pl. 35, figs. 5–8).

The holotype (UC 8796), and only known specimen, of *Bellerophon cincinnatiensis* Miller and Faber (1894) is illustrated here (pl. 35, figs. 15, 16), and that species is placed in synonymy with *S. mohri*. *Bellerophon parksi* Foerste (1924) is also placed in synonymy with *S. mohri*.

Ulrich's (Ulrich and Scofield, 1897) hypotypes (USNM 45702) are nine calcitic casts and internal molds, some of which probably do not belong in this species or genus. Two of the better preserved specimens belong to *S.*

*mohri*, have been removed from this collection, and are now cataloged under USNM 315610 (pl. 35, figs. 12-14) and USNM 315611 (pl. 35, figs. 9-11).

Numerous specimens were found in the collections of the University of Cincinnati and Miami University. Specimens used here are UCGM 44303 (pl. 36, figs. 14, 15), an internal mold; MU 14539 (pl. 36, fig. 13), apparently an external mold but seeming to retain some part of the shell; and MU 252T (pl. 41, figs. 3-5), a calcitic cast.

New silicified material is from USGS samples 6139-CO, which yielded more than 200 specimens and fragments, and 6140-CO, which contains about 30 poor fragments. From the 6139-CO collection, 5 specimens were selected for illustration (USNM 315629-315633) (pls. 36, 41), and 22 other specimens were measured (USNM 315656).

*Distribution.*—*S. mohri* is distributed throughout Richmondian-age strata in the Indiana-Ohio-Kentucky tristate area, and also occurs in lower Maysvillian rocks. It is best known from the Whitewater Formation in the vicinity of Richmond, Ind., but has also been recognized in the Saluda Formation, and the Liberty and Waynesville biofacies of the Dillsboro Formation.

The holotype of *Bellerophon cincinnatiensis* (= *S. mohri*) is from the Maysvillian Fairview Formation at Cincinnati, Ohio. *Bellerophon parksi* Foerste, 1924 (= *S. mohri*) is from Richmondian-age strata of Ontario, Canada.

*Comparison.*—*S. mohri* differs from *S. capax* in having closed umbilici, a more rapidly expanded shell, a more prominent selenizone, and a smaller, narrower whorl floor ridge. *S. recurvus*, which also has a closed umbilicus, is less inflated and expanded than *S. mohri*, and does not have as prominent a selenizone.

*Discussion.*—Miller (1874) referred to *S. mohri* as involute, implying the presence of umbilici, but his type specimens, particularly UC 8793c (pl. 35, figs. 6-8), clearly show that the umbilici are closed by the parietal lip. Likewise, Ulrich and Scofield (1897, p. 920) mentioned small umbilici, but the two specimens from their collections shown here (pl. 35, figs. 9-11, 12-14) also show the umbilici closed. Foerste (1924, p. 208) named *Bellerophon parksi* from Richmondian-age strata in Ontario, saying that it differed from *S. mohri* in its closed umbilici. As it is clear that the umbilici of *S. mohri* are closed, Foerste's specimens are essentially identical to *S. mohri*.

Miller and Faber (1894) named *Bellerophon cincinnatiensis* for rare specimens from the Maysvillian Fairview Formation at Cincinnati, Ohio. The holotype, and only specimen of *B. cincinnatiensis*, is a vertically compressed specimen comparing favorably with *S. mohri* in its closed umbilicus, high selenizone, and distinct, closely spaced growth lines, as well as in its general shell form.

Miller and Faber (1894) described the aperture as expanded and probably wider than long, but their specimen is not well enough preserved that the shape or size of the aperture could be determined accurately. Because *B. cincinnatiensis* has no distinctive morphological traits to distinguish it from *S. mohri*, the two species names are considered to be synonyms. This extends the range of *S. mohri* from late Richmondian to early Maysvillian.

*S. mohri* is the most common member of the genus *Sphenosphaera* in the Cincinnati Series, being abundant in the late Richmondian Whitewater Formation in southeastern Indiana. Specimens from Indiana can be common locally, but they are generally poorly preserved. Many are internal molds (pl. 36, figs. 14, 15), encrusted by bryozoan colonies. In the upper Dillsboro Formation (USGS 6139-CO; Richmondian), some specimens are silicified. They can be recrystallized (pl. 35, figs. 9-11), and many are crushed and distorted by compression (pl. 35, figs. 5, 6-8). Similar preservation is characteristic of other bellerophonaceans and gastropods in Indiana Ordovician faunas (see *Salpingostoma richmondensis*, *Bucania simulatrix*, *Cyrtolites ornatus*). On the other hand, many groups, such as the articulate brachiopods and horn corals, are well preserved in these beds. These circumstances support the conclusion that these bellerophonaceans and gastropods had predominantly aragonitic shells. This aspect of preservation compounds the problem of dealing with rather simple, subtly different morphologies. Consider the subtle differences in the whorl forms of USNM 315631 and 315629 (pl. 36, figs. 1-3 and 4-7, respectively); the specimens are from the same collection, but USNM 315631 is more inflated and robust than USNM 315629. The bryozoan-encrusted paralectotypes of *S. capax* (pl. 34, figs. 4-7) are quite difficult to distinguish from *S. mohri*. The two species are closely related. Both are larger than their Middle Ordovician ancestors, both have rapidly expanding shells with marked lateral expansion in adulthood, and both occur in rubbly, bioclastic limestone sequences associated with a diverse fauna. Many are completely encrusted by bryozoans. The expanded, thickened adult apertures of these species suggest that they were sluggish vagrant benthos living in moderately high energy environments, probably grazing on benthic algae.

#### Family CARINAROPSIDAE Ulrich and Scofield, 1897

*Diagnosis.*—Shell greatly expanded, coil nearly or completely reduced; interior posteromedian septum developed within aperture; slit as short notch with selenizone, or as raised hollow keel.

*Stratigraphic range.*—Middle Ordovician–Middle Devonian.

*Genera included.*—*Carinaropsis* Hall, 1847; *Gyrospira* Boucot, 1956; *Pterotheca* Salter, 1853;

*Cyclothea* Teichert, 1935; *Aspidothea* Teichert, 1935; and *Pedasiola* Spriesterbach, 1919.

**Discussion.**—Ulrich and Scofield (1897) placed *Carinaropsis* and *Pterotheca* in the Carinaropsidae. Teichert (1928, 1930, 1935) also concluded that, after a series of studies of *Pterotheca*, the two genera were closely related. Wenz (1938) and Golikov and Starobogatov (1975) recognized two families, the Carinaropsidae and Pterothecidae, but treated the two as closely related.

Knight and others (1960) included the Carinaropsinae and Pterothecinae as subfamilies of the Bellerophonitidae. In the Carinaropsinae, they included a number of genera showing a tendency toward rapid expansion of whorls and reduction of coiling, and generally having development of the parietal lip into a platelike extension, with a whorl floor keel, and a selenizone on a moderately developed dorsal crest. As noted later in the discussion of *Carinaropsis cymbula* (Hall), the internal septum of *Carinaropsis* is not simply a reflexed parietal lip, as in *Bucanopsis* and *Sphenosphaera*, but is a greatly extended outgrowth of the parietal region that protrudes into the apertural opening as a separate structural element. Rollins (1967) came to a similar conclusion regarding the Carinaropsinae (sensu Knight and others, 1960). He stated (p. 149): "The Carinaropsinae reflect an unnatural grouping of genera. *Gyrospira* and *Carinaropsis* are quite distinct, by virtue of an incipient aperture plate, from *Bucanopsis* and *Sphenosphaera*. The former genera reflect a trend that culminated in the Pterothecidae, with the development of a *Crepidula*-like platform." However, Rollins (1967) did not formally propose redefinition of the Carinaropsinae (sensu Knight and others, 1960). That step is taken here, with *Bucanopsis* and *Sphenosphaera* transferred to the new subfamily Bucanopsinae of the Bellerophonitidae, and *Carinaropsis* and *Gyrospira* left in the Carinaropsinae.

The Carinaropsidae is here treated as a family, and is considered to contain three distinct but closely related subfamilies: Carinaropsinae, Pterothecinae, and Pedasiolinae. It is believed that the Carinaropsinae was ancestral to the other two subfamilies, which include the genera assigned to the Pterothecinae by Knight and others (1960). The Carinaropsinae are characterized by the possession of a small coil and the development of an apertural platform. The Pterothecinae is restricted to genera having a completely reduced coil and a marginal apex, and includes the genera *Pterotheca* Salter, 1853, and *Cyclothea*, Teichert, 1935. The Pedasiolinae is proposed here as a new subfamily of the Carinaropsidae.

#### Subfamily PEDASIOLINAE new subfamily

**Diagnosis.**—Carinaropsidae having completely reduced coil, submarginal elevated apex, and slit developed as raised median keel.

**Stratigraphic range.**—Lower-Middle Devonian.

**Type genus.**—*Pedasiola* Spriesterbach (1919).

**Genera included.**—*Pedasiola* Spriesterbach (1919), Middle Devonian; and *Aspidothea* Teichert (1935), Lower Devonian.

**Discussion.**—The stratigraphic position of these genera suggests that they developed from the Pterothecinae. However, their elevated submarginal apex would seem to be a less advanced condition, being morphologically intermediate between the shell forms of the Carinaropsinae and Pterothecinae. The Pedasiolinae probably evolved from the Carinaropsinae separately from the Pterothecinae, which also evolved from the Carinaropsinae. No genera of this subfamily occur in the Ordovician rocks in the area included in this study.

#### Subfamily CARINAROPSINAE Ulrich and Scofield, 1897

**Diagnosis.**—Shell having small but distinct phanerocephalous coil, then broadly expanding rapidly; posteromedian septum well developed within aperture, but relatively small; slit as short notch, generating distinct selenizone.

**Stratigraphic range.**—Middle Ordovician-?Devonian.

**Genera included.**—*Carinaropsis* Hall, 1847, which occurs in the Middle and Upper Ordovician of North America and Europe; and *Gyrospira* Boucot, 1956, whose occurrence in South America is probably in Devonian rocks (Knight and others, 1960).

**Discussion.**—The retention of a small coil and a distinct selenizone, and the relatively small apertural septum, show the Carinaropsinae to be the most morphologically primitive taxon within the family; thus, phylogenetic roots for the family depend on comparisons with *Carinaropsis*. A genus that may fit the role of ancestor to *Carinaropsis* is the Lower Ordovician *Eobucania* Kobayashi (1955), which has a small, involute coil, a moderately expanded adult aperture, and a distinct selenizone with bordering threads; partial reduction of the coil and greater expansion of the aperture of a species of *Eobucania* would result in a *Carinaropsis*-like shell. This appears to be the direction of the general morphologic trend within the Carinaropsidae. The Bucanopsinae appear to have a common ancestry with the Carinaropsinae; however, in the Carinaropsinae, coil reduction and rapid shell expansion developed much further than in bucanopsins. *Sphenosphaera* shows incipient outbuilding of the parietal area, as well as a tendency toward an increasing rate of whorl expansion, and a species of that genus is considered to be the most likely ancestor to *Carinaropsis*.

#### Genus CARINAROPSIS Hall, 1847

**Diagnosis.**—Shell having small carinate coil, followed by greatly expanded adult whorl; slit short; selenizone

moderately wide, bordered by small ridges; posteromedian platform in apertural cavity bearing dorsomedian keel.

*Description*.—Shell having small juvenile coil with carinate dorsum, convex lateral slopes, and open umbilicus, followed at maturity by rapid, broad expansion of whorl, producing a patelliform appearance, having broadly convex dorsum; expanded aperture widest posteriorly; slit a short notch; selenizone moderately wide, with lunulae; posteromedian platform protruding into apertural cavity, the anterior margin being straight to concave-upward, having sharp keel dorsomedially; parietal lip excavated to varying degrees; shell thin; growth lines broadly sweeping.

*Type species*.—*C. carinata* Hall, 1847, by subsequent designation of Fischer (1885).

*Other North American species*.—*C. acuta* Ulrich and Scofield, 1897; *C. carinata* (Hall), 1847; *C. cunulæ* (Hall), 1861; *C. cymbula* Hall, 1861; *C. explanata* Ulrich, 1897; *C. minima* Ulrich and Scofield, 1897; *C. phalera* (Sardeson, 1892).

*European species*.—*C. gracilis* Reed, 1921; *C. maccoyi* Reed, 1921.

*Distribution*.—Rocklandian-Edenian of Eastern North America (New York, Kentucky, Tennessee, Minnesota) and Great Britain.

*Discussion*.—Hall (1847, p. 183) described the genus *Carinaropsis* as "symmetrical, subconical, patelliform, subangulated or carinated on the dorsal line; apex incurved or convolute; aperture oval, narrowed posteriorly." In modern terms, the coil would be considered involute. Also, it is now known that the aperture is broader posteriorly. Hall (1847) named two species, *C. carinata* and *C. patelliformis*, the latter of which is now the type species for the Ordovician monoplacophoran genus *Archinacelliopsis* Horny, 1963a.

Hall (1861, p. 93–95) named two additional species from the Ordovician of Kentucky and Tennessee that he said resembled *Carinaropsis* externally, but also showed "a kind of septum as in *Crepidula*, extending from the posterior side one-third the distance across the cavity." Concerning this feature, Hall commented: "Should these prove to be identical with those which I have designated as *Carinaropsis*, that generic term will have precedence; but should this important character not be found in those forms, I propose for those now under consideration the generic name of *Phragmostoma*, from the septum within the aperture." These two species are now regarded as *Carinaropsis cunulæ* and *C. cymbula*.

Ulrich and Scofield (1897, p. 926, 927) briefly discussed the possible relation of *Carinaropsis* to *Bellerophon* (by which they meant the Ordovician species now assigned to *Sphenosphaera*). They pointed out that both genera have an expanded aperture with a parietal plate, a carinate

dorsum, and a selenizone. However, they concluded that these features had an outward resemblance, but differed greatly in their development. Therefore, they believed *Carinaropsis* to represent a distinct family. They also proposed that *Pterotheca*, a genus that most authors of that time believed to be a pteropod, belonged to the same family as *Carinaropsis*; they based their opinion on their observation that both genera have a greatly expanded adult shell, a well-developed parietal platform, a reduced coil, and a carinate dorsum.

Teichert (1935), after studying *Pterotheca* in detail, also concluded that *Carinaropsis* and *Pterotheca* were closely related phylogenetically. Wenz (1938) supported this conclusion and placed the families Carinaropsidae and Pterothecidae in close association. Wenz placed *Pedasiola* with *Carinaropsis* in the Carinaropsidae. *Pedasiola* was placed with *Pterotheca* in the Pterothecinae by Knight and others (1960). Herein, *Pedasiola* is placed with *Aspidotheca* Teichert (1935), in the new subfamily Pedasiolinae of the Carinaropsidae.

Knight and others (1960) allied *Carinaropsis* with *Bucanopsis*, *Sphenosphaera*, *Gyrospira*, and *Phragmosphaera* in the subfamily Carinaropsinae. This interpretation stressed the reflected parietal lips and whorl floor keel common to these genera. Their figure 98, 3a, is misleading, as it makes the parietal lip of *Carinaropsis* appear as a simple reflected apertural margin, as in *Bucanopsis* and *Sphenosphaera*, when the parietal platform of *Carinaropsis* actually is developed quite differently. This parietal platform, or septum as it is commonly called, does not simply reflex around the ventral coil, but grows anteriorly into the apertural cavity during ontogeny. As seen in *C. cymbula* (Hall) (pl. 38, figs. 1, 2), the septum is developed from the parietal lip, but apparently as a separate structural element. The dorsolateral septal surface attaches to the interior shell roof, sloping downward convexly; it then folds back tightly upon itself, sloping posteriorly as a concave surface to meet the shell wall, and linking that wall to the parietal shell margin. As shown on plate 38, figures 1, 2, there appears to be a cavity within the septum. Whether this cavity was open is uncertain, because it may be a product of silicification; this cavity was seen on other silicified specimens also. Sections through well-preserved calcitic material, which was not available for this study, are needed to confirm the presence of this cavity. It is likely that the septum of *Carinaropsis* is quite different from the reflexed parietal lips of *Bucanopsis* and *Sphenosphaera*, and is similar to the interior platform of *Pterotheca*, as noted here and as illustrated by Teichert (1935). It is conceivable that *Carinaropsis* is intermediate in form between such genera as *Sphenosphaera* and *Pterotheca*. Supporting this notion is the presence of a keel on the dorsal septal floor of *Carinaropsis*.

Comparison between the septa of *Crepidula* and those of *Carinaropsis* and *Pterotheca* has been made ever since Hall's (1861) descriptions of *Carinaropsis cymbula* and *C. cunulae*. Hoagland (1977, p. 358), in her review of the Calyptraeidae, stated: "The septum of *Crepidula* is homologous to the columella. Migration of the point of muscle insertion to the junction of the septum and the shell proper, or onto the shell, is a specialization for sedentary limpet like existence, as is the derivation of new muscles for shell attachment. The presence of an insertion on either side of the septum as shown by the presence of two muscle scars is a third solution to the problem of attachment of body to shell and substrate." She further explained: "The septum supports the viscera and provides for muscle attachment. It divides the body into three parts; the foot, the viscera, and the head and brood chamber regions....The disc like foot covers the area of the septum and no more; thus the larger the septum proportional to the size of the shell, the greater will be the area of the foot. Also, the deeper the septum is inserted into the shell, the thicker may be the foot." Hoagland was able to use the morphology of the septum (median ridge, notches and curves in the margin, positions of muscle attachment) for the differentiation of species. However, she noted that the depth of insertions and the depth of the notches show some intraspecific variation, and that changes in septal area to apertural area in ontogeny must be carefully distinguished from interspecific differences. Many of her observations probably have application to the Carinaropsidae. It seems likely that the carinaropsids were adapted to a largely sedentary existence, and the morphology of the carinaropsid septum can be used in specific differentiation. Moreover, the increase in the size of the septum from *Carinaropsis* to *Pterotheca* probably indicates a concomitant increase in the size of the foot, and may denote increased specialization for a purely limpetlike existence with stronger clamping power. However, it should be recognized that although the septa of *Crepidula* and *Carinaropsis* seem to have analogous functional significance, the septum of *Carinaropsis* is not columellar (as suggested for *Crepidula*), and the two structures have quite different origins.

**Carinaropsis acuta Ulrich and Scofield, 1897**

Plate 4, figures 18–25

*Carinaropsis acuta* Ulrich and Scofield, 1897, p. 928, pl. 62, figs. 6–9.

**Diagnosis.**—Shell small (up to 13 mm long), submature coil greatly compressed laterally and having sharply angular dorsum; adult shell rapidly expanded; apertural outline becoming subcircular; septum short.

**Description.**—Shell small for genus, thin, smooth; submature whorls greatly compressed laterally, produc-

TABLE 84.—Measurements (in millimeters) of *Carinaropsis acuta*

USNM No.	Shell length	Shell width	Shell height	Coil width	Septum length	Septum width
265992	13.05	15.15	8.35	—	6.0	6.3
265993	—	17.15	8.00	3.6	—	—
265994	—	10.10	—	3.5	—	—

ing relatively high, narrow coil with sharply angular dorsal crest; umbilici subcircular and deep; with rapid expansion of adult whorl, apertural outline changes from triangular to subcircular, dorsal angle becomes less acute quickly and broadens to accommodate moderately wide selenizone; anterior slope of shell rather steep; posterior lip not reflected strongly, but rather explanate; septum short.

**Measurements.**—Measurements of *C. acuta* are listed in table 84. Because the specimens are fragmentary, the measurements are approximations.

**Material.**—*C. acuta* was recognized in USGS silicified samples 5023-CO, 5100-CO, 5101-CO, 7784-CO, and possibly (*C. cf. C. acuta*) in 6134-CO and 6419-CO; the total number of fragmentary specimens was 15. Figured specimens are USNM 265992, 265993, 265994, and 265995 (pl. 4, figs. 18–25).

**Distribution.**—Ulrich and Scofield (1897) described *C. acuta* from the Decorah Formation (Rocklandian-Kirkfieldian) of Minnesota. In Kentucky the species was recognized in five samples from the Curdsville Limestone Member (5023-CO, 5100-CO, 5101-CO, 6134-CO, 7784-CO), and another possible specimen was found in a sample from the Logana Member (6419-CO) of the Lexington Limestone (Kirkfieldian).

**Comparison.**—The consistently small size of all the specimens of *Carinaropsis* in the Curdsville Limestone Member samples suggests that they differ from the larger species *C. cymbula* in the Grier Limestone Member. Close examination of the Curdsville specimens shows that, compared with *C. cymbula*, they have a more laterally compressed submature coil and a more prominent dorsal carina (pl. 4, figs. 20, 24), and that their expanded whorl is relatively higher and has a subcircular outline (pl. 4, figs. 18, 19).

Ulrich and Scofield (1897) differentiated *C. acuta* from *C. phalera* (Sardeson) by the former's narrower coil and shorter septum. The septum of all the Kentucky specimens of *C. acuta* is poorly preserved, but where visible, it is quite short.

**Discussion.**—This is the first identification of *C. acuta* outside Minnesota. The species is distinguished from juveniles of *C. cymbula* and *C. cunulae* mainly by its narrow, sharply crested submature coil. For its small size, *C. acuta* had a rather wide selenizone (pl. 4, figs. 18, 24), which broadened rapidly as the mature whorl

TABLE 85.—*Measurements (in millimeters) of Carinaropsis cunulae*

USNM No.	Shell length	Shell width	Shell height	Coil width	Septum length	Septum width	Selenizone width
45738	20.5	22.4	9.2	5.1	9.85	13.5	2.0
45738	18.9	22.5	8.9	4.95	10.0	—	2.0
45738	16.2	17.75	8.1	5.2	7.9	10.5	2.0
45738	15.2	18.8	—	4.5	9.05	11.3	—

expanded rapidly into its steep, subcircular form (pl. 4, figs. 18, 19).

***Carinaropsis cunulae* (Hall, 1861)**

Plate 37, figures 12–14

*Phragmostoma cunulae* Hall, 1861, p. 95; Miller, 1889, p. 415.

*Carinaropsis cunulae* (Hall) Ulrich and Scofield, 1897, p. 927, pl. 62, figs. 10–13; Grabau and Shimer, 1909, p. 626, pl. 845a-c.

**Diagnosis.**—Shell having relatively large initial coil; septum relatively small and flat, with shallow excavation posteroventrally; posterior apertural margin broad and straight.

**Description.**—Shell moderate in size (up to 20 mm long); submature coil relatively large, with sharp dorsal crest and rounded lateral whorl slopes, umbilici small but deep; coil projects distinctly beyond broad, straight posterior apertural margin; dorsum of rapidly expanded adult whorl broadly convex; median selenizone distinct and moderately wide; septum relatively short, dorsally nearly flat with slightly concave upward anterior margin and sharp median keel, ventrally with shallow posteroventral excavation; ornament unknown.

**Measurements.**—Measurements of *C. cunulae* are listed in table 85. Note that all shell length measurements are minimum values, as the anterior shell margin was not preserved in any available specimen.

**Material.**—Hall's types are not at the American Museum of Natural History, and could not be located at any other museum. Ulrich and Scofield's (1897) hypotypes, USNM 45738, were the only specimens of the species located and examined. Their four silicified specimens are all incomplete. Three specimens (USNM 45738) preserve the expanded dorsum and the septum. The fourth specimen, which is missing the dorsum, reveals the dorsal side of the septum, and is the only one to preserve the submature coil (pl. 37, figs. 12–14); this specimen is separated from the hypotypic suite and is cataloged under the new number USNM 265998.

**Distribution.**—Ulrich and Scofield's (1897) hypotypes (USNM 45738 and 265998) are listed on the museum label as from the Cannon facies of the Bigby-Cannon Limestone (Kirkfieldian-Shermanian) at Nashville, Tenn. The authors cited the species as from the "Upper Trenton

group, Nashville, Tennessee, and Boyle County, Kentucky."

**Comparison.**—*C. cunulae* differs from *C. cymbula* (Hall) in having a more inflated submature coil, a shorter and flatter septum, and a shallower posteroventral excavation. The last difference is the most distinctive distinguishing morphological feature (compare pl. 37, figs. 9–11 and 12–14). Ulrich and Scofield (1897, p. 928) compared *C. cunulae* to *C. phalera* (Sardeson) from the Decorah Formation of Minnesota. They stated that *C. phalera* has a less reflected apertural margin which is scarcely truncated posteriorly, a more circular outline, and a greater depth to the concavity of the septum.

**Discussion.**—*C. cunulae* appears to be less advanced than *C. cymbula* when the major morphological trends of the family Carinaropsidae are considered. These trends are mainly the reduction of the coil and the increased development of the septum. *C. cunulae* has a more inflated coil and a smaller septum.

***Carinaropsis cymbula* (Hall, 1861)**

Plate 37, figures 1–11, 15–23; Plate 38, figures 1–12

*Phragmostoma cymbula* Hall, 1861, p. 94.

*Phragmostoma natator* Hall (in error for *cymbula*), 1862, pl. 6, figs. 12–14.

*Phragmostoma cymbula* Hall, Miller, 1889, p. 415, fig. 693.

*Carinaropsis cymbula* (Hall), Ulrich and Scofield, 1897, p. 927, pl. 62, figs. 1–4; Grabau and Shimer, 1909, p. 626, figs. 845d-g; Bassler, 1932, p. 222, pl. 20, figs. 21, 22.

**Diagnosis.**—Shell having relatively narrow initial coil; septum relatively large, angled downward toward anterior, anterior margin slightly concave upward; shell deeply excavated posteroventrally to rear of septum.

**Description.**—Shell moderately large (up to about 30 mm long); submature coil relatively small and narrow, with sharp dorsum, convex (but not inflated) lateral whorl slopes, umbilici small and deep; coil protruding slightly beyond posterior shell margin; dorsum of rapidly expanded adult whorl broadly convex, having median crest upon which slightly raised selenizone rests, the crest becoming increasingly rounded during growth; selenizone moderately wide, bordered by low, sharp ridges, with median groove, lunulae in some specimens distinct; septum relatively large, angled strongly downward

TABLE 86.—Measurements (in millimeters) of *Carinaropsis cymbula*

USNM No.	Shell length	Shell width	Shell height	Coil width	Septum width
45739	27.8	21.3	10.8	—	—
45739	—	—	—	4.4	9.5
45739	—	—	8.8	4.6	9.5
265997	—	13.4	—	4.55	9.4
265996	—	—	—	3.55	6.8
265984	—	42.6	—	3.9	22.3
265986	—	47.0	—	4.0	21.5
265987	—	39.3	—	4.2	19.3
265990	—	—	—	—	—
265988	—	31.0	—	4.35	14.4
265985	—	31.9	—	3.6	15.1
265987a	—	27.7	—	—	14.8
265987b	—	38.2	—	—	17.9
265987b	—	36.2	—	—	16.4
265987c	—	30.7	—	—	17.6

toward anterior, dorsally convex in side view, anterior margin nearly straight to strongly concave upward, having dorsomedian keel; posteroventral excavation deep; growth lines broadly sweeping, showing greatest width of shell to be posterolateral, and curving strongly backward near selenizone, reflecting rather broad, shallow sinus housing short slit; growth lines in some specimens as low, broad wrinkles; radiating threads visible in some specimens; posterior shell margin slightly arched in a few specimens; shell thin.

**Measurements.**—Measurements of *C. cymbula* are listed in table 86. Although a number of specimens were available, most were not measured because of the fragmentary condition of the shell margins.

**Material.**—Type specimens examined were Hall's (1861) holotype (pl. 37, figs. 1–4; AMNH 37723a) and paratypes (AMNH 37724, 37725a–c) and Ulrich and Scofield's (1897) hypotypes (USNM 45739). Two specimens from the latter suite figured here are given the new catalog numbers USNM 265996 (pl. 37, figs. 7, 8) and USNM 265997 (pl. 37, figs. 9–11). All of these types are silicified specimens. USNM 87778 is also figured (pl. 37, fig. 23).

A number of excellent specimens were found in the following USGS silicified collections from Kentucky: D-1196-CO, 5096-CO (USNM 265984, 265986, 265991), 4879-CO (USNM 265987, 265985, 265988, 265990), 4880-CO, 4852-CO, 4876-CO, 4883-CO, 5107-CO, 4073-CO, 5094-CO, 5074-CO, 5099-CO, 5067-CO, 4959-CO, 5015-CO, 7783-CO, ?7809-CO (pls. 37, 38).

**Distribution.**—Hall's (1861) types are labeled as coming from the "Trenton Limestone at Allen's Bluff, Tennessee." Ulrich and Scofield's (1897) hypotypes are labeled "Trenton Group, near Danville, Kentucky." It should be noted that Hall (1861) had originally mistak-

only recorded the species as from the "Hudson River Group," which at that time was the equivalent to the Cincinnati. The so-called "Trenton Group" in Tennessee would be the Nashville Group of modern usage, and in Kentucky would be the Lexington Limestone.

In the USGS silicified collections from Kentucky, *C. cymbula* was recognized from the Logana Member (D-1196-CO), the Grier Limestone Member (4073-CO, 4852-CO, 4876-CO, 4879-CO (USNM 265987), 4880-CO, 4883-CO, 4959-CO (USNM 265987a), 5067-CO, 5074-CO, 5094-CO, 5096-CO, 5099-CO, 5107-CO), the Salvisa Bed of the Perryville Limestone Member (5015-CO (USNM 265987b)), and the Tanglewood Limestone Member (7783-CO (USNM 265987c) and possibly 7809-CO) of the Lexington Limestone. All occurrences of the species are Kirkfieldian-Shermanian in age.

**Comparison.**—The only species in the study area that bears any close resemblance to *C. cymbula* is *C. cunulæ*. The primary basis for distinguishing these two species is the deep excavation of the posteroventral septum (pl. 37, figs. 3, 4, 11, 18, 19; pl. 38, figs. 4, 5) of *C. cymbula*, compared with the shallow indentation of the posteromedian septum of *C. cunulæ* (pl. 37, fig. 14). The septum of *C. cymbula* is larger, protrudes farther into the apertural cavity, and is more convex, sloping strongly anteriorly. The submature coil of *C. cymbula* is slightly smaller and distinctly narrower than that of *C. cunulæ*.

*C. phalera* (Sardeson) was originally described as having indistinct radial folds on the dorsal surface of the shell, but Ulrich and Scofield (1897) did not find any such markings on their specimens. However, a single specimen of *C. cymbula* from USGS sample 5096-CO (Grier Limestone Member) does show radial markings, these being in the form of faint, widely spaced threads (pl. 38, fig. 8). Ulrich and Scofield (1897, p. 928) stated that *C. phalera* is very similar to *C. cunulæ*, which in turn is very similar to *C. cymbula*. These species apparently form a closely related group. If new material of *C. phalera* becomes available, it should be compared closely with the Cincinnati arch species, as it could be a synonym of one of them.

**Discussion.**—*C. cymbula* seems to be more advanced than *C. cunulæ*, as shown by the former's smaller coil and larger septum. Hoagland (1977) correlated the size of the septum of modern *Crepidula* with the size of the foot. This relationship may hold true for the analogous carinaprosid septum. The deep posteroventral excavation of the septum of *C. cymbula* may have helped to house an enlarged foot when the animal clamped its shell to the substrate.

Although a few specimens of *C. cymbula* were found in samples from the Logana, Perryville Limestone, and



Tanglewood Limestone Members of the Lexington Limestone, the species is most abundant, and is often fairly well preserved, in samples from the Grier Limestone Member. This suggests that the species inhabited a wide range of environments but thrived in shallow, only moderately agitated, normal marine environments, such as those represented by the Grier Limestone Member.

All specimens examined were readily placed in *C. cymbula* if the ventral septum having the deep excavation was visible. As pointed out by Ulrich and Scofield (1897), this excavation is the main distinguishing feature of the species. The dorsal shell of the species is thin and easily fragmented. No specimen having a complete shell is known. The most commonly preserved portion of the shell is the septum, which is thickened by the recumbent folding of the shell layers that construct it. Through most of the breadth of the septum, two shell layers are sandwiched together; as the species grew larger, the lateral areas of the septum apparently opened into a small cavity (pl. 38, figs. 1, 2). The double-walled septum and parietal lip of the shell is all that is preserved intact in most specimens. Therefore, the dimensions of the shells and the actual characteristics of the shell margins are poorly known, and variability within the species is difficult to assess.

The septum of *C. cymbula* does not show much variation in size and form, even within a single population. If these animals led a clinging mode of life, as proposed by Rollins (1967), the host object or the energy of the environment may have at least partly governed the morphology of the septum. This would have been particularly true if the septum were the attachment base for the shell muscles. For example, compare specimens USNM 265984 (pl. 37, figs. 15–21) and USNM 265988 (pl. 38, figs. 3–6), both from the Grier Limestone Member of the Lexington Limestone but from different samples. The general form of the septa of the two specimens is quite similar, but that of the former is noticeably larger. The anteromedian part of the septum generally is protuberant, as in these two specimens, but this “nose” is missing from some specimens, particularly of juveniles (pl. 37, figs. 3, 9, 11; pl. 38, figs. 11, 12). Also, the anterior margin of the septum apparently increases in concavity (from an anterior view) during growth.

The submature coil does not appear to have a selenizone, but because of its size it is difficult to tell. The selenizone develops quickly with the rapid expansion of the shell to a certain width, and then remains essentially the same width through the remainder of growth (pl. 37, fig. 1). There is a median groove on the selenizone, the origin of which is unknown (pl. 37, fig. 1; pl. 38, fig. 10).

The growth lines in the species vary somewhat. In most specimens they are only fine lines, giving the surface of the shell a rather smooth appearance (pl. 37,

figs. 15, 16, 20; pl. 38, figs. 3, 10). However, in some they are developed as low wrinkles (pl. 37 figs. 1, 2; pl. 38, figs. 7, 8).

Except for the sharp, low ridges bordering the selenizone (pl. 37, fig. 1), few specimens of *Carinaropsis* preserve the radial ornament. Contrary to the opinion of Ulrich and Scofield (1897), and confirming that of Sardeson that there are indistinct radial wrinkles in *C. phalera* (Sardeson), one USGS silicified specimen of *C. cymbula* from the Grier Limestone Member (USNM 265991) shows faint but distinct, widely spaced, radial threads (pl. 38, figs. 7, 8). This confirmation of radial ornament in the genus supports the opinion that the Carinaropsinae had a common origin with, or evolved from, the Bucanopsinae.

#### *Carinaropsis explanata* Ulrich, 1897

Plate 40, figures 10–14

*Carinaropsis explanata* Ulrich in Ulrich and Scofield, 1897, p. 939, pl. 62, fig. 5.

**Diagnosis.**—Shell having large, prominent, triangular beak area with sharp dorsal crest and steep slopes; lateral shell slopes gently convex and outward sloping.

**Description.**—Shell moderately large for genus (minimum of 32 mm long); beak area large, prominently elevated, triangular in dorsal view, with sharp dorsal crest and steep lateral slopes (although crest broadens with growth, median axis of shell remains elevated above lateral slopes of shell); broadly but strongly convex in side view; contact between beak area and lateral shell slopes marked by sharp break in slope, lateral shell slopes very gently convex and sloping at much gentler angle outward; characteristics of shell and septum unknown.

**Measurements.**—The lectotype (USNM 45740) is a minimum of 32 mm long, 41.2 mm wide, and 14.4 mm high. The lectotype is a fragmentary internal mold.

**Material.**—Only two specimens of this species are known, both originally cataloged under the number USNM 45740. The specimen shown on plate 40, figures 10–14, is here designated the lectotype (USNM 45740); the other specimen is a paralectotype (USNM 315531). Both specimens are internal molds.

**Distribution.**—Ulrich and Scofield (1897, p. 929) cited the species as occurring in the “upper part of the Trenton Group, Covington, Kentucky.” These beds are now covered by the Ohio River and its tributaries, because of the damming of the Ohio River; in the present stratigraphic framework they would be placed in the Point Pleasant Tongue of the Clays Ferry Formation, which is latest Shermanian in age.

**Comparison.**—The large triangular beak area distinguishes the species from all others known.

*Discussion.*—As far as can be told from examination of the type material, Ulrich's (Ulrich and Scofield, 1897, pl. 62, fig. 5) description of the species is highly interpretive, as is his illustration. The types are fragmentary and do not retain the growth lines, so the outline of the shell of the species is unknown. Likewise, the nature of the septum is unknown. Nevertheless, the form of the specimens strongly supports their assignment to *Carinaropsis*. The species coil must have been very small (pl. 40, figs. 13, 14).

#### Subfamily PTEROTHECINAE Wenz, 1938

*Diagnosis.*—Shell with coil completely reduced, apex marginal and curved downward; slit developed as raised, hollow keel.

*Stratigraphic range.*—Middle Ordovician–Upper Silurian.

*Genera included.*—*Pterotheca* Salter, 1853; *Cyclothea* Teichert, 1935.

*Discussion.*—This is the most advanced subfamily in the Carinaropsidae, having a completely reduced coil. The broad explanate shells and large parietal platforms of genera in the Pterothecinae are analogous to the morphology of the modern slipper limpet *Crepidula*, which leads a nearly sedentary life. This analogy suggests that species in the Pterothecinae were also sedentary, or nearly so. Species of *Pterotheca* are commonly associated with abundant leperditiid ostracodes (discussed further below), and they probably inhabited shallow lagoons and tidal flats. Based upon their paleoenvironmental occurrence and their shell form, it is generally believed that these animals were algal grazers, but deposit feeding cannot be ruled out.

#### Genus PTEROTHECA Salter, 1853

*Diagnosis.*—Shell broadly expanded, outline ovate to subtriangular to subquadrangular; coil completely reduced, apex marginal and incurved to varying degrees; slit in elevated dorsomedian keel; septum triangular, with two short, diverging prongs on upper surface at apex.

*Description.*—Many shell large (up to 50 mm long and wide), broadly expanded, generally wider than long, outline varying from ovate to subtriangular to subquadrangular; coil absent; apex marginal, incurved to varying degrees, in many cases hooklike; slit more or less vertical to apertural plane, generating a prominent elevated dorsomedian keel from apex to anteromedian apertural margin, which is generally sinuate; lateral shell surfaces convex, with comarginal growth lines, lamellae, or undulations, and in some cases with radial markings on either side diverging from apex along lines of attachment between ventral septum and ventral shell surface, thus defining a slightly elevated triangular area of dorsal

shell overlying septum; radial threads or cords unknown; septum triangular, proportionate size and angles variable, flat to convex-upward, with two short, diverging prongs at apical end in narrow space between septum and shell surface; space between shell dorsum and septum very narrow.

*Type species.*—*Atrypa transversa* Portlock, 1843, by subsequent designation of Miller (1889, p. 392).

*Distribution.*—Middle Ordovician (Chazy) to Upper Ordovician (Richmondian) of Eastern North America and Europe (Great Britain, Czechoslovakia, Germany, Estonia).

*Comparison.*—*Pterotheca* is easily distinguished from similar genera by its prominent dorsomedian keel, its lack of a coil, its marginal incurved apex, and its large triangular septum with its short apical supports.

*Discussion.*—Species of *Pterotheca* have been erroneously described as brachiopods (*Atrypa transversa* Portlock, 1843), and the genus itself has often been classified with the pteropod or heteropod gastropods.

Hall (1861, p. 96–98), not knowing of the genus *Pterotheca*, Salter (1853), described a number of North American species under the generic name *Clidoderma*. Hall (1861) did note that the species he described under that name were related to *Carinaropsis*, and that they were more distantly related to *Bellerophon* (*Sphenosphaera* of modern usage); thus, he recognized the ancestry and relations of the genus. Ulrich and Scofield (1897) also regarded *Pterotheca* as related to the bellerophonitids, placing it with *Carinaropsis* in the family Carinaropsidae. Notwithstanding these views, the genus was still often regarded as a pteropod or heteropod by their contemporaries. For example, such influential workers as Miller (1889) and Dall (in Eastman, 1913) assigned the genus to the Pteropoda.

Teichert (1928), in his initial study of the genus, considered *Pterotheca* a heteropod. However, upon examination of better material (Teichert, 1935), he concluded that the genus was actually closely related to *Carinaropsis*, as proposed by Ulrich and Scofield (1897), and was therefore a bellerophonitacean gastropod. Teichert (1935) suggested that *Pterotheca* had descended from *Carinaropsis* and had given rise to the genera *Cyclothea* Teichert (1935) and *Aspidotheca* Teichert (1935) (Silurian and Devonian, respectively). I agree with Teichert's opinion on the ancestry of *Pterotheca*, and that *Cyclothea* evolved from a species of *Pterotheca*; however, the genera *Aspidotheca* and *Pedasiola* Spriesterbach (1919) seem to have developed along a line of evolution separate from the Carinaropsinae. *Pterotheca* and *Cyclothea* are characterized by shells having a marginal incurved apex, whereas *Aspidotheca* and *Pedasiola* are characterized by a distinctly submarginal elevated apex.

Teichert (1935, fig. 1b) showed a transverse cross section of a *Pterotheca* shell with the following caption (translated from German): "The cross-section goes through the shell and septum, and shows how the shell rests in a cavity of the septum." If I understand Teichert's diagram and caption correctly, I must disagree with his interpretation. The line that Teichert apparently regarded as separating the shell from the septum is simply the line along which the septum attached to the ventral surface of the shell. Hall (1861, p. 98) described this structure correctly when he stated, "The divergent grooves are apparently caused by the thickening at the junction of the ventral partition with the outer shell." In internal molds, these lines of attachment are represented by narrow grooves that look like sutures. As shown on plate 26, figures 9, 10, these suturelike grooves do not reach to the shell margin, but only the length of the septum.

*Pterotheca* is a genus in great need of complete restudy. Most species were named in the mid- to late 19th century (many by Hall, 1861), and their sketchy descriptions and poor illustrations make identifications and comparisons very difficult. Wilson (1951) also noted this difficulty, as well as the problem of poor preservation.

Foerste (1924, p. 218-220) made some instructive observations and comparisons concerning American and European species of *Pterotheca*. He informally divided the genus into two groups. The first consisted of ovate to subtriangular species, including *P. attenuata* (Hall), *P. saffordi* (Hall) (pl. 39, figs. 1-5, 13), and *P. harviei* Foerste (pl. 26, figs. 9, 10). The second group consisted of more subquadrate forms, whose lateral angles were sharper and lateral margins were more or less parallel. In this latter group he included *P. clochensis* Foerste, *P. canaliculata* (Hall), *P. expansa* (Emmons) (pl. 39, figs. 10, 11), *P. anatifformis* (Hall), *P. undulata* (Hall), *P. angusta* Raymond (pl. 39, figs. 8, 9), and *P. transversa* Salter (as identified by Billings, 1866, from the Richmondian strata of Anticosti Island, Canada). Some species in the second group (such as *P. expansa*) are more ovate and would be better placed in the first group.

Foerste (1924) employed a taxobasis that is very useful for specific differentiation within *Pterotheca*; the angle at which the lateral septal margins diverge from the apex. He also used the angle made by the posterior shell margins, but this angle is less commonly preserved, as the shell margins of most specimens are incomplete. However, if growth lines are preserved, they can be used. The septal angle seems to be the most useful way to differentiate species, because it can be measured (1) when only the dorsal shell is preserved or exposed by using the radial markings along the line of septal attachment, (2) when only the septum is preserved or exposed, and (3) even when only internal molds are available,

because of the suturelike grooves left along lines of septal attachment. Where possible, the septal angle is used with other morphological features to distinguish species. Herein, comparisons were made partly from septal angle measurements taken from drawings in older works; such drawings may be highly subjective. A restudy of the types of all species is necessary so that both interspecific and intraspecific variability can be assessed.

Four species are distinguished herein. *P. saffordi* (Hall) (Blackriveran-Rocklandian) is distinguished from *P. expansa* (Emmons) (Blackriveran-Kirkfieldian) mainly on the basis of the angularity and abruptness of the dorsal keel of the former and on differences in ornament features; both species have a septal angle of about 80 degrees. *P. angusta* Raymond (which occurs with *P. expansa* in the USGS silicified collections from Kentucky) was distinguished from other species in the study area by its low septal angle of about 60 degrees. *P. harviei* Foerste bears a low angular keel, broad shell form, and septal angle of about 85 degrees. It occurs in the Edenian beds of Kentucky.

By analogy with *Crepidula*, it is likely that *Pterotheca* led a largely sedentary life. Hoagland (1977) noted that juvenile *Crepidula* are somewhat mobile, but adults are sedentary clingers that filter feed. The high keel of *Pterotheca*, with its more or less vertical slit, may have been an adaptation to a filter-feeding mode of life. However, it seems more likely that *Pterotheca* was an algal grazer. *Pterotheca* is consistently associated with the ostracodes *Leperditia* and *Leperditella* (identified by Jean Berdan, USGS) (pl. 39, figs. 5, 12, 13; pl. 40, figs. 8, 9) in the Middle Ordovician of Tennessee and Kentucky. This common association suggests that *Pterotheca* inhabited intertidal to shallow nearshore subtidal environments, possibly in waters of increased salinities (Berdan, 1984). Gastropods living in such restricted environments are mostly algal grazers.

#### *Pterotheca saffordi* (Hall, 1861)

Plate 39, figures 1-5, 13; Plate 40, figures 8, 9

*Clioderma saffordi* Hall, 1861, p. 96, pl. 6, figs. 15-17.

*Pterotheca* (*Clioderma*) *saffordi* (Hall), Lesley, 1889, p. 821, figs.

*Pterotheca saffordi* (Hall), Shimer and Shrock, 1944, p. 445, pl. 180, figs. 17, 18.

**Diagnosis.**—Shell ovate-triangular in outline; dorso-median keel high, rising abruptly from lateral shell slopes, subangular crest becoming rounded through ontogeny; septum large, extending two-thirds the shell length; growth lines lamellose.

**Description.**—Shell moderately large (up to 49.5 mm long), outline ovate-triangular, length and width more or less equal; posterior shell margins slightly concave, extending into slightly protuberant beak area, diverging from apex at about 114 degrees; shell margins broadly

TABLE 87.—Measurements (in millimeters) of *Pterotheca saffordi*

Museum No.	Plate	Figure	Shell length	Shell width	Septal angle	Keel width	Keel height
Hall (1861)	6	15	35.0	44.7	85	6.4	6.5
USNM							
79262	39	1, 2	37.5	34.7	77–80	7.2	11.9
79268	39	5	49.5	50.4	85	6.6	9.8
50093	39	13	14.0	14.5	78	—	—

rounded anterolaterally, having anteromedian sinus; dorsolateral slopes moderately arched; dorsomedian keel high, rising abruptly from lateral slopes, subangular crest becoming rounded through ontogeny; septum large and triangular, convex-upward, extending from apex to two-thirds the shell length, the lateral margins diverging from apex at angle of 80–85 degrees; shell surface having strongly lamellose comarginal growth lines.

*Measurements.*—Hall (1861, p. 96) stated that the species had a shell length of about 1.5 in (3.8 cm), with the width being nearly the same.

Most measurements of *Pterotheca saffordi* are approximate, because many of the thin shell margins are broken. The most reliable measurement probably is the septal angle, this being easily taken from photographs. The measurements of *P. saffordi* are listed in table 87. The row labeled “Hall (1861)” includes measurements taken from his plate 6, figure 15. It is obvious from these measurements that Hall’s (1861) original figures do not agree well with the specimens figured here in their length-width proportions; however, I note that USNM 79262 (pl. 39, figs. 1, 2) is a plaster cast of the holotype of *P. saffordi*, and it agrees favorably with other specimens measured. Thus, care must be taken when making measurements from older hand-drawn interpretive illustrations.

*Material.*—The holotype was not examined. However, Shimer and Shrock (1944, pl. 180, figs. 17, 18) show good photographs of the specimen. A plaster cast of the holotype (USNM 79262, pl. 39, figs. 1, 2) is figured here.

A fine calcitic specimen (USNM 79268; pl. 39, figs. 3, 4) from the Tyrone Limestone at High Bridge, Ky., was found in the U.S. National Museum collections. It is embedded in the upper few millimeters of a small slab in a matrix of gray micrite, while a few millimeters beneath the specimen (on the other side of the slab) is an ostracodal biomicrite (packstone) (pl. 39, fig. 5). According to the museum label, specimen USNM 50093 (pl. 39, fig. 13) is from the “top of [the] Tyrone just beneath [the] lower bentonite beds” at High Bridge, Ky. This small slab is mainly micrite, but the surface is covered by a densely packed layer of leperditicopid ostracodes, a few brachiopod fragments, and a fragment of a small *P. saffordi*, all silicified. Specimen USNM 50099 (pl. 40, figs. 8, 9) is also from the Tyrone Limestone at High

Bridge, and occurs in association with ostracodes. Some of the specimens identified here as *P. cf. P. expansa* (Emmons) may actually be assignable to *P. saffordi*. For further comments about these specimens, see the discussion of *P. cf. P. expansa*.

*Distribution.*—*P. saffordi* was originally described from the Lebanon Limestone (Blackriveran-Rocklandian) at Lebanon, Tenn. The species is recognized here from the Tyrone Limestone (Rocklandian) of central Kentucky.

*Comparison.*—*P. saffordi* is distinguished mainly on the basis of its high, rounded dorsomedian keel, its ovate shell outline, and its lamellose growth lines. Wilson (1951, p. 33) stressed the narrow keel of *P. expansa* in distinguishing it from *P. saffordi*.

Foerste (1924) grouped *P. saffordi* with *P. attenuata* (Hall) and *P. harviei* Foerste on the basis of their relatively ovate shells in comparison with other American species, which he claimed were subquadrangular in outline. From Chamberlin’s (1883, fig. 33g) figure of *P. attenuata*, it appears that that species is in reality more triangular, and relatively longer than *P. saffordi*, and has a smaller septum. Foerste (1924) also stated, “*P. harviei* resembles *P. saffordi* most nearly in outline, but it is a much larger species, of less convexity, and the median carina is relatively narrower and less strongly elevated.”

*Discussion.*—The specimen USNM 79268 (pl. 39, figs. 3, 4) confirms the presence of *P. saffordi* in Kentucky. Specimen USNM 50093 (pl. 39, fig. 13) was just one of five such small slabs in a collection from the same locality. All of these specimens are associated with ostracodes, strongly suggesting a very shallow, onshore to nearshore habitat for the species.

#### *Pterotheca expansa* (Emmons, 1842)

Plate 39, figures 6, 7, 10–12; Plate 40, figures 1–7

*Delthyris expansus* Emmons, 1842, p. 397, fig. 109, 2; Owen, 1844, p. 368, fig. 2; 1844b, p. 84, pl. 17, fig. 14.

*Clidoderma expansa* (Emmons), Hall, 1861, p. 98.

*Pterotheca expansa* (Emmons), Lesley, 1889, p. 821, fig.; Raymond, 1902, p. 19, fig. 12; Weller, 1903, p. 179, pl. 12, fig. 35; Branson, 1909, p. 45, pl. 7, fig. 14; Shrock and Raasch, 1937, p. 570, 571, pl. 5, figs. 8, 9, 13; Shimer and Shrock, 1944, p. 445, pl. 180, figs. 15, 16; Wilson, 1951, p. 33, pl. 2, figs. 19, 20; Steele and Sinclair, 1971, p. 20, pl. 10, figs. 5–8.

TABLE 88.—Measurements (in millimeters) of *Pterotheca expansa*

Museum No.	Plate	Figure	Shell length	Shell width	Septal angle	Keel width	Keel height
USNM							
79283	39	6-7	23-27	31-32	—	4.7	7.0
315534	40	6-7	—	—	82	—	—
315536	40	1-3	50-51	58-59	80	11.0	13.0
315537	40	4	40-44	51-52	80	—	—
Steele and Sinclair (1971)							
GSC 22372	10	5	—	—	83	—	—
GSC 22375	10	8	—	—	80	—	—

**Diagnosis.**—Shell moderately large (up to 50 mm long), with broad, subovate outline; dorsomedian carina high, subangular at crest, basal slopes of keel gently concave; septum large, convex upward, septal angle about 80 degrees.

**Description.**—Shell relatively large, subovate in outline, anterior broadly rounded, posterior margins somewhat straighter; dorsum broadly convex; dorsomedian keel highly elevated, having gently concave basal slopes, crest subangular; septum large, extending from apex at about 80 degrees, dorsally convex; growth lines fine, very closely spaced.

**Measurements.**—Because of the fragmentary condition of available specimens of *P. expansa*, measurements are approximate. Examination of figures on plates 39 and 40 of measured specimens will aid in understanding the reliability of measurements listed in table 88.

**Material.**—Most of Emmons' type invertebrate fossils have been lost (Pojeta, written commun., Dec. 1983), and *P. expansa* has no known types. The best preserved specimen known, which shows the greatest number of morphological taxobases, was illustrated by Steele and Sinclair (1971, Pl. 10, figs. 5-7) and is cataloged by the Geological Survey of Canada under GSC 22372. That specimen is herein designated the neotype.

All material studied here is from the USNM collections and the new USGS silicified collections. Specimens assigned to *P. expansa* include those in USGS sample 6034-CO, such as USNM 315532 (pl. 40, fig. 5), USNM 315533 (pl. 39, fig. 11), and USNM 315534 (pl. 40, figs. 6, 7), and a fragment from 6134-CO (USNM 315535, pl. 39, fig. 10). Specimens designated *P. cf. P. expansa* were found in USGS sample 7784-CO, and include USNM 315536 (pl. 40, figs. 1-3) and 315537 (pl. 40, fig. 4). Other specimens designated *P. cf. P. expansa* include USNM 50100 (pl. 39, fig. 12) and 79283 (pl. 39, figs. 6, 7).

**Distribution.**—*P. expansa* has been reported from Blackriveran- to Kirkfieldian-age strata in New York, Ontario, Wisconsin, Illinois, Missouri, New Jersey, and herein from Kentucky. The Kentucky material is from the Tyrone Limestone (6034-CO) (Rocklandian), and from the lowest 3 ft of the Curdsville Limestone Member of the Lexington Limestone (7784-CO and 6134-CO)

(early Kirkfieldian). Specimen USNM 50100 (pl. 39, fig. 12) is from the Murfreesboro Limestone (Blackriveran) at Murfreesboro, Tenn. Specimen USNM 79283 (pl. 39, figs. 6, 7) is from the Curdsville Member of the Lexington Limestone at Curdsville, Ky.

**Comparison.**—*P. expansa* was the first described species of the genus *Pterotheca* in North America. Emmons (1842, p. 397, fig. 109, 2) figured a drawing of an internal mold without a description, placing the new species in the brachiopod genus *Delthyris*. Hall (1861) placed the species in the *Clodermma* Hall, as a gastropod, but did not include a figure and stated only that the species had "great lateral expansion and a very strong dorsal carina" with a shell "length of more than an inch and three-fourths on the carina." Lesley (1889, p. 821) was the first to publish the species under the generic name *Pterotheca*, but did not include a description and used only Emmons' original figure. It should be noted that this original illustration shows a broad specimen having a septal angle of about 85-90 degrees. Raymond (1902) presented a new figure of the species which showed a septal angle of about 81 degrees and stated only: "This obscure fossil is figured here in hope that the attention of other workers will be called to it. Its affinities seem to be rather doubtfully understood." Weller (1903) figured a single fragment having a sharp carina and a septal angle of about 83 degrees.

The first detailed description of *P. expansa* was by Shrock and Raasch (1937, p. 571). The type specimens were not examined and are probably lost; instead, Shrock and Raasch used new material from Wisconsin and the quarries at Kentland, Ind. They said their specimens had an average width of 42 mm, an average length of 32 mm, and a septal angle of 78-82 degrees. They described the two short, diverging, ridgelike supports between the apices of the shell and the septum in *P. expansa*, which had previously been described in *P. attenuata* (Hall, 1861). These authors also used the distance between the lateral edge of the septum and the posterolateral shell margin as a taxobasis. The distance was said to be 7-9 mm in *P. expansa*, only 5 mm in *P. attenuata*, and 10 mm or more in *P. intermedia* Shrock. These authors concluded: "The angle made by the lateral

edges of the septum, the distance from the anterior and lateral margins of the shell to the anterior and lateral edges of the septum, the distance the septum reaches into the cavity, the general outline of the shell, and the convexity of the carinate exterior surface are the features which are of most value in the identification of this form."

Wilson (1951, p. 33) remarked that all known species of *Pterotheca* have been inadequately described and figured owing to poor preservation. She stated: "*Pterotheca expansa*, however, is more explanate than other forms. The sides of the platform make a greater angle than that of *Pterotheca transversa*. The sharp surface ridge seems narrower than that of *Pterotheca saffordi*, and the sides of the interior platform do not seem to be so close to the shell margin." Shrock and Raasch (1937) worked with internal and external molds, but Wilson (1951) had silicified shell material similar to that studied here.

Steele and Sinclair (1971, pl. 10, figs. 5-8) also described *P. expansa* from Wilson's (1951) study area in Ontario, and recognized the species sensu Wilson (1951). Their material is silicified and appears to conform exactly to specimens figured here as *P. expansa*. The form of the dorsal keels, the septa, and the septal angles, the presence of the apical supports, and shell markings are essentially identical in the Ontario and Kentucky specimens. There can be no doubt that the Kentucky specimens are *P. expansa* sensu Wilson, but it is uncertain if they are *P. expansa* sensu Emmons. Most of Emmons' types of invertebrate fossils are lost (Pojeta, written commun., Dec. 1983). Thus, the designation of a neotype for *P. expansa* made above solves a zoological problem by tying the name to a specimen and developing a concept for the species. For most of the time since *P. expansa* was proposed, it has been a popular name to affix to incomplete specimens. Now that its concept has been tied down (Wilson, 1951; Steele and Sinclair, 1971; and herein), its purported wide geographic and stratigraphic ranges can be tested.

*P. expansa* differs from *P. attenuata* (Hall), *P. transversa* Salter, and *P. angusta* Raymond by having a septal angle of about 80 degrees, this being 13-20 degrees greater than in the other species. *P. canaliculata* (Hall) and *P. undulata* apparently have never been figured, so no comparison can be made. From Hall's (1847, pl. 34, fig. 7) illustration of *P. anatifformis* (Hall), that species appears to be quite broad and may be closely related to, or a synonym of, *P. expansa* (Emmons). *P. clochensis* Foerste is quite distinct in its small size and different outline. *P. harviei* has a much lower and more angular keel.

*P. saffordi* (Hall) appears to be more equidimensional than *P. expansa*, but both have a septal angle of about 80-85 degrees, and both have high, subangular to

rounded keels. It appears that the keel of *P. saffordi* arises more abruptly from the lateral slopes (pl. 39, figs. 3, 4), whereas the basal keel slopes of *P. expansa* are more gently concave (pl. 39, figs. 10, 11). *P. saffordi* seems to have a rather more broadly rounded abrupt keel throughout growth, whereas the keel of *P. expansa* is subangular through most of its ontogeny. However, as seen in specimen USNM 315535 (pl. 40, figs. 1-3), in large mature specimens of *P. expansa* the keel appears to become much broader, and is similar to that of *P. saffordi*, but such specimens of *P. expansa* still retain the gently concave basal slopes. The surface markings of *P. saffordi* were described by Hall (1861) as "lamellose-striate" (pl. 39, figs. 1-4, herein), and differ from the shell markings of *P. expansa*, which are fine, closely spaced growth lines (pl. 40, fig. 5; Steel and Sinclair, 1971, pl. 10, figs. 5, 8). Although *P. expansa* and *P. saffordi* are similar morphologically, there are recognizable differences, which I use as species differentia.

**Discussion.**—If all the specimens identified as *P. expansa* or *P. cf. P. expansa* represent a single species, then this species was quite successful, ranging throughout Eastern North America from the Blackriveran to the Kirkfieldian Stages. Throughout this stratigraphic range in the present study area, *P. expansa* is repeatedly associated with leperditiid ostracod assemblages, as is *P. saffordi*. If such an association can be demonstrated to be characteristic of other species of *Pterotheca*, it would have an important bearing on the paleoautecologic interpretations of the taxon.

#### *Pterotheca angusta* Raymond, 1921

Plate 39, figures 8, 9

*Pterotheca angusta* Raymond, 1921, p. 29, pl. 8, fig. 8.

**Diagnosis.**—Shell relatively small (up to 24 mm long), with sharply angular, moderately high dorsal keel; septal angle about 60 degrees.

**Description.**—Shell relatively small for genus, ovate-subquadrangular in outline, anterolateral margins imperfectly known but appear to be quite obtuse; antero-medial sinus shallow; dorsomedian keel moderately high, with sharply angular crest and steep, flat to concave slopes, having an inverted V-shape; septum long but narrow, the sides diverging from the apex at about 60 degrees; dorsolateral shell surface generally of low convexity, the greatest arching over ventral septum, so that margins of septum are deflected dorsally by distinct radial undulation on either side of shell; shell surface with rather widely spaced, weakly undulating, comarginal growth lines.

**Measurements.**—Raymond (1921) gave the length of the holotype (GSC 3266) as 16 mm, with a nearly equal width, and the septal angle as about 60 degrees. The

single specimen identified here as *P. angusta*, USNM 315538, measures as follows: shell length 24 mm, shell width 24.9 mm, maximum keel height above lateral shell slopes 4.5 mm, and septal angle 60 degrees.

*Material*.—Only one specimen was examined, USNM 315538 (pl. 39, figs. 8, 9) from USGS silicified sample 7784-CO from Kentucky.

*Distribution*.—Raymond (1921) reported the holotype from "the highest layers of the Cobourg at Collingwood," Ontario. Sweet and Bergstrom (1971) correlated the Coburgian strata of New York with the Edenian and earliest Maysvillian strata of the type Cincinnati section of the present study area. The single specimen found in the USGS silicified samples from Kentucky is from the basal 2 ft of the Curdsville Limestone Member of the Lexington Limestone (early Kirkfieldian) (7784-CO).

*Comparison*.—This species is immediately separable from other species of the study area by its narrow septal angle of about 60 degrees and its very narrow, sharply angular dorsomedian keel (pl. 39, figs. 8, 9).

The only other species of *Pterotheca* that has a comparatively low septal angle is *P. attenuata*, that also being about 60 degrees. Hall (1861), in discussing *P. attenuata* (Hall), stated, "This species closely resembles *P. canaliculata* in form, but has no depressions of the shell parallel to the sides, and the surface is apparently less distinctly striated." There are no known illustrations of *P. canaliculata* (Hall) for comparison with *P. attenuata*, but the differences stated by Hall are probably due to preservation, and the two species names may be synonyms. In any case, *P. attenuata* is probably closely related to *P. angusta*, as shown by their common possession of extremely acute septal angles.

*Discussion*.—This report of *P. angusta* from the Kirkfieldian strata of Kentucky is only the second known occurrence of the species. The two occurrences are widely separated geographically and stratigraphically, the first being in the latest Edenian or earliest Maysvillian of Ontario, but the diagnostic morphologic features of the two specimens are in close agreement.

#### *Pterotheca harviei* Foerste, 1924

Plate 26, figures 9, 10

*Pterotheca harviei* Foerste, 1924, p. 219, pl. 26, fig. 6.

*Diagnosis*.—Shell large (up to 60 mm long), broadly ovate in outline; dorsomedian keel of moderate height, with sharply angular crest and flat slopes; septal angle about 85 degrees; shell surface marked by broadly rounded, gently undulating rugose growth increments.

*Description*.—Shell relatively large, broadly ovate-subtriangular in outline, with moderately low convexity; anterolateral margins broadly rounded, posterolateral margins nearly straight but slightly convex; beak area

not particularly protuberant but moderately incurved; median sinus fairly deep; dorsomedian keel of moderate height, but rather low compared with width of shell, with sharply angular crest and flat slopes having inverted V-shape; septum large, lateral margins diverging from apex at about 85 degrees and curving outward slightly; shell surface marked by low but distinct, broad, comarginal rugae.

*Measurements*.—Foerste (1924) gave the following approximate measurements for the species: shell length 60 mm, shell width 75 mm, length of lateral margins of septum 40 mm, and septal angle 98 degrees. This measurement of the septal angle appears to be in error, as the septal angle of the holotype on his plate 26, figure 6, measures about 85 degrees.

The single specimen examined here also yields only approximate measurements: shell length 31 mm, shell width 50 mm, length of lateral septum margins 28 mm, and septal angle 85 degrees.

*Material*.—The specimen identified here as *P. harviei*, USNM 50092 (pl. 26, figs. 9, 10), is a composite mold, possibly retaining some shell and coated by a thin, resistant, glossy layer that probably consists mainly of residual organic matter. As Wilson (1951) pointed out, the line of attachment of the septum with the shell is a thickening of the shell, which leaves a narrow groove on internal molds, such as seen in this specimen. The specimen is embedded in gray micrite.

*Distribution*.—Foerste (1924) originally described *P. harviei* from "two miles northwest of St. Hughes on Yamaska, in the *Cryptolithus* zone of the Lorraine Formation," in Ontario, Canada. The specimen figured here is from the Kope Formation at Covington, Ky. Both occurrences are Edenian in age (lower Upper Ordovician).

*Comparison*.—The Kentucky specimen agrees well with the holotype of *P. harviei* (as figured by Foerste, 1924, p. 219, pl. 26, fig. 6), the two having shell length/width ratios of 1.29 and 1.25, respectively, septal angles of about 85 degrees, and similar shell outlines and keel forms. Foerste (1924) stated, "*P. harviei* resembles *P. saffordi* most nearly in outline, but is a much larger species, of less convexity, and the median carina is relatively narrower and less strongly elevated."

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## APPENDIX: LOCALITY REGISTER

During the geologic mapping of the State of Kentucky by the Kentucky and U.S. Geological Surveys, Ordovician fossils were collected from nearly 1,100 localities. Pojeta (1979, p. A19-A46) listed 317 of these localities from which Ordovician fossils were collected and studied. Coordinates for the localities use the system of Pojeta (1979, p. A19). Below is a list of the USGS localities from which the fossils studied for this report were collected. The localities are arranged sequentially by collection number assigned to each in the USGS register of Cambrian and Ordovician localities (-CO). The following abbreviations are used in this locality listing for convenience: C.n., Collection number; G.l., Geographic location; C., Coordinates; F., Formation; S.p., Stratigraphic position; Q.n., 7.5 min quadrangle name; S.n., Section name; S.no., Section number. Not all localities have information in all categories. Do., ditto.

## U.S. GEOLOGICAL SURVEY LOCALITIES

- |  |         |  |  |
|--|---------|--|--|
| C.n. — 4073-CO.  |         |  | ern termination of Kentucky Route 595 at Kentucky River. |
| G.l. — Proceed east from Milner, Ky., 0.75 mi and turn right (southwest) on Shryock Ferry Road. Continue down Shryock Ferry Road about 1 mi to top of section. | C. —    | Base of section at 19 mm east, 176 mm north.   |  |
| C. — 153 mm east, 99 mm north (base of section at 134 mm east, 87 mm north).   | F. —    | Grier Limestone Member, Lexington Limestone.   |  |
| F. — Grier Limestone Member, Lexington Limestone.  | S.p. —  | 30 ft above base of section.   |  |
| S.p. — 148 ft above base of Curdsville Limestone Member, Lexington Limestone.  | Q.n. —  | Valley View, Ky.   |  |
| Q.n. — Tyrone, Ky.   | S.n. —  | Valley View C (Antioch Church Road).   |  |
| S.n. — Tyrone A.   | S.no. — | 180.   |  |
| S.no. — 89.  |         |  |  |
| C.n. — 4852-CO.  | C.n. —  | 4876-CO.   |  |
| G.l. — Section along Interstate 75, 1.4 mi south of Georgetown, Ky., exit.   | G.l. —  | Name as for 4874-CO.   |  |
| C. — 364 mm east, 321 mm north.  | C. —    | Do.  |  |
| F. — Grier Limestone Member, Lexington Limestone.  | F. —    | Grier Limestone Member, Lexington Limestone.   |  |
| S.p. — 25 ft below top of Grier Limestone Member.  | S.p. —  | 35 ft above base of section.   |  |
| Q.n. — Georgetown, Ky.   | Q.n. —  | Valley View, Ky.   |  |
| S.n. — Georgetown A.   | S.n. —  | Valley View C (Antioch Church Road).   |  |
| S.no. — 151.   | S.no. — | 180.   |  |
| C.n. — 4865-CO.  | C.n. —  | 4879-CO.   |  |
| G.l. — U.S. Route 62 at crossing of Kentucky River; from east side of Blackburn Memorial Bridge, take side road north 0.1 mi to railroad roadcut exposure.     | G.l. —  | Same as for 4874-CO.   |  |
| C. — Base of section at 108 mm east, 197 mm north.   | C. —    | Do.  |  |
| F. — Logana Member, Lexington Limestone.   | F. —    | Grier Limestone Member, Lexington Limestone.   |  |
| S.p. — Lower 12 ft of Logana Member.   | S.p. —  | 43-45 ft above base of section.  |  |
| Q.n. — Tyrone, Ky.   | Q.n. —  | Valley View, Ky.   |  |
| S.n. — Tyrone C, or Ky. Utilities Plant.   | S.n. —  | Valley View C (Antioch Church Road).   |  |
| S.no. — 174.   | S.no. — | 180.   |  |
| C.n. — 4874-CO.  | C.n. —  | 4880-CO.   |  |
| G.l. — Road exposures between Trinity Church and Antioch Church, southwest quadrant, Valley View quadrangle, Kentucky, 1 mi southwest of north-                | G.l. —  | Same as for 4874-CO.   |  |
|  | C. —    | Do.  |  |
|  | F. —    | Grier Limestone Member, Lexington Limestone.   |  |
|  | S.p. —  | 47 ft above base of section.   |  |
|  | Q.n. —  | Valley View, Ky.   |  |
|  | S.n. —  | Valley View C (Antioch Church Road).   |  |
|  | S.no. — | 180.   |  |
|  | C.n. —  | 4883-CO.   |  |
|  | G.l. —  | Same as for 4874-CO.   |  |
|  | p. —    | Do.  |  |
|  | F. —    | Grier Limestone Member, Lexington Limestone.   |  |
|  | S.p. —  | 60.5 ft above base of section.   |  |
|  | Q.n. —  | Valley View, Ky.   |  |
|  | S.n. —  | Valley View C (Antioch Church Road).   |  |
|  | S.no. — | 180.   |  |
|  | C.n. —  | 4928-CO.   |  |
|  | G.l. —  | Road exposure 0.5 mi east and 1.6 mi south of northwestern corner of Salvisa quadrangle, Kentucky. |  |
|  | C. —    | 32 mm east, 467 mm north.  |  |
|  | F. —    | Grier Limestone Member, Lexington Limestone.   |  |
|  | S.p. —  | 22 ft below base of Brannon Member, Lexington Limestone.   |  |
|  | Q.n. —  | Salvisa, Ky.   |  |
|  | S.n. —  | Salvisa A.   |  |
|  | S.no. — | 175.   |  |
|  | C.n. —  | 4929-CO.   |  |
|  | G.l. —  | Same as for 4928-CO.   |  |
|  | C. —    | Do.  |  |
|  | F. —    | Grier Limestone Member, Lexington Limestone.   |  |
|  | S.p. —  | 8 ft below base of Brannon Member, Lexington Limestone.  |  |
|  | Q.n. —  | Salvisa, Ky.   |  |
|  | S.n. —  | Salvisa A.   |  |

- S.no. — 175.
- C.n. — 4940-CO.
- G.l. — Road exposure on western side of Kentucky River at bridge crossing of Central Kentucky Parkway on northern side of parkway.
- C. — Base of section at 186 mm east, 508 mm north.
- F. — Curdsville Limestone Member, Lexington Limestone.
- S.p. — 7 ft above top of Tyrone Limestone.
- Q.n. — Salvisa, Ky.
- S.n. — Salvisa B.
- S.no. — 176.
- C.n. — 4959-CO.
- G.l. — Same as for 4940-CO.
- C. — Do.
- F. — Grier Limestone Member, Lexington Limestone.
- S.p. — 149–152 ft above top of Tyrone Limestone.
- Q.n. — Salvisa, Ky.
- S.n. — Salvisa B.
- S.no. — 176.
- C.n. — 5015-CO.
- G.l. — Quarry exposure 0.4 mi south of Perryville, Ky., on eastern side of Mitchellsburg Road, eastern side of Chaplin River.
- C. — 191 mm east, 92 mm north.
- F. — Salvisa Bed, Perryville Limestone Member, Lexington Limestone.
- S.p. — 5 ft above base of Salvisa Bed.
- Q.n. — Perryville, Ky.
- S.n. — Perryville B (Perryville South)
- S.no. — 30 B.
- C.n. — 5016-CO.
- G.l. — Same as for 5015-CO.
- C. — Do.
- F. — Cornishville Bed, Perryville Limestone Member, Lexington Limestone.
- S.p. — 14 ft above base of Salvisa Bed, Perryville Limestone Member, Lexington Limestone.
- Q.n. — Perryville, Ky.
- S.n. — Perryville B (Perryville South).
- S.no. — 30 B.
- C.n. — 5022-CO.
- G.l. — Section in quarry and road exposures near Clear Creek, 0.2 mi east and 2.5 mi south of northwestern corner of Keene quadrangle, Kentucky.
- C. — Base of section at 21 mm east, 326 mm north.
- F. — Curdsville Limestone Member, Lexington Limestone.
- S.p. — Float from lower 22 ft of Curdsville Limestone Member.
- Q.n. — Keene, Ky.
- S.n. — Keene A.
- S.no. — 150.
- C.n. — 5023-CO.
- G.l. — Same as for 5022-CO.
- C. — Do.
- F. — Curdsville Limestone Member, Lexington Limestone.
- S.p. — 30 ft above base of Curdsville Limestone Member.
- Q.n. — Keene, Ky.
- S.n. — Keene A.
- S.no. — 150.
- C.n. — 5024-CO.
- G.l. — Same as for 5022-CO.
- C. — Do.
- F. — Logana Member, Lexington Limestone.
- S.p. — Float from lower Logana Member.
- Q.n. — Keene, Ky.
- S.n. — Keene A.
- S.no. — 150.
- C.n. — 5036-CO.
- G.l. — Small stream exposure on Squires Road, 1.8 mi southwest of intersection with U.S. Route 421 (upstream 0.1 mi).
- C. — 151 mm east, 494 mm north.
- F. — Devils Hollow Member, Lexington Limestone.
- S.p. — 60 ft above base of Brannon Member, Lexington Limestone.
- Q.n. — Coletown, Ky.
- C.n. — 5067-CO.
- G.l. — Hillside pasture exposure on western side of U.S. Route 227, 0.4 mi south of intersection of Ford-Hampton Road and U.S. 227, north of Ford, Ky.
- C. — 423 mm east, 187 mm north.
- F. — Grier Limestone Member, Lexington Limestone.
- S.p. — 140 ft above top of Tyrone Limestone.
- Q.n. — Ford, Ky.
- C.n. — 5072-CO.
- G.l. — Immediately behind Old Crow Distillery, northern bluff of Glenns Creek Road, 0.7 mi west of intersection with Hanley Lane.
- C. — 107 mm east, 102 mm north.
- F. — Lower Lexington Limestone; mostly basal Curdsville Limestone Member, but with some float blocks of Logana Member included in sample.
- Q.n. — Frankfort East, Ky.
- S.n. — Frankfort East B.
- S.no. — 87.
- C.n. — 5073-CO.
- G.l. — Northwest of Old Crow Distillery on first sharp north bend of Glenns Creek Road, 0.9 mi west of intersection with Hanley Lane.
- C. — 82 mm east, 111 mm north.
- F. — Upper Logana Member, Lexington Limestone.
- S.p. — Just below 4-ft-thick dalmanellid coquina.
- Q.n. — Frankfort East, Ky.
- S.n. — Frankfort East B.
- S.no. — 87.
- C.n. — 5074-CO.
- G.l. — Small quarry on western side of Tates Creek Pike, north of Gainesway, Ky., and 2 mi south of intersection with Cooper Road.
- C. — 15.5 mm east, 545 mm north.
- F. — Grier Limestone Member, Lexington Limestone.
- S.n. — Tates Creek Rd. quarry.

- C.n. — **5075-CO.**  
 G.l. — 2d Quarry, Jessamine Creek, southeast of Wilmore, Ky.  
 C. — 372 mm east, 425.5 mm north.  
 F. — Tyrone Limestone.  
 S.p. — Tyrone Limestone.  
 Q.n. — Wilmore, Ky.
- C.n. — **5080-CO.**  
 G.l. — First crossing of Southern Railroad tracks by unnamed road running due south from two right-angle turns in Kentucky Route 342, 1.2 mi west of Herrington Lake spillway.  
 C. — 88 mm east, 158 mm north.  
 F. — Upper part of Curdsville Limestone Member, Lexington Limestone.  
 Q.n. — Wilmore, Ky.
- C.n. — **5084-CO.**  
 G.l. — From eastern side of Blackburn Memorial Bridge crossing Kentucky River, take first road north toward Kentucky Utilities Plant; section in railroad and road exposures.  
 C. — 108 mm east, 214 mm north (railroad exposures).  
 F. — Curdsville Limestone Member, Lexington Limestone.  
 S.p. — 5 ft above base of Curdsville Limestone Member.  
 Q.n. — Tyrone, Ky.  
 S.n. — Tyrone C, or Ky. Utilities Plant.  
 S.no. — 174.
- C.n. — **5085-CO**  
 G.l. — Same as for 5084-CO.  
 C. — Do.  
 F. — Curdsville Limestone Member, Lexington Limestone.  
 S.p. — 16 ft above Tyrone-Lexington contact.  
 Q.n. — Tyrone, Ky.  
 S.n. — Tyrone C, or Ky. Utilities Plant.  
 S.no. — 174.
- C.n. — **5086-CO.**  
 G.l. — Same as for 5084-CO.  
 C. — Do.  
 F. — Logana Member, Lexington Limestone.  
 S.p. — 18–20 ft above base of Logana Member.  
 Q.n. — Tyrone, Ky.  
 S.n. — Tyrone C.  
 S.no. — 174.
- C.n. — **5087-CO.**  
 G.l. — Small road exposure on U.S. Route 421, 0.5 mi east of U.S. Routes 60 and 421 junction.  
 C. — 242 mm east, 287 mm north.  
 F. — Upper part of Devils Hollow Member, Lexington Limestone.  
 Q.n. — Frankfort East, Ky.
- C.n. — **5091-CO.**  
 G.l. — Behind Old Stagg Distillery, north of lock 4 on Kentucky River.  
 C. — 3.5 mm east, 434 mm north.  
 F. — Logana Member, Lexington Limestone.  
 S.p. — 20 ft above base of Logana Member.  
 Q.n. — Frankfort East, Ky.
- S.n. — Stagg Distillery.
- C.n. — **5092-CO.**  
 G.l. — Same as for 5084-CO.  
 C. — 108 mm east, 197 mm north.  
 F. — Logana Member, Lexington Limestone.  
 S.p. — 10–12 ft above base of Logana Member.  
 Q.n. — Tyrone, Ky.  
 S.n. — Tyrone C, or Ky. Utilities Plant.  
 S.no. — 174.
- C.n. — **5094-CO.**  
 G.l. — Roadcuts along Devils Hollow Road, 0.7 mi south of Buttimer Hill.  
 C. — 411 mm east, 318 mm north.  
 F. — Grier Limestone Member, Lexington Limestone.  
 S.p. — Float 45 ft above Macedonia Bed.  
 Q.n. — Frankfort West, Ky.  
 S.n. — Devils Hollow Road.
- C.n. — **5095-CO.**  
 G.l. — Road exposure on northern side of westbound lanes of Interstate 64, 0.5 mi east of bridge over Kentucky River.  
 C. — 123 mm east, 195 mm north.  
 F. — Devils Hollow Member, Lexington Limestone.  
 S.p. — 6–8 ft above base of Devils Hollow Member.  
 Q.n. — Frankfort East, Ky.  
 S.n. — Frankfort East A.  
 S.no. — 86.
- C.n. — **5096-CO.**  
 G.l. — Just before ferry crossing of Tates Creek Road and Kentucky River, take road west toward Daniel Boone YMCA Camp; collection from near top of northern bluff of Kentucky River, 0.4 mi south-east of YMCA Camp, in abandoned railroad bed.  
 C. — 151 mm east, 432 mm north.  
 F. — Grier Limestone Member, Lexington Limestone.  
 Q.n. — Valley View, Ky.
- C.n. — **5099-CO.**  
 G.l. — Roadcuts along Hunters Ferry Road, 0.85 mi north-east of Trinity Church.  
 C. — 54 mm east, 262 mm north.  
 F. — Grier Limestone Member, Lexington Limestone.  
 S.p. — 78–80 ft above base of section.  
 Q.n. — Valley View, Ky.  
 S.n. — Hunters Ferry Road (Valley View B).  
 S.no. — 34.
- C.n. — **5100-CO.**  
 G.l. — Crisman Mill Road, 0.2 mi west of Hickman Creek crossing.  
 C. — 411 mm east, 451 mm north.  
 F. — Lower part of Curdsville Limestone Member, Lexington Limestone.  
 Q.n. — Little Hickman, Ky.  
 S.n. — Little Hickman B.
- C.n. — **5101-CO.**  
 G.l. — Kentucky Route 169 just west of Hickman Creek crossing.  
 C. — 398 mm east, 81 mm north.

- F. — Lower part of Curdsville Limestone Member, Lexington Limestone.  
 Q.n. — Nicholasville, Ky.
- C.n. — **5107-CO.**  
 G.l. — Hillside exposure in farm road leading south from U.S. Route 60, just west of Keeneland Racetrack; collected at 900-ft contour.  
 C. — 43 mm east, 194 mm north.  
 F. — Grier Limestone Member, Lexington Limestone.  
 Q.n. — Lexington West, Ky.
- C.n. — **6034-CO.**  
 G.l. — Section on New Watts Mill Road, 0.1 mi southwest of intersection with Kentucky Route 39.  
 C. — Base of section at 260 mm east, 346 mm north.  
 F. — Tyrone Limestone.  
 S.p. — 112 ft above base of section.  
 Q.n. — Little Hickman, Ky.  
 S.n. — Little Hickman A.
- C.n. — **6035-CO.**  
 G.l. — Same as for 6034-CO.  
 C. — Do.  
 F. — Tyrone Limestone.  
 S.p. — 89–94 ft above base of section.  
 Q.n. — Little Hickman, Ky.  
 S.n. — Little Hickman A.
- C.n. — **6127-CO.**  
 G.l. — Southernmost tributary of Landing Run, 2,000 ft east of intersection of U.S. Route 31E and Kentucky Route 46, between Balltown and Culver-town, Ky.  
 C. — 381 mm east, 436 mm north.  
 F. — Rowland Member, Drakes Formation.  
 Q.n. — New Haven, Ky.
- C.n. — **6128-CO.**  
 G.l. — Outcrop at farm pond 2,000 ft west of intersection of Mt. Horeb and Carrick Roads, 1,000 ft north of Carrick Road.  
 C. — 183 mm east, 387 mm north.  
 F. — Tongue of Clays Ferry Formation between underlying Millersburg Member, Lexington Limestone, and overlying Tanglewood Limestone Member, Lexington Limestone.  
 S.p. — 5–10 ft above base of Clays Ferry Formation tongue, 15–20 ft above *Allonychia flanaganesis* zone in Millersburg Member.  
 Q.n. — Centerville, Ky.
- C.n. — **6131-CO.**  
 G.l. — Section on Kentucky Route 33 just north of bridge crossing of Mocks Branch, 2.5 mi north of Danville, Ky.  
 C. — 405 mm east, 307 mm north.  
 F. — Upper part of Curdsville Member, Lexington Limestone.  
 S.p. — 23 ft above Tyrone Limestone-Lexington Limestone contact.  
 Q.n. — Danville, Ky.  
 C.n. — **6134-CO.**
- G.l. — Road exposures 0.2 mi west of Dix River crossing of Kentucky Route 52.  
 C. — 315 mm east, 78 mm north.  
 F. — Curdsville Limestone Member, Lexington Limestone.  
 S.p. — Lower 3 ft of Curdsville Limestone Member.  
 Q.n. — Bryantsville, Ky.  
 S.n. — Bryantsville D.
- C.n. — **6136-CO.**  
 G.l. — Roadcut on Kentucky Route 52, 1.45 mi east of junction with U.S. Route 150; 0.15 mi east of crossing of Kentucky Route 52 and Balls Branch Run.  
 C. — 74 mm east, 35 mm north.  
 F. — Faulconer Bed, Perryville Limestone Member, Lexington Limestone.  
 S.p. — Basal 3–4 ft of Perryville Limestone Member, immediately above Tanglewood Limestone Member, Lexington Limestone.  
 Q.n. — Bryantsville, Ky.  
 S.n. — Bryantsville B.
- C.n. — **6138-CO.**  
 G.l. — Same as for 6136-CO.  
 C. — Do.  
 F. — Cornishville Bed, Perryville Limestone Member, Lexington Limestone.  
 S.p. — 16 ft above Perryville Limestone Member-Tanglewood Limestone Member contact.  
 Q.n. — Bryantsville, Ky.  
 S.n. — Bryantsville B.
- C.n. — **6139-CO.**  
 G.l. — Southern bank of Salt Creek, 900 ft upstream from covered bridge on Enochsburg-Oldenburg (Ind.) Road.  
 C. — 328 mm east, 378 mm north.  
 F. — Upper part of Dillsboro Formation.  
 Q.n. — New Point, Ind.
- C.n. — **6140-CO.**  
 G.l. — Northern bank of Salt Creek, 0.4 mi upstream from covered bridge on Enochsburg-Oldenburg (Ind.) Road.  
 C. — 315 mm east, 380 mm north.  
 F. — Upper part of Dillsboro Formation.  
 Q.n. — New Point, Ind.
- C.n. — **6142-CO.**  
 G.l. — Road exposure on eastern side of Kentucky Route 982, 0.4 mi south of junction of Kentucky Routes 32, 36, and 982 in Cynthiana, Ky. (across from River View Mission and Liggett and Meyers tobacco warehouse).  
 C. — 290 mm east, 39 mm north.  
 F. — Lower tongue of Clays Ferry Formation.  
 S.p. — 18–20 ft above base of section.  
 Q.n. — Cynthiana, Ky.
- C.n. — **6143-CO.**  
 G.l. — Same as for 6142-CO.  
 C. — Do.  
 F. — Upper tongue of Clays Ferry Formation.  
 S.p. — 30–35 ft above base of section.

- Q.n. — Cynthiana, Ky.
- C.n. — **6144-CO.**  
G.l. — Same as for 6142-CO.  
C. — Do.  
F. — Base of upper tongue of Millersburg Member, Lexington Limestone.  
S.p. — 24 ft above base of section.  
Q.n. — Cynthiana, Ky.
- C.n. — **6145-CO.**  
G.l. — Kentucky Route 8, 1 mi south of Carntown, Ky.  
C. — 28 mm east, 326 mm north.  
F. — Point Pleasant Tongue, Clays Ferry Formation.  
S.p. — About 50 ft below base of Kope Formation.  
Q.n. — Moscow, Ohio-Kentucky.
- C.n. — **6411-CO.**  
G.l. — U.S. Route 27, 0.1 mi northeast of crossing of Dix River.  
C. — 42.5 mm east, 342 mm north.  
F. — Gilbert Member, Ashlock Formation.  
S.p. — 5 ft above base of Gilbert Member.  
Q.n. — Lancaster, Ky.  
S.n. — Ashlock Cemetery.  
S.no. — 21 B.
- C.n. — **6412-CO.**  
G.l. — Same as for 6411-CO.  
C. — Do.  
F. — Gilbert Member, Ashlock Formation.  
S.p. — 11.5 ft above base of Gilbert Member.  
Q.n. — Lancaster, Ky.  
S.n. — Ashlock Cemetery.  
S.no. — 21 B.
- C.n. — **6414-CO.**  
G.l. — Exposures of Kentucky Route 21, 0.9 mi south of junction of Walnut Meadow Branch and Paint Lick Creek.  
C. — 18 mm east, 372 mm north.  
F. — Gilbert Member, Ashlock Formation.  
S.p. — 1-2-ft silicified zone at top of Gilbert Member.  
Q.n. — Berea, Ky.
- C.n. — **6419-CO.**  
G.l. — 1.4 mi east of Wilmore, Ky., 500 ft north of main road.  
C. — 420 mm east, 534 mm north.  
F. — Lower part of Logana Member, Lexington Limestone.  
Q.n. — Wilmore, Ky.
- C.n. — **6915-CO.**  
G.l. — Boyle County quarry, western side of U.S. Route 68, 1.3 mi northeast of Perryville, Ky.  
C. — p17 mm east, 176 mm north.  
F. — Salvisa Bed, Perryville Limestone Member, Lexington Limestone.  
S.p. — Basal 2 ft of Salvisa Bed; northwestern wall of quarry.  
Q.n. — Perryville, Ky.  
S.n. — Perryville A (Perryville North).
- S.no. — 30 A.
- C.n. — **6916-CO.**  
G.l. — Same as for 6915-CO.  
C. — Do.  
F. — Salvisa Bed, Perryville Limestone Member, Lexington Limestone.  
S.p. — Same as for 6915-CO, but from eastern wall of quarry.  
Q.n. — Perryville, Ky.  
S.n. — Perryville A (Perryville North).  
S.no. — 30 A.
- C.n. — **6990-CO.**  
G.l. — Western side of U.S. Route 27, 1,700 ft from highway, 0.9 mi south of Lair, Ky.  
C. — 245 mm east, 369 mm north.  
F. — Top of tongue of Clays Ferry Formation, which lies between a lower tongue of Millersburg Member, Lexington Limestone, and an upper tongue of Tanglewood Limestone Member, Lexington Limestone.  
S.p. — 60 ft above top of Grier Limestone Member, Lexington Limestone.  
Q.n. — Shawhan, Ky.  
S.n. — Section at White Farm.
- C.n. — **7044-CO.**  
G.l. — 0.7 mi southwest of junction of Kentucky Route 974 and Dry Fork Road on Dry Fork Road. Section begins in valley of East Fork of Fourmile Creek in Tanglewood Limestone Member, Lexington Limestone, just below *Allonychia flanaganesis* zone of Millersburg Member, Lexington Limestone. Main part of section is north of East Fork, along Dry Fork Road above 823-ft elevation mark.  
C. — Base of section at 394 mm east, 268 mm north.  
F. — Tongue of Clays Ferry Formation.  
S.p. — 25 ft above *Allonychia flanaganesis* horizon.  
Q.n. — Winchester, Ky.  
S.n. — Winchester A (Dry Fork Road).  
S.no. — 1004.
- C.n. — **7343-CO.**  
G.l. — Same as for 6990-CO.  
C. — Do.  
F. — Top of tongue of Clays Ferry Formation, which lies between a lower tongue of Millersburg Member, Lexington Limestone, and an upper tongue of Tanglewood Limestone Member, Lexington Limestone.  
S.p. — 60 ft above top of Grier Limestone Member, Lexington Limestone.  
Q.n. — Shawhan, Ky.  
S.n. — Section at White Farm.
- C.n. — **7344-CO.**  
G.l. — Eastern side of U.S. Route 27, 900 ft from highway, 0.4 mi north of Lair, Ky.  
C. — 246 mm east, 439 mm north.  
F. — Near top of lower tongue of Millersburg Member, Lexington Limestone.  
Q.n. — Shawhan, Ky.



- C.n. — **7345-CO.**  
 G.l. — Same as for 6142-CO.  
 C. — Do.  
 F. — Lower tongue of Clays Ferry Formation.  
 S.p. — 20–22 ft above base of section.  
 Q.n. — Cynthiana, Ky.
- C.n. — **7348-CO.**  
 G.l. — 4,300 ft east and 6,300 ft south of northwestern corner of Shawhan quadrangle.  
 C. — 54 mm east, 493 mm north.  
 F. — Tongue of Clays Ferry Formation underlain by tongue of Millersburg Member, Lexington Limestone, and overlain by tongue of Tanglewood Limestone Member, Lexington Limestone.  
 S.p. — Float, 4 ft above 810-foot contour.  
 Q.n. — Shawhan, Ky.
- C.n. — **7349-CO.**  
 G.l. — Same as for 7348-CO.  
 C. — Do.  
 F. — Do.  
 S.p. — Float, 5 ft above 810-ft contour.  
 Q.n. — Shawhan, Ky.
- C.n. — **7350-CO.**  
 G.l. — Same as for 7348-CO.  
 C. — Do.  
 F. — Do.  
 S.p. — Float, 6 ft above 810-foot contour.  
 Q.n. — Shawhan, Ky.
- C.n. — **7353-CO.**  
 G.l. — 1 mi northeast of junction of Cook Road and Lair Road in stock pond.  
 C. — 428 mm east, 471 mm north.  
 F. — Lower tongue of Millersburg Member, Lexington Limestone.  
 Q.n. — Shawhan, Ky.
- C.n. — **7450-CO.**  
 G.l. — Section along road to U.S. Route 25, 0.4 mi west of Sadieville, Ky.  
 C. — Base of section at 295 mm east, 63 mm north.  
 F. — Tongue of Clays Ferry Formation.  
 S.p. — 5 ft above base of section.  
 Q.n. — Sadieville, Ky.  
 S.n. — Sadieville C.  
 S.no. — 192.
- C.n. — **7452-CO.**  
 G.l. — Same as for 7450-CO.  
 C. — Do.  
 F. — Tongue of Clays Ferry Formation.  
 S.p. — 10 ft above base of section.  
 Q.n. — Sadieville, Ky.  
 S.n. — Sadieville C.  
 S.no. — 192.
- C.n. — **7454-CO.**  
 G.l. — Same as for 7450-CO.  
 C. — Do.  
 F. — Millersburg Member, Lexington Limestone.
- S.p. — 20 ft above base of section.  
 Q.n. — Sadieville, Ky.  
 S.n. — Sadieville C.  
 S.no. — 192.
- C.n. — **7455-CO.**  
 p.l. — Same as for 7450-CO.  
 C. — Do.  
 F. — Millersburg Member, Lexington Limestone.  
 S.p. — 22 ft above base of section.  
 Q.n. — Sadieville, Ky.  
 S.n. — Sadieville C.  
 S.no. — 192.
- C.n. — **7457-CO.**  
 G.l. — Same as for 7450-CO.  
 C. — Do.  
 F. — Millersburg Member, Lexington Limestone.  
 S.p. — 32 ft above base of section.  
 Q.n. — Sadieville, Ky.  
 S.n. — Sadieville C.  
 S.no. — 192.
- C.n. — **7458-CO.**  
 G.l. — Same as for 7450-CO.  
 C. — Do.  
 F. — Tongue of Clays Ferry Formation.  
 S.p. — 35 ft above base of section.  
 Q.n. — Sadieville, Ky.  
 S.n. — Sadieville C.  
 S.no. — 192.
- C.n. — **7461-CO.**  
 G.l. — Same as for 7450-CO.  
 C. — Do.  
 F. — Tongue of Clays Ferry Formation.  
 S.p. — 50–55 ft above base of section.  
 Q.n. — Sadieville, Ky.  
 S.n. — Sadieville C.  
 S.no. — 192.
- C.n. — **7782-CO.**  
 G.l. — Same as for 5084-CO.  
 C. — Do.  
 F. — Curdsville Limestone Member, Lexington Limestone.  
 S.p. — Lower 5 ft of Curdsville Limestone Member.  
 Q.n. — Tyrone, Ky.  
 S.n. — Tyrone C, or Ky. Utilities Plant.  
 S.no. — 174.
- C.n. — **7783-CO.**  
 G.l. — Southern side of westbound lanes of Interstate 64, 0.5 mi south of bridge across Kentucky River.  
 C. — 123 mm east, 195 mm north.  
 F. — Top bed, upper tongue of Tanglewood Limestone Member, Lexington Limestone.  
 S.p. — Tanglewood Limestone Member, just below Devils Hollow Member, Lexington Limestone.  
 Q.n. — Frankfort East, Ky.  
 S.n. — Frankfort East A.  
 S.no. — 86.

- C.n. — **7784-CO.**  
 G.l. — U.S. Route 27, 0.3 mi southeast of crossing of Kentucky River bridge on southern side of road.  
 C. — 41 mm east, 75 mm north.  
 F. — Curdsville Limestone Member, Lexington Limestone.  
 S.p. — Basal 2 ft of Curdsville Limestone Member.  
 Q.n. — Little Hickman, Ky.
- C.n. — **7785-CO.**  
 G.l. — Same as for 7784-CO.  
 C. — Do.  
 F. — Curdsville Limestone Member, Lexington Limestone.  
 S.p. — 11-12 ft above base of Curdsville Limestone Member.  
 Q.n. — Little Hickman, Ky.
- C.n. — **7787-CO.**  
 G.l. — Southern side of westbound lanes of Interstate 64, about 0.8 mi east of bridge over Kentucky River.  
 C. — 123 mm east, 195 mm north.  
 F. — Top bed of upper tongue of Tanglewood Limestone Member, Lexington Limestone.  
 Q.n. — Frankfort East, Ky.  
 S.n. — Frankfort East A.  
 S.no. — 86.
- C.n. — **7789-CO.**  
 G.l. — Northern and southern sides of eastbound lanes of Interstate 64, 0.8 mi east of Kentucky River.  
 C. — 123 mm east, 195 mm north.  
 F. — Upper part of Devils Hollow Member, Lexington Limestone.  
 Q.n. — Frankfort East, Ky.  
 S.n. — Frankfort East A.  
 S.no. — 86.
- C.n. — **7791-CO.**  
 G.l. — Same as for 4940-CO.  
 C. — Do.  
 F. — Lower part of Logana Member, Lexington Limestone.  
 S.p. — 35 ft above Tyrone Limestone-Lexington Limestone contact.  
 Q.n. — Salvisa, Ky.  
 S.n. — Salvisa B.  
 S.no. — 176.
- C.n. — **7796-CO.**  
 G.l. — Exposures on Interstate 75, 1.3 mi south of exit to Kentucky Route 418.  
 C. — 434 mm east, 313 mm north.  
 F. — Lowermost tongue of Tanglewood Limestone Member, Lexington Limestone, below Brannon Member, Lexington Limestone.  
 S.p. — 3-9 ft above base of Cane Run Bed, Grier Limestone Member, Lexington Limestone.  
 Q.n. — Coletown, Ky.
- C.n. — **7809-CO.**  
 G.l. — 75 ft south of junction of Kentucky Route 388 and U.S. Route 227.  
 C. — 384 mm east, 113 mm north.
- F. — Tanglewood Limestone Member, Lexington Limestone.  
 S.p. — First bed above Brannon Member-Tanglewood Limestone Member contact.  
 Q.n. — Ford, Ky.  
 S.n. — Boonesboro Beach.
- C.n. — **7812-CO.**  
 G.l. — Farm pond 250 ft west of U.S. Route 27, 500 ft south of junction of U.S. Routes 27 and 62.  
 C. — 220 mm east, 548 mm north.  
 F. — Clays Ferry Formation.  
 Q.n. — Shawhan, Ky.
- C.n. — **7817-CO.**  
 G.l. — Section on Kentucky Route 39, 0.3 mi southeast of Black Bridge crossing over Hickman Creek.  
 C. — Base of section at 260 mm east, 346 mm north.  
 F. — Curdsville Limestone Member, Lexington Limestone.  
 S.p. — 6 in above contact of Tyrone Limestone and Curdsville Member, Lexington Limestone.  
 Q.n. — Little Hickman, Ky.  
 S.n. — Little Hickman A.
- C.n. — **7843-CO.**  
 G.l. — Exposures on Kentucky Route 35 (U.S. Route 127), north of Moreland about 2.5 mi.  
 C. — 260 mm east, 173.5 mm north.  
 F. — Gilbert Member, Ashlock Formation.  
 Q.n. — Junction City, Ky.
- C.n. — **D-1172-CO.**  
 G.l. — Old road to lower Clays Ferry, Ky. Bridge section beginning about 1,750 ft west of high bridge piers for Interstate 75 bridge crossing of Kentucky River.  
 C. — Base of section at 132 mm east, 31 mm north.  
 F. — Clays Ferry Formation.  
 S.p. — 24 ft above top of Tanglewood Limestone Member, Lexington Limestone.  
 Q.n. — Ford, Ky.  
 S.n. — Clays Ferry (lower part); Ford A.  
 S.no. — 22 B.
- C.n. — **D-1196-CO.**  
 G.l. — Eastbound lanes of Interstate 64 from Kentucky River bridge crossing to end of exposure.  
 C. — Base of section at 88 mm east, 164 mm north.  
 F. — Top of Logana Member, Lexington Limestone.  
 S.p. — 50 ft above top of Tyrone Limestone.  
 Q.n. — Frankfort East, Ky.  
 S.n. — Frankfort East A.  
 S.no. — 86.
- C.n. — **D-1206-CO.**  
 G.l. — Southern side of westbound lanes of Interstate 64, 0.5 mi south of bridge across Kentucky River.  
 C. — 123 mm east, 195 mm north.  
 F. — Top of upper tongue of Tanglewood Limestone Member, Lexington Limestone.  
 S.p. — Just below 7783-CO.  
 Q.n. — Frankfort East, Ky.  
 S.n. — Frankfort East A.  
 S.no. — 86.

## NON-USGS COLLECTIONS

- C.n. — **OH-1** (= 6211-CO, Pojeta, 1979).  
 G.l. — Bear Creek Quarry, an abandoned quarry along bluffs on northern side of Ohio River, at intersection of Bear Creek Road and U.S. Route 52, 3 mi east of Neville and 1.1 mi west of Chilo, Washington Co., Ohio.  
 F. — Kope Formation.  
 S.p. — 10–15 ft above contact of Kope Formation and Point

Pleasant Tongue, Clays Ferry Formation.

- Q.n. — Moscow, Ohio-Ky.  
 S.n. — Bear Creek.  
 C.n. — **KY-1**.  
 G.l. — Roadcut on western side of Interstate 71, at Carrollton, Ky., exit.  
 F. — Kope Formation.  
 S.p. — Mollusk-rich lens along bench in roadcut.  
 Q.n. — Carrollton, Ky.



# INDEX

[*Italic page numbers indicate major references*]

Page		Page		Page
<b>A</b>				
Abstract.....	1	<i>Archinacella</i> —Continued		
Abundance of species .....	36, 37, 38	<i>kagawongensis</i> .....	84	
<i>acuta</i> , <i>Carinaropsis</i> .....	28, 36, 37, 177; pl.4	<i>laevis</i> .....	80	
<i>acutilira</i> , <i>Sinuities</i> .....	51, 52, 54, 87	<i>patelliformis</i> .....	27, 29, 74, 76, 78	
<i>acutus</i> , <i>Sinuities cancellatus</i> .....	34, 112	79, 81		
( <i>Aglaoglypta</i> ), <i>Bellerophon</i> .....	159	<i>perovalis</i> .....	80	
Aldanella.....	56	<i>powersi</i> .....	75, 76, 79, 82	
Algae.....	31, 35	<i>pulaskiensis</i> .....	pl.2	
archaeogastropod browsing .....	34	<i>richmondensis</i> .....	82, 83, 84	
drifting masses.....	31	<i>rugatina</i> .....	29, 81; pl.2	
feeding habit.....	30, 41	<i>semicarinata</i> .....	81	
films .....	31	<i>simmonsii</i> .....	72	
flora .....	31	<i>simulatrix</i> .....	28, 36, 37, 76, 77, 80;	
foliage dwellers .....	31, 32, 40, 45	pl.2		
48, 89		<i>subrotunda</i> .....	80, 84	
grazers .....	26, 30, 34, 45	<i>valida</i> .....	27, 39, 78, 81; pl.2	
<i>alphaeus</i> , <i>Tremanotus</i> .....	52	sp. ....	29, 33, 38	
<i>alta</i> , <i>Archinacella</i> .....	28, 80; pl.3	( <i>Carinaropsis</i> ) <i>patelliformis</i> .....	79	
<i>amabilis</i> , <i>Petrotrochus</i> .....	30	<i>Archinacellacea</i> .....	55, 59, 60, 61, 65	
Amphigastropoda.....	54, 58	73, 74, 75		
<i>Amplexopora septosa</i> .....	22	<i>Archinacellida</i> .....	59, 74	
<i>Amygdalocystites</i> bed.....	79	<i>Archinacellidae</i> .....	58, 59, 61, 75	
<i>Anapetopsis</i> .....	48	<i>Archinacellina</i> .....	74, 75	
<i>anatiformis</i> , <i>Pterotheca</i> .....	182, 185	<i>modesta</i> .....	75	
<i>Anconochilus</i> .....	116	<i>Archinacelliopsis</i> .....	59, 74, 75, 76	
<i>angularis</i> , <i>Sinuities cancellatus</i> .....	112	<i>patelliformis</i> .....	75	
<i>angusta</i> , <i>Pterotheca</i> .....	28, 36, 182, 185;	<i>Archinacelloidea</i> .....	59, 74	
pl.39		<i>Archinella pulaskiensis</i> .....	81	
Anisostrophic coiling .....	45, 56	<i>simulatrix</i> .....	81	
Anterior siphon, caenogastropods .....	31	<i>Argillaceous facies</i> , Leipers		
Apertures, explanate.....	47, 48	Formation .....	12	
margins.....	43, 44, 85	<i>Argillaceous member</i> , laminated,		
platform.....	46, 51, 175	Hermitage Formation.....	9	
radial.....	47, 151	<i>Arnheim Formation</i> , Richmond		
sinus.....	44	Group .....	12, 18, 21, 23, 24	
tangential .....	48	<i>Ashlock Formation</i> .....	18, 20, 23	
<i>Aporrhais</i> .....	48	<i>Ashlock Formation</i>		
Appalachian geosyncline .....	4	(See also particular member)		
<i>arca</i> , <i>Archinacella</i> .....	28, 29, 82; pl.3	<i>Aspidobranch ctenidia</i> .....	115	
Archaeogastropoda .....	30, 31, 63, 115	<i>Aspidobranch gastropoda</i> .....	49	
<i>Archaeophiala</i> .....	59, 71, 72	<i>Aspidobranchia</i> .....	115, 116	
Archaeophialidae .....	59, 60, 61, 65, 71, 72	<i>Aspidotheca</i> .....	175, 176, 181	
<i>Archaeopruga</i> .....	74	<i>attenuata</i> , <i>Pterotheca</i> ....	182, 183, 184, 186	
<i>Archinacella</i> .....	28, 59, 74, 75, 76, 78, 80;	<i>ausus</i> , <i>Sphenosphaera</i> .....	28	
pls.2, 3, 4, 5		Autoecology, bellerophontaceans .....	30	
<i>alta</i> .....	28, 80; pl.3	Autoecology, monoplacophorans .....	26, 27	
<i>arca</i> .....	28, 29, 82; pl.3			
<i>cingulata</i> .....	28, 78, 79; pl.2	<b>B</b>		
<i>davisi</i> .....	29, 80; pl.3	Bardstown Member, Drakes		
<i>deleta</i> .....	77, 80, 81	Formation .....	21	
<i>depressa</i> .....	27, 80, 84; pl.2	Basin siltstones .....	35	
<i>indianensis</i> .....	28, 29, 40, 76, 82, 83	<i>Bellerophon</i> .....	46, 47, 49, 50, 53, 54, 61	
84, 85; pls.3, 4, 5		127, 141, 158, 159, 166; pl.18		
		<i>bilineatus</i> .....	160	
		<i>Bellerophon</i> —Continued		
		<i>bilobatus</i> .....	111	
		<i>cancellatus</i> .....	111	
		<i>capax</i> .....	172	
		<i>carinifera</i> .....	164	
		<i>cincinnatiensis</i> .....	167, 173, 174; pl.35	
		<i>clausus</i> .....	166, 167	
		<i>diabloensis</i> .....	165	
		<i>gibsoni</i> .....	52	
		<i>globularis</i> .....	114	
		<i>gorbyi</i> .....	141	
		<i>megalostoma</i> .....	150	
		<i>mohri</i> .....	173	
		<i>parksii</i> .....	173, 174	
		<i>punctifrons</i> .....	141, 142	
		<i>primaeva</i> .....	141	
		<i>recticostatus</i> .....	52	
		<i>recurvus</i> .....	171	
		<i>rogersensis</i> .....	166, 167, 168; pl.32	
		<i>subangularis</i> .....	171	
		<i>subglobulus</i> .....	159	
		<i>sulcatinus</i> .....	127	
		<i>troosti</i> .....	168	
		<i>burginensis</i> .....	170	
		<i>vasulites</i> .....	158	
		sp. ....	52	
		( <i>Aglaoglypta</i> ).....	159	
		( <i>Bellerophon</i> ).....	61, 158, 159, 166;	
		pls.28, 33		
		<i>bilineatus</i> .....	159, 160; pl.28	
		<i>nana</i> .....	159, 160	
		<i>subglobulus</i> .....	159; pl.33	
		<i>subpatula</i> .....	159, 161	
		sp. ....	35	
		( <i>Pharkidonotus</i> ) .....	158, 159	
		<i>percarinatus</i> .....	35	
		<i>Bellerophon</i> .....	61, 158, 159, 166;	
		pls.28, 33		
		<i>Bellerophon</i> sp. ....	35	
		<i>bilineatus</i> , <i>Bellerophon</i> .....	159, 160;	
		pl.28		
		<i>nana</i> , <i>Bellerophon</i> .....	159, 160	
		<i>Bucania</i> .....	pl.18	
		<i>subglobulus</i> , <i>Bellerophon</i> ....	159; pl.33	
		<i>subpatula</i> , <i>Bellerophon</i> .....	159, 161	
		<i>Bucania</i> .....	pl.18	
		<i>Bellerophont conundrum</i> .....	53	
		<i>Bellerophontacea</i> .....	35, 40, 44, 46	
		61, 62, 63, 115, 116		
		functional morphology .....	44	
		shell coiling.....	44	
		<i>Bellerophontidae</i> .....	45, 50, 60, 61, 62, 63	
		64, 156, 158, 175		
		<i>Bellerophontina</i> .....	63, 116	
		<i>Bellerophontinae</i> .....	62, 63, 158	

	Page		Page		Page
Bellevue Limestone Member,		<i>Bucania</i> —Continued		<i>canadense</i> , <i>Salpingostoma</i> .....	150
McMillan Formation .....	18, 22, 23, 24	<i>lindsleyi</i> —Continued		<i>canaliculata</i> , <i>Pterotheca</i> .....	182, 185
<i>bellulus</i> , <i>Conradella</i> .....	123	group .....	64, 127, 128, 135, 138	<i>cancellata</i> , <i>Protowarthia</i> .....	111
<i>Phragmolites</i> .....	29, 123, 124; pl.44	<i>micronema</i> .....	28, 45, 132, 136; pl.19	<i>cancellatus acutus</i> , <i>Sinuities</i> .....	34, 112
<i>bidorsata</i> , <i>Bucania</i> .....	145	<i>nana</i> .....	160, 161	<i>angularis Sinuities</i> .....	112
<i>Tetranota</i> .....	27, 29, 39, 41, 46, 47	<i>nashvillensis</i> .....	27, 28, 37, 46, 51, 131	<i>Bellerophon</i> .....	111
114, 125, 145, 146, 147, 148, 149;		132, 137, 140; pls.13, 14, 15, 27		<i>cancellatus</i> , <i>Sinuities</i> .....	112
pls.21, 22		group .....	45, 47, 127	<i>corrugatus</i> , <i>Sinuities</i> .....	112
Bigby facies, Bigby-Cannon		<i>peracuta</i> .....	27, 51, 134, 135, 137, 138;	<i>liratus</i> , <i>Sinuities</i> .....	34, 112
Limestone, Nashville Group .....	9	pl.16		<i>Sinuities</i> .....	28, 29, 34, 52, 53, 54, 110
Bigby-Cannon Limestone,		<i>pojetai</i> .....	29, 138, 139; pl.20	111, 112, 115; pl.11	
Nashville Group .....	9, 39	<i>punctifrons</i> .....	142	<i>cancellatus</i> .....	112
(See also particular member)		<i>rugatina</i> .....	28, 38, 127, 131, 132	<i>trentonensis</i> , <i>Sinuities</i> .....	112
<i>bilineatus</i> , <i>Bellerophon</i> .....	160	136, 137; pls.16, 17		Cannon facies, Bigby-Cannon	
( <i>Bellerophon</i> ) .....	159, 160; pl.28	<i>simulatrix</i> .....	29, 138, 139, 156	Limestone, Nashville Group .....	10, 39
<i>Sphenosphaera</i> .....	28, 37	157, 174; pl.19		<i>capax</i> , <i>Bellerophon</i> .....	172
<i>billingsi</i> , <i>Salpingostoma</i> .....	150, 154, 156	<i>singularis</i> .....	27, 135, 137; pl.19	<i>Sphenosphaera</i> .....	29, 166, 172, 174;
<i>bilobatus</i> , <i>Bellerophon</i> .....	111	<i>subangulata</i> .....	28, 36, 37, 130, 131;	pl.34	
<i>corrugatus</i> , <i>Sinuities</i> .....	34	pls.14, 15		Carbonate environments .....	34
<i>Cyrtolites</i> .....	111	<i>sublata</i> .....	28, 37, 38, 135; pl.13	Carinaropsidae .....	61, 62, 63, 64, 116
<i>Sinuities</i> .....	110	<i>subpatula</i> .....	161	158, 162, 174, 176, 181	
Biostratigraphic classification .....	3	<i>sulcatina</i> .....	46, 150	Carinaropsinae .....	62, 63, 175, 176
Biotremus .....	117	group .....	45, 47, 50, 55, 64, 118	<i>Carinaropsis</i> .....	38, 47, 48, 51, 55
Bipectinate ctenidia .....	49	120, 127, 128, 130, 132		62, 80, 158, 162, 166, 167, 174	
Bipectinate gill .....	31	135, 137, 141, 143, 150		175, 176, 177, 181; pls.4, 37, 38, 40	
Bipulvinidae .....	61	sp. ....	27, 32, 33, 36, 37, 38, 40	<i>acuta</i> .....	28, 36, 37, 177; pl.4
<i>bjalyi</i> , <i>Nyuella</i> .....	75	( <i>Bellerophon</i> ) <i>nana</i> .....	pl.18	<i>cunulae</i> .....	27, 176, 177, 178, 179;
Blackriveran Stage, upper Middle		<i>subpatula</i> .....	pl.18	pl.37	
and Upper Ordovician rocks .....	4	<i>Bucaniella</i> .....	53	<i>cymbula</i> .....	28, 37, 38, 46, 131, 162
Blue clay-shale member, Hermitage		<i>esthona</i> .....	140	167, 176, 177, 178, 179; pls.37, 38	
Formation, Nashville Group .....	9	<i>Bucaniidae</i> .....	45, 50, 61, 62, 63, 64, 126, 143	<i>explanata</i> .....	28; pl.40
<i>bohemica</i> , <i>Cyclotheca</i> .....	33	<i>Bucaniinae</i> .....	62, 63, 64, 126, 149	<i>explanatus</i> .....	180
<i>bohemicum</i> , <i>Grandostoma</i> .....	33	<i>Bucanopsinae</i> .....	63, 64, 127, 158, 161	<i>phalera</i> .....	177, 179
<i>Boiotremus</i> .....	62, 117, 149	162, 175		sp. ....	37, 38
<i>boreale</i> , <i>Salpingostoma</i> .....	150	<i>Bucanopsis</i> .....	38, 46, 47, 61, 127, 144, 158	( <i>Carinaropsis</i> ) <i>patelliformis</i> ,	
Brannon Member, Lexington		161, 162, 166, 175, 176; pl.27		<i>Archinacella</i> .....	79
Limestone .....	16	<i>calypso</i> .....	33	<i>carinatus</i> , <i>Cyrtolites</i>	
<i>brevilineata</i> , <i>Sinuities</i> .....	52	<i>carinifera</i> .....	27, 28, 37, 38, 133	( <i>Paracyrtolites</i> ) .....	29, 44, 87, 89
Brookville Formation .....	19	162, 163, 164, 165; pl.27		99, 103, 108, 109, 126; pls.7, 8	
Brown, quoted .....	18	<i>diabloensis</i> .....	28, 38, 162, 165; pl.27	<i>carinifera</i> , <i>Bellerophon</i> .....	164
Bryozoan-encrusted shell .....	42	sp. ....	33, 35	<i>Bucanopsis</i> .....	27, 28, 37, 38, 133
Bryozoans .....	41	<i>budleighensis</i> , <i>Cyrtolites</i> .....	90	162, 163, 164, 165; pl.27	
<i>Bubovicus</i> .....	158	<i>buelli</i> , <i>Bucania</i> .....	150	<i>carrickensis</i> , <i>Tetranota</i> .....	144
<i>Bucanella</i> .....	116, 140, 143	<i>Salpingostoma</i> .....	52, 150, 151, 153	Carters Limestone, Stones River	
<i>Bucanellidae</i> .....	59, 63, 109, 116	154, 156; pl.24		Group .....	7
<i>Bucanellinae</i> .....	62	Bull Fork Formation .....	18, 23	Catheys Formation,	
<i>Bucania</i> .....	38, 45, 46, 47, 61, 118	<i>burginensis</i> , <i>Bellerophon troosti</i> .....	170	Nashville Group .....	11, 39
120, 122, 126, 127, 128, 133, 140		<i>Sphenosphaera</i> .....	37, 166, 170; pl.28	(See also particular facies)	
141, 144, 149, 150, 166; pls.12				<i>cellulosa</i> , <i>Conradella dyeri</i> .....	122
13, 14, 15, 16, 17, 18, 19, 20, 27				<i>cellulosum</i> , <i>Tetradium</i> , in Carters	
<i>bidorsata</i> .....	145			Limestone lower member .....	7
<i>buelli</i> .....	150			<i>cellulosus</i> , <i>Phragmolites</i> .....	27, 39, 122;
<i>christianae</i> .....	52, 53			pl.43	
<i>cornu</i> group .....	150			<i>dyeri</i> .....	122
<i>crassa</i> .....	29, 130, 137, 139, 140;			Central Tennessee bank .....	5
pl.19				Central Tennessee high .....	5
<i>emmonsii</i> .....	27, 128, 130, 135; pl.12			Central Tennessee, Ordovician	
<i>frankfortensis</i> .....	27, 28, 38			lithostratigraphy .....	6
131, 133, 134, 140; pls.13, 16				paleoecology .....	39
<i>halli</i> .....	28, 36, 129, 130, 135, 143; pl.12			<i>Chalarostrepsis</i> .....	45, 57, 58, 64, 117, 142
<i>intexta</i> .....	129			<i>praecursor</i> .....	117
<i>lindsleyi</i> .....	27, 131, 132, 133			Champlainian Series .....	4
136, 137, 140; pl.18				<i>christianae</i> , <i>Bucania</i> .....	52, 53

	Page		Page		Page
Ciliary suspension feeders .....	30	Corryville Member, McMillan		<i>Cyrtolites</i> —Continued	
Cincinnati arch .....	4	Formation .....	18, 23	<i>ornatus</i> .....	29, 42, 51, 52, 5
Cincinnatian Ordovician rocks, classification		Corryville to Oregonia sequence .....	19	62, 86, 87, 90, 174	
(see Upper Ordovician)		<i>costalis</i> , <i>Kokenospira</i> .....	29, 140, 141, 144;	<i>retrorsus</i> .....	29, 38, 39, 87, 90
Cincinnatian Series .....	4	pl.20		<i>subacutus</i> .....	118
<i>cincinnatiensis</i> , <i>Bellerophon</i> .....	167, 173	<i>craigensis</i> , <i>Cyrtolites</i> .....	90	<i>subplanus</i> .....	90
174; pl.35		<i>crassa</i> , <i>Bucania</i> .....	29, 130, 137, 139, 140;	<i>thraivensis</i> .....	91
<i>cingulata</i> , <i>Archinacella</i> .....	28, 78, 79; pl.2	pl.19		sp. ....	33, 36, 37, 38
Circumbilical muscles .....	43, 52, 55	<i>Crenistriella</i> .....	116	( <i>Cyrtolites</i> ) .....	41, 87, 88, 89, 91;
Classification .....	52, 53	<i>Crepidula</i> .....	46, 51, 55, 176, 177, 181, 182	pls.4, 5, 6, 7, 8	
Bellerophontacea .....	61	<i>Crepidula fornicata</i> .....	48	<i>claysferryensis</i> .....	28, 29, 38, 42, 44
monoplacophora .....	58	<i>cristatus</i> , <i>Cyrtolites</i> .....	119	87, 89, 90, 99, 100, 101	
suprageneric, bellerophontacean		<i>Oxydiscus</i> .....	119	104, 109, 146; pls.4, 8	
gastropoda .....	61	<i>Tropidodiscus</i> .....	27, 119; pl.41	<i>disjunctus</i> .....	44, 90, 92
Clastic environments, Ordovician .....	32	<i>Cryptolithus</i> .....	22	104, 106; pl.6	
<i>clausus</i> , <i>Bellerophon</i> .....	166, 167	sp. ....	pl.21	<i>hornyi</i> .....	29, 40, 90, 92, 102
<i>Sphenosphaera</i> .....	27, 37, 38, 39, 46	Ctenidia .....	115	104, 105; pl.8	
51, 55, 125, 159, 166, 167		<i>Ctenodonta hermitagensis</i> .....	9	<i>minor</i> .....	29, 87, 88, 89, 90
168, 170, 171; pls.30, 31, 32		<i>Ctenodonta</i> member, Hermitage		92, 102, 103; pl.7	
Clays Ferry Formation, Lexington		Formation, Nashville Group .....	9	<i>ornatus</i> .....	29, 44, 67, 69
Limestone .....	18, 19, 20, 37, 38, 41	<i>cunulae</i> , <i>Carinaropsis</i> .....	27, 176, 177	88, 89, 90, 91, 92, 93	
<i>claysferryensis</i> , <i>Cyrtolites</i> .....	41	178, 179; pl.37		94, 103, 104, 106; pls.6, 7	
( <i>Cyrtolites</i> ) .....	28, 29, 38, 42	<i>Phragmostoma</i> .....	178	<i>retrorsus</i> .....	27, 28, 36, 37, 38
44, 87, 89, 90, 99, 100		Curdsville Limestone Member,		44, 87, 89, 90, 94	
101, 104, 109, 146; pls.4, 8		Hermitage Formation, Nashville		96, 98, 99, 100, 101	
<i>Clidoderm</i> .....	181, 184	Group .....	8	104, 108, 109; pls.5, 7	
<i>expansa</i> .....	183	Lexington Limestone .....	15, 37	<i>fillmorensis</i> .....	89, 99
<i>saffordi</i> .....	182	abundance of species .....	36	<i>subplanus</i> .....	99
( <i>Clidoderm</i> ) <i>saffordi</i> , <i>Pterotheca</i> .....	182	<i>Cyclocyrtionellidae</i> .....	59, 61	( <i>Paracyrtolites</i> ) .....	87, 88, 89, 107;
<i>clochensis</i> , <i>Pterotheca</i> .....	182, 185	<i>Cyclomya</i> .....	59, 60	pls.7, 8	
<i>Cloudia</i> .....	86, 109	<i>Cyclonema</i> .....	30	<i>carinatus</i> .....	29, 44, 87, 89, 99
<i>Cocculinaea</i> .....	49, 116	<i>Cyclothea</i> .....	175, 181	103, 108, 109, 126; pls.7, 8	
<i>Codiaceae</i> .....	31	<i>bohemica</i> .....	33	<i>parvus</i> .....	28, 87, 108, 109, 126;
<i>Coelocyclus</i> .....	126, 158	( <i>Cymatospira</i> ) <i>montfortianus</i> ,		pl.7	
Coiling, anisostrophic .....	45, 56	<i>Knightites</i> .....	35	<i>subplanus</i> .....	28, 37, 87, 89
Bellerophontacea .....	44	<i>cymbula</i> , <i>Carinaropsis</i> .....	28, 37, 38	107, 108; pls.7, 8	
disjunct .....	44, 45, 58, 106	46, 131, 162, 167, 176		( <i>Cyrtolites</i> ) <i>claysferryensis</i> ,	
isostrophic .....	45, 51, 52, 56	177, 178, 179; pls.37, 38		<i>Cyrtolites</i> .....	28, 29, 38, 42, 44
Columellar muscles and scars .....	52, 53	<i>Phragmostoma</i> .....	178	87, 89, 90, 99, 100, 101	
54, 64		<i>Cymbularia</i> .....	35	104, 109, 146; pls.4, 8	
<i>Columnaria</i> , in Carters Limestone		sp. ....	33	<i>Cyrtolites</i> .....	41, 87, 88, 89, 91;
lower member .....	7	<i>Cymbulariidae</i> .....	62	pls.4, 5, 6, 7, 8	
Composite molds .....	82, 93, 126, 130	<i>Cymbulariinae</i> .....	62, 126, 158	<i>disjunctus</i> , <i>Cyrtolites</i> .....	44, 90, 92
<i>compressa</i> , <i>Conradella</i> .....	120	Cynthiana Formation .....	18, 19	104, 106; pl.6	
Compression, lateral .....	45, 117, 118	<i>Cyrtolitacea</i> .....	86	<i>hornyi</i> , <i>Cyrtolites</i> .....	29, 40, 90, 92
<i>compressus</i> , <i>Cyrtolites</i> .....	120	<i>Cyrtolites</i> .....	29, 36, 38, 42, 43, 44, 49	102, 104, 105; pl.8	
<i>Phragmolites</i> .....	28, 34, 120, 121;	53, 55, 59, 60, 69, 86, 116, 135		<i>minor</i> , <i>Cyrtolites</i> .....	29, 87, 88, 89
pls.42, 44		<i>bilobatus</i> .....	111	90, 92, 102, 103; pl.7	
Conodont zonation .....	3	<i>budleighensis</i> .....	90	<i>ornatus</i> , <i>Cyrtolites</i> .....	29, 44, 67, 69
<i>Conradella</i> .....	61, 117, 120	<i>claysferryensis</i> .....	41	88, 89, 90, 91, 92, 93, 94	
<i>bellulus</i> .....	123	<i>compressus</i> .....	120	103, 104, 106; pls.6, 7	
<i>compressa</i> .....	120	<i>craigensis</i> .....	90	<i>retrorsus</i> , <i>Cyrtolites</i> .....	27, 28, 36, 37
<i>dyeri</i> .....	124	<i>cristatus</i> .....	119	38, 44, 87, 89, 90, 94, 96, 98, 99	
<i>cellulosa</i> .....	122	<i>disjunctus</i> .....	87	100, 101, 104, 108, 109; pls.5, 7	
<i>elegans</i> .....	123	<i>dyeri</i> .....	123, 124	<i>fillmorensis</i> , <i>Cyrtolites</i> .....	89, 99
<i>grandis</i> .....	121	<i>elegans</i> .....	123	<i>subplanus</i> , <i>Cyrtolites</i> .....	99
<i>similis</i> .....	120, 121	<i>hornyi</i> .....	40	<i>Cyrtolitidae</i> .....	59, 61, 62, 86, 116
<i>consobrina</i> , <i>Pterotheca</i> .....	33	<i>lamellifer</i> .....	125	<i>Cyrtolitina</i> .....	86, 125
<i>cornu</i> , <i>Bucania</i> , group .....	150	<i>magnus</i> .....	119	<i>nitidula</i> .....	125
<i>Cornulites</i> .....	41	<i>nitidula</i> .....	125	<i>Cyrtionella</i> .....	51, 58, 61
<i>corrugatus</i> , <i>Sinuities bilobatus</i> .....	34	<i>nodosus llandoveria</i> .....	91	<i>mitella</i> .....	52, 54
<i>cancellatus</i> .....	112	<i>nodosus</i> .....	91		
Corryville Formation .....	24				



	Page		Page		Page
Cyrtonelella.....	59, 61	<i>elegans</i> —Continued		<i>fissicostata, Helcionopsis</i> .....	66
Cyrtonelellida.....	43, 55, 59, 60, 61, 86	Phragmolites.....	29, 123, 124; pls.44, 45	( <i>Fissurella</i> ), <i>Diodora</i> .....	49
functional morphology.....	43	Elkhorn Formation.....	18, 25	Fissurellacea.....	49
Cyrtonelellidae.....	61	Emargination, labral.....	49, 54, 60, 115, 116	Fissurellidae.....	30, 31, 49, 115
D		<i>Emarginula</i> .....	49, 54	Flanagan Chert, Lexington	
<i>Dalmanella coquina</i> member,		<i>eminens, Helcionopsis</i> .....	68	Limestone.....	16, 119, 131, 135, 136
Hermitage Formation,		<i>emmonsi, Bucania</i> .....	27, 128, 130, 135;	<i>fornicata, Crepidula</i> .....	48
Nashville Group.....	9	pl.12		<i>frankfortensis, Bucania</i> .....	27, 28, 38, 131
Dasycladaceae.....	31	<i>Encrinurus</i> .....	34	133, 134, 140; pls.13, 16	
<i>davisi, Archinacella</i> .....	29, 80; pl.3	Encrustation.....	28, 29, 41, 42, 67, 69	<i>fraternus, Salpingostoma</i> .....	150
<i>Dekayia aspera</i> .....	22	88, 137		Fulton beds, Kope Formation.....	22
<i>deleta, Archinacella</i> .....	77, 80, 81	Endogastric orientation.....	42, 55	Fulton Shale.....	19
Delta fronts, environment.....	32, 35, 36	<i>Entemnotrochus</i> .....	50	Functional morphology.....	42
fauna.....	34	Environments, carbonate,		G	
<i>Delthyris expansus</i> .....	183	Ordovician.....	34	<i>galathea, Neopilina</i> .....	43, 58
<i>dentatum, Rhynchotrema</i> , beds,		clastic, Ordovician.....	32	Garrard Siltstone.....	18, 20
Whitewater Formation.....	156	<i>Eobucania</i> .....	58, 64, 117, 118, 126	Gastropods.....	63
Deposit feeders.....	27, 30, 35, 47	149, 175		predation.....	41
<i>depressa, Archinacella</i> .....	27, 80, 84; pl.2	Eotomariidae.....	57	size restrictions.....	32
Detorsion, regulatory.....	45	<i>esthona, Bucaniella</i> .....	140	Geologic setting.....	3
Detritus feeders.....	30, 36, 40	Euomphalaceans.....	35	<i>gibsoni, Bellerophon</i> .....	52
Devils Hollow Member,		Euomphalid archaeogastropods.....	30	Gilbert Member, Ashlock	
Lexington Limestone.....	17	<i>Euphemites</i> .....	47, 61, 117	Formation.....	21
abundance of species.....	38	Euphemitidae.....	62, 63, 116, 117	<i>Girvanella</i> .....	15
<i>diabloensis, Bellerophon</i> .....	165	Euphemitinae.....	62	<i>globata, Phragmosphaera</i> .....	35
<i>Bucanopsis</i> .....	28, 38, 162, 165; pl.27	<i>Euphemitopsis</i> .....	117	<i>globularis, Bellerophon</i> .....	114
<i>dilatatus, Salpingostoma</i> .....	150	Exogastric orientation.....	42, 55	<i>Sinuities</i> .....	29, 114, 115; pl.10
Dillsboro Formation.....	18, 23, 24, 40	<i>expansa, Clidoderm</i> .....	183	<i>Glyptotomaria (Glyptotomaria)</i>	
<i>Diodora (Fissurella)</i> .....	49	<i>Pterotheca</i> .....	27, 28, 36, 39, 182, 183	<i>marginata</i> .....	30
Diotocardia.....	115	184, 185; pls.39, 40		( <i>Glyptotomaria</i> ) <i>marginata</i> ,	
<i>Dirachopea</i> .....	58	<i>Salpingostoma</i> .....	150, 154, 155, 156	<i>Glyptotomaria</i> .....	30
Disjunct coiling.....	44, 45, 58, 106	<i>expansus, Delthyris</i> .....	183	<i>gorbyi, Bellerophon</i> .....	141
<i>disjunctus, Cyrtolites</i> .....	87	<i>explanata, Carinaropsis</i> .....	28; pl.40	<i>Undulabucania</i> .....	29, 141, 142, 143;
( <i>Cyrtolites</i> ).....	44, 90, 92, 104	Explanate apertures.....	47, 48	pl.23	
106; pl.6		Explanate bellerophonaceans.....	30, 33, 35	<i>grande, Grandostoma</i> .....	33
Dove-colored facies.....	39	Explanate shells.....	33, 38, 47, 48, 50, 116	<i>grandis, Conradella</i> .....	121
Bigby-Cannon Limestone,		<i>explanatus, Carinaropsis</i> .....	180	<i>Phragmolites</i> .....	27, 121, 122, 123;
Nashville Group.....	10	External molds.....	66, 76, 77, 78, 83	pls.42, 43	
Catheys Formation,		F		<i>Grandostoma</i> .....	116
Nashville Group.....	11	Facies, Bigby-Cannon Limestone.....	9	<i>bohemicum</i> .....	33
Drahomiridae.....	61	Catheys Formation.....	11	<i>grande</i> .....	33
Drakes Formation.....	18, 21, 24, 25	Leipers Formation.....	12	Grandostomatidae.....	62, 63, 116
<i>dyeri cellulosus, Conradella</i> .....	122	Fairmont beds, Fairview		Grandostomatinae.....	62
<i>cellulosus, Phragmolites</i> .....	122	Formation.....	22	<i>granistriatus, Sinuities</i> .....	29, 51, 111, 113
<i>Conradella</i> .....	124	Fairmount Formation.....	24	114, 115, 146; pls.11, 21, 45	
<i>Cyrtolites</i> .....	123, 124	Fairview Formation.....	18, 22	Grant Lake Limestone.....	18, 23
<i>dyeri, Phragmolites</i> .....	122	Faulconer Bed, Perryville		(See also McMillan Formation)	
<i>Phragmolites</i> .....	29, 41, 122, 123, 124;	Limestone Member,		Granular facies, Catheys Formation,	
pls.44, 45		Lexington Limestone.....	15, 16	Nashville Group.....	11
<i>dyeri</i> .....	122	Faunas, upper Ordovician,		Hermitage Formation,	
<i>Phragmolithes</i> .....	124	paleoecology.....	40	Nashville Group.....	9
E		Feeders, algal.....	26, 30, 34, 41, 45	Leipers Formation.....	12
<i>eatoni, Triarthrus</i> .....	22	ciliary suspension.....	30	Grazers.....	47
Economy Shale, Kope Formation.....	22	deposit.....	27, 30, 35, 47	Greendale Lentil, Lexington	
Eden Group, Inman Formation.....	12	detritus.....	30, 36, 40	Limestone.....	16
Eden Shales.....	17, 22	grazing.....	47	Grier Limestone Member,	
Edenian Stage, upper Middle and		suspension.....	48	Lexington Limestone.....	15, 37, 38
Upper Ordovician rocks.....	4	Fernvale Limestone,		<i>Gyrospira</i> .....	174, 175, 176
<i>elegans, Conradella</i> .....	123	Richmond Group.....	13	H	
<i>Cyrtolites</i> .....	123	<i>fillmorensis, Cyrtolites (Cyrtolites)</i>		Haliotidae.....	52
		<i>retrorsus</i> .....	89, 99	<i>Haliotis</i> .....	49

	Page		Page		Page
<i>halli</i> , <i>Bucania</i> .....	28, 36, 129, 130, 135 143; pl.12	Kentucky, middle Ordovician		<i>Liljevallospira</i> .....	158
<i>harviei</i> , <i>Pterotheca</i> .....	29, 182, 183, 185 186; pl.26	lithostratigraphy.....	6	<i>lindsleyi</i> , <i>Bucania</i> .....	27, 131, 132 133, 136, 137, 140; pl.18
<i>Helcionella</i> .....	69	north-central, upper Ordovician		group.....	64, 127, 128, 135, 138
<i>Helcionellacea</i> .....	61, 62	lithostratigraphy.....	22	Lineback, quoted .....	18
<i>Helcionellaceans</i> .....	118	south-central, upper Ordovician		<i>Liospira</i> .....	34, 168
<i>Helcionellidae</i> .....	61	lithostratigraphy.....	19	<i>liratus</i> , <i>Sinuities</i> .....	112
<i>Helcionopsis</i> .....	28, 43, 65, 66, 68, 69; pl.2	upper Ordovician		cancelatus .....	34, 112
<i>fissicostata</i> .....	66	lithostratigraphy.....	17	<i>Litavina</i> .....	68
<i>eminens</i> .....	68	<i>kentuckyense</i> , <i>Salpingostoma</i> .....	28, 36 37, 47, 51, 150, 151, 152 153, 154, 156; pls.24, 25, 26	<i>llandoveria</i> , <i>Cyrtolites nodosus</i> .....	91
<i>radiata</i> .....	66	<i>Kirengella</i> .....	71	<i>locator</i> , <i>Salpingostoma</i> .....	150
<i>reticulatus</i> .....	66	<i>Kirengellacea</i> .....	60, 61, 65, 71, 72, 75	Logana Member, Lexington	
<i>striata</i> .....	28, 29, 66, 67; pl.2	<i>Kirengellida</i> .....	59, 60, 71, 72	Limestone .....	15
<i>subcarinata</i> .....	66	<i>Kirengellidae</i> .....	59, 60, 61, 71	abundance of species .....	37
sp. ....	66	<i>Kirengelloidea</i> .....	59	Lophosphirid gastropods.....	41
<i>Heliospongia vokesi</i> .....	31	Knight, quoted .....	76	<i>Lophospira</i> .....	168
Hermitage Formation,		<i>Knightites</i> .....	47, 158, 161, 162, 166	<i>medialis</i> .....	17
Nashville Group .....	8, 39	( <i>Cymatospira</i> ) <i>montfortianus</i> .....	35	Low-spined shells.....	58
(See also particular member)		<i>Knightitidae</i> .....	62	<i>Loxobucania</i> .....	127, 128
<i>hermitagensis</i> , <i>Ctenodonta</i> .....	9	<i>Knightitinae</i> .....	62, 158, 161	<i>Loxonomataceans</i> .....	35
Heteropod .....	181	<i>Kodymites</i> .....	158	Lunulae .....	50
High Bridge Group .....	13	<i>Kokenia</i> .....	61, 140		
(See also particular member)		<i>Kokenospira</i> .....	47, 61, 126, 140, 144, 158; pl.20	M	
Hill quarry beds (Fairview		<i>costalis</i> .....	29, 140, 141, 144; pl.20	Macluritid archaeogastropods.....	30
Formation) .....	22	Kope to Bellevue sequence.....	19	<i>Macroscenella</i> .....	72
<i>hippapus</i> , <i>Tetranota</i> .....	144	Kope Formation .....	18, 20, 22, 23, 24, 41	<i>magnus</i> , <i>Cyrtolites</i> .....	119
Holopeids .....	35	Kope Formation (Indiana) .....	24	<i>Oxydiscus</i> .....	119
Homolotid-Plectonotus		<i>Kotysium</i> .....	68	<i>Tropidodiscus</i> .....	29, 119, 120; pl.42
community.....	34			<i>manitoulini</i> , <i>Vallatotheca</i> .....	28, 29, 67, 68 69, 70, 71; pl.1
<i>hornyi</i> , <i>Cyrtolites</i> .....	40			Mantle cavity .....	49
( <i>Cyrtolites</i> ).....	29, 40, 90, 92 102, 104, 105; pl.8	L		<i>marginata</i> , <i>Glyptotomaria</i>	
Hypseloconiae .....	61	<i>labioreflexus</i> , <i>Pharkidonotus</i> .....	52	( <i>Glyptotomaria</i> ) .....	30
Hypseloconidae .....	58, 59, 74	Labral emargination.....	49, 54, 60, 115, 116	Material used in study .....	25
<i>Hypseloconus</i> .....	59, 71, 72, 73, 74	Labral sinus.....	49, 62	Maysville Group, Leipers	
		Labral slit .....	54	Formation .....	12
I		<i>laevis</i> , <i>Archinacella</i> .....	80	McMicken Member, Kope	
<i>Iapetus</i> (proto-Atlantic) Ocean .....	4	<i>lamellifer</i> , <i>Cyrtolites</i> .....	125	Formation .....	22
<i>imbricata</i> , <i>Salpingostoma</i> .....	150	<i>Temnodiscus</i> .....	117	McMillan Formation .....	18, 20
Indiana, southeastern, upper		Laminated argillaceous member,		(See also particular member)	
Ordovician lithostratigraphy .....	17, 24	Hermitage Formation,		Measurements.....	26
<i>indianensis</i> , <i>Archinacella</i> .....	28, 29, 40, 76 82, 83, 84, 85; pls.3, 4, 5	Nashville Group .....	9	<i>medialis</i> , <i>Lophospira</i> .....	17
Inductural deposits .....	47, 117	Laminated siltstone facies, Catheys		<i>Megalomphala</i> .....	54, 61
Inman Formation, Eden Group .....	12	Formation .....	12	<i>taenia</i> .....	52
<i>inornatum</i> , <i>Salpingostoma</i> .....	150	<i>Lapsus calami</i> .....	66	<i>megalostoma</i> , <i>Bellerophon</i> .....	150
<i>intermedia</i> , <i>Pterotheca</i> .....	184	<i>lata</i> , <i>Salpingostoma</i> .....	150	<i>Metoptoma</i> .....	75
Internal molds.....	84, 93, 110, 111, 112 146, 150, 155, 156	Laterally compressed shells.....	45, 117, 118	Miamitown Shale .....	18, 23, 23
<i>intexta</i> , <i>Bucania</i> .....	129	Lebanon Limestone, Stones River		Micrite envelopes.....	26
Introduction.....	2	Group .....	7	Micromorphic bellerophonaceans .....	30
<i>Isopleura</i> .....	58	Leipers Formation, Maysville		<i>miconema</i> , <i>Bucania</i> .....	28, 45, 132, 136; pl.19
Isostrophic shell coiling.....	45, 51, 52, 56	Group .....	12	Microphagous scavenging,	
J		<i>lemchei</i> , <i>Sylvestrosphaera</i> .....	52	<i>Mikadotrochus</i> .....	30
Jessamine dome, Cincinnati arch .....	5	<i>lenaensis</i> , <i>Multifariites</i> .....	59	<i>Micropileus</i> .....	72; pl.1
K		<i>Leperditella</i> .....	182	<i>obesus</i> .....	73
<i>kagawongensis</i> , <i>Archinacella</i> .....	84	<i>Leperditia</i> .....	182	<i>variabilis</i> .....	28, 36, 73; pl.1
		Lexington Limestone .....	14, 20, 37	<i>midas</i> , <i>Petrotrochus</i> .....	30
		paleoecology .....	36	Middle Ordovician lithostratigraphy,	
		(See also particular member)		Kentucky .....	6
		Liberty bed, Drakes Formation .....	21	<i>Mikadotrochus</i> .....	30
		Liberty Formation .....	18, 23, 24	microphagous scavenging .....	30
		Drakes Formation.....	21		

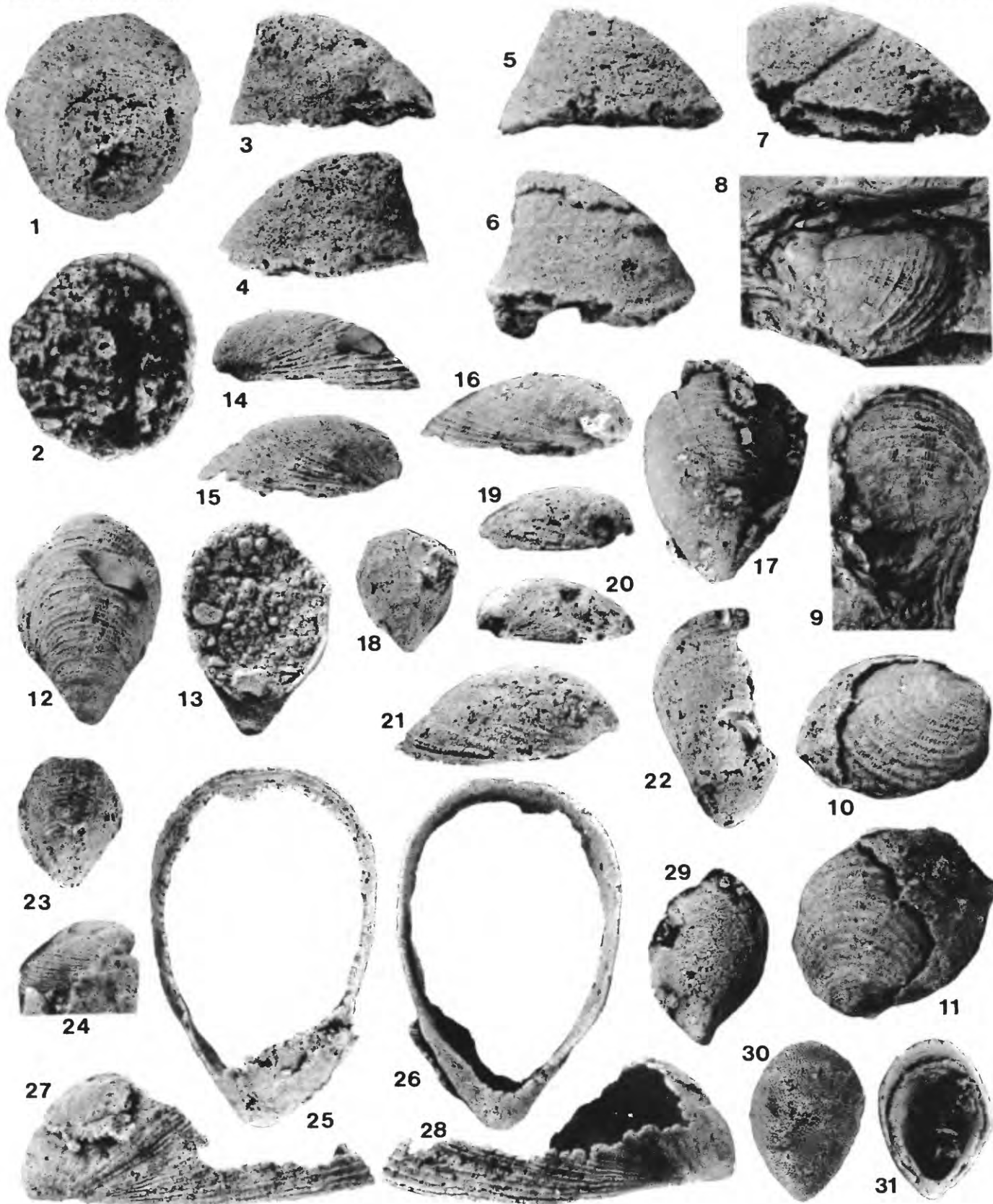
	Page		Page		Page
Millersburg Member, Lexington		<i>nitidula</i> —Continued		Paleoecology, central Tennessee—	
Limestone .....	17	<i>Temnodiscus</i> .....	125, 126; pl.42	Continued	
Million Shale .....	18, 19	<i>Temnodiscus</i> .....	28	Tyrone Limestone.....	36
<i>minor</i> , <i>Cyrtolites</i> ( <i>Cyrtolites</i> ) .....	29, 87	<i>nodosus</i> , <i>Cyrtolites nodosus</i> .....	91	upper Ordovician faunas .....	40
88, 89, 90, 92, 102, 103; pl.7		<i>llandoveria</i> , <i>Cyrtolites</i> .....	91	Paleozoic borings .....	41
<i>mitella</i> , <i>Cyrtolites</i> .....	52, 54	<i>nodosus</i> , <i>Cyrtolites</i> .....	91	<i>Paleuphemites</i> .....	117
Mode of life, and shell form .....	44, 45, 47	Nodular facies, Catheys Formation,		Pallial system.....	49
<i>modesta</i> , <i>Archinacellina</i> .....	75	Nashville Group .....	12	( <i>Paracyrtolites</i> ) <i>carinatus</i> ,	
<i>Mogulia</i> .....	61	Noncalcareous marine algae.....	31	<i>Cyrtolites</i> .....	29, 44, 87, 89, 99
<i>mohri</i> , <i>Bellerophon</i> .....	173	<i>Nylanderina</i> .....	143	103, 108, 109, 126; pls.7, 8	
<i>Sphenosphaera</i> .....	29, 40, 41, 166	<i>Nyuella</i> .....	71, 72	<i>Cyrtolites</i> .....	87, 88, 89, 107; pls.7, 8
167, 172, 173, 174; pls.35, 36, 41		<i>Nyuella bjalyi</i> .....	75	<i>parvus</i> , <i>Cyrtolites</i> .....	28, 87
Molds .....	26			108, 109, 126; pl.7	
Monopectinate ctenidia,		O		<i>subplanus</i> , <i>Cyrtolites</i> .....	28, 37
caenogastropods .....	31	<i>obesus</i> , <i>Micropileus</i> .....	73	87, 89, 107, 108; pls.7, 8	
Monoplacophora .....	61, 116	<i>Protowarthia</i> .....	112	Parietal deposits .....	50, 55
autoecology .....	26	<i>Sinuities</i> .....	28, 36, 37, 111	Parietal inductura .....	51
classification and phylogeny.....	58	112, 113; pl.9		Parietal platform .....	176, 181
functional morphology .....	42	<i>obliqua</i> , <i>Phragmolites</i> .....	121	(See also Septum)	
Tryblidiid .....	28	<i>obseleta</i> , <i>Tetranota</i> .....	28, 37	<i>parksii</i> , <i>Bellerophon</i> .....	173, 174
<i>montfortianus</i> , <i>Knightites</i>		<i>obseleta</i> , <i>Tetranota</i> .....	146, 147, 148, 149; pls.20,	<i>parvus</i> , <i>Cyrtolites</i>	
( <i>Cymatospira</i> ) .....	35	22		( <i>Paracyrtolites</i> ) .....	28, 87, 108
Morphology, functional .....	41	Ohio, southwestern, upper		109, 126; pl.7	
Mount Auburn Formation .....	24	Ordovician lithostratigraphy .....	17, 22	Patellacea .....	49, 116
Mount Auburn Member, McMillan		Ophiletinæ .....	58	Patellacean archaeogastropods .....	30
Formation .....	18, 21, 23	Ordovician carbonate environments .....	34	Patellacean gastropods .....	43, 52, 55
Mount Hope beds, Fairview		Ordovician clastic environments .....	32	Patellaceans .....	30
Formation .....	22	Ordovician lithostratigraphy,		<i>patelliformis</i> , <i>Archinacella</i> .....	27, 29
Mount Hope Formation .....	24	central Tennessee .....	6	74, 76, 78, 79, 81	
<i>Moyerokania</i> .....	59, 71	Ordovician-Silurian unconformity.....	25	( <i>Carinaropsis</i> ) .....	79
Multifariidae .....	59, 60, 61	Oregon Formation, High Bridge		<i>Archinacelliopsis</i> .....	75
<i>Multifariites lenaensis</i> .....	59	Group .....	13	<i>Patellilabia</i> .....	48
Murchisoniaceans .....	35	Oregonia Member, Arnheim		<i>Patellostium</i> .....	61, 117
Murchisoniids .....	35	Formation .....	21	<i>Pedasiola</i> .....	175, 176, 181
Murfreesboro Limestone, Stones		<i>orientalis</i> , <i>Salpingostoma</i> .....	150	<i>Pedasiolinae</i> .....	63, 175, 176
River Group .....	6	<i>ornatus</i> , <i>Cyrtolites</i> .....	29, 42, 51, 52, 54	Pellagiellaceans .....	56
Muscles, bands .....	55	62, 86, 87, 90, 174		<i>peracuta</i> , <i>Bucania</i> .....	27, 51, 134
retractor .....	53	( <i>Cyrtolites</i> ) .....	29, 44, 67, 69	135, 137, 138; pl.16	
scars .....	43, 51, 52, 53, 54	88, 89, 90, 91, 92, 93, 94		<i>percarinatus</i> , <i>Bellerophon</i>	
55, 58, 65, 75, 87		103, 104, 106; pls.6, 7		( <i>Pharkidonotus</i> ) .....	35
N		Ostracodes .....	182	<i>Perotrochus</i> .....	50
<i>nana</i> , <i>Bellerophon</i>		Otter Creek Coral Bed, Drakes		<i>amabilis</i> .....	30
( <i>Bellerophon</i> ).....	159, 160	Formation .....	21	<i>midas</i> .....	30
<i>Bucania</i> .....	160, 161	<i>Owenella</i> .....	116	<i>perovalis</i> , <i>Archinacella</i> .....	80
<i>Bucania</i> ( <i>Bellerophon</i> ) .....	pl.18	<i>Oxydiscus</i> .....	61, 117, 118	Perryville Limestone Member,	
<i>Sphenosphaera</i> .....	160	<i>cristatus</i> .....	119	Lexington Limestone .....	15
Nashville dome, Cincinnati arch .....	5	<i>magnus</i> .....	119	abundance of species .....	37
Nashville Group .....	8	<i>subacutus</i> .....	118	<i>pervoluta</i> , <i>Protowarthia</i> .....	110
paleoecology .....	39	Ozark dome .....	5	<i>Sinuities</i> .....	28, 110, 111
<i>nashvillensis</i> , <i>Bucania</i> .....	27, 28, 37, 46, 51			<i>pervolutus</i> , <i>Sinuities</i> .....	110
131, 132, 137, 140; pls.13, 14, 15, 27		P		<i>Phagmosphaera</i> .....	176
group.....	45, 47, 127	Palaeacmeidae .....	59	<i>phalera</i> , <i>Carinaropsis</i> .....	177, 179
<i>natator</i> , <i>Phragmostoma</i> .....	178	Pale-colored facies, Catheys		<i>Pharetrulites</i> .....	35, 55
<i>Neomphalus</i> .....	30	Formation, Nashville Group .....	11	<i>Pharkidonotus</i> .....	54
<i>Neopilina</i> .....	27	Leipers Formation .....	12	<i>labioreflexus</i> .....	52
<i>Neopilina</i> .....	43, 51, 58, 59, 60, 65, 74	Paleoecological studies .....	32, 34	( <i>Pharkidonotus</i> ), <i>Bellerophon</i> .....	158, 159
<i>galathea</i> .....	43, 58	Paleoecology, central Tennessee.....	39	<i>percarinatus</i> , <i>Bellerophon</i> .....	35
<i>Neopilinoidea</i> .....	61	Lexington Limestone .....	36	<i>Phragmolites</i> .....	41, 45, 47, 61, 117, 118
<i>Neopilinoidea</i> .....	59	post-Ordovician studies .....	34	120, 125, 128, 141, 142; pls.42, 43, 44, 45	
Neritacea .....	49, 52, 115, 116	previous Ordovician studies .....	32	<i>bellulus</i> .....	29, 123, 124; pl.44
<i>nitidula</i> , <i>Cyrtolites</i> .....	125	of symmetrical univalved		<i>cellulosus</i> .....	27, 39, 122; pl.43
<i>Cyrtolites</i> .....	125	mollusks .....	27		

	Page
<i>retrorsus</i> —Continued	
<i>fillmorensis</i> , <i>Cyrtolites</i> ( <i>Cyrtolites</i> ).....	89, 99
<i>Rhynchotrema dentatum</i> beds,	
Whitewater Formation .....	156
Richmond Group.....	12
<i>richmondensis</i> , <i>Archinacella</i> .....	82, 83, 84
<i>Salpingostoma</i> .....	29, 41, 47, 48
138, 139, 150, 151, 155	
156, 157, 174; pls.24, 26	
Richmondian Stage, upper Middle and Upper Ordovician rocks .....	4
Ridley Limestone, Stones River Group .....	7
Rocklandian Stage, upper Middle and Upper Ordovician rocks .....	4
<i>rogersensis</i> , <i>Bellerophon</i> .....	166, 167, 168; pl.32
<i>Romaniella</i> .....	59, 71, 72
Romaniellidae .....	59, 60, 61, 71, 74
Rosov, quoted .....	71
Rowland Member, Drakes Formation .....	21
Rugae.....	134, 138
<i>rugatina</i> , <i>Archinacella</i> .....	29, 81; pl.2
<i>Bucania</i> .....	28, 38, 127, 131, 132
136, 137; pls.16, 17	
S	
<i>saffordi</i> , <i>Clioderma</i> .....	182
<i>Pterotheca</i> .....	27, 28, 39, 46, 182, 183
185, 186; pls.39, 40	
( <i>Clioderma</i> ).....	182
<i>Salpingostoma</i> .....	40, 47, 48, 50, 54
61, 62, 64, 117, 119, 127	
128, 149, 150; pls.24, 25, 26	
<i>billingsi</i> .....	150, 154, 156
<i>boreale</i> .....	150
<i>buelli</i> .....	52, 150, 151, 153, 154
156; pl.24	
<i>canadense</i> .....	150
<i>dilatatus</i> .....	150
<i>expansa</i> .....	150, 154, 155, 156
<i>fraternus</i> .....	150
<i>imbricata</i> .....	150
<i>inornatum</i> .....	150
<i>kentuckyense</i> .....	28, 36, 37, 47, 51, 150
151, 152, 153, 154, 156; pls.24, 25, 26	
<i>lata</i> .....	150
<i>locator</i> .....	150
<i>orientalis</i> .....	150
<i>richmondensis</i> .....	29, 41, 47, 48
138, 139, 150, 151, 155	
156, 157, 174; pls.24, 26	
<i>sculptilis</i> .....	150
sp. ....	36
Salpingostomatidae .....	62, 149
Salpingostomatinae .....	63, 64, 126, 149
Saluda Dolomite Member, Drakes Formation .....	21
Saluda Formation .....	19, 24, 25
Salvisa Bed, Perryville Limestone Mem- ber, Lexington Limestone .....	15, 16

## PLATE I

[All dorsal and ventral views have anterior end down]

- FIGURES 1–7. *Micropileus variabilis* new species (p. 073).
- 1–4. Dorsal, ventral, and left- and right-lateral views of holotype ( $\times 3$ ). Curdsville Limestone Member, Lexington Limestone (Kirkfieldian), USGS 7817-CO. USNM 265926.
  5. Left-lateral view of a paratype ( $\times 3$ ). Curdsville Limestone Member, Lexington Limestone (Kirkfieldian), USGS 7784-CO. USNM 265928.
  6. Left-lateral view of a paratype ( $\times 3$ ). Same collection as figure 5 above. USNM 265929.
  7. Left-lateral view of a paratype ( $\times 3$ ). Same sample as figure 5 above. USNM 265927.
  - 8–11. *Vallatotheca manitoulini* Foerste, 1914a (p. 069).
    - 8, 9. Oblique left-lateral and dorsal views of calcitic cast ( $\times 3$ ). Elkhorn biofacies, Preachersville Member, Drakes Formation, from creek just south of Morning Sun, Ohio. MU 244T.
    - 10, 11. Right-dorsolateral and dorsal views of calcitic cast ( $\times 3$ ). Upper Whitewater Formation, from tributary of Paint Creek near Camden, Ohio. MU 245T.
  - 12–31. *Vallatotheca unguiformis* (Ulrich, 1897) (p. 070).
    - 12–15. Dorsal, ventral, and left- and right-lateral views of lectotype ( $\times 3$ ). Museum label gives horizon and locality as “Upper Trenton, Harrodsburg Junction, C.S. Railroad, Kentucky.” USNM 45990.
    - 16, 17. Right-lateral and dorsal views of silicified specimen ( $\times 4$ ). Salvisa Bed, Perryville Limestone Member, Lexington Limestone, USGS 6915-CO. USNM 265934.
    - 18–20. Dorsal and right- and left-lateral views of silicified specimen ( $\times 3$ ). Salvisa Bed, Perryville Limestone Member, Lexington Limestone, USGS 5015-CO. USNM 265932.
    - 21, 22. Right-lateral and dorsal views of a paralectotype ( $\times 3$ ). Same collection as figures 12–15 above. USNM 265930.
    - 23, 24. Dorsal and right-lateral views of a paralectotype ( $\times 3$ ). Same collection as figures 12–15 above. USNM 265931.
    - 25–28. Dorsal, ventral, and left- and right-lateral views of large silicified specimen ( $\times 3$ ). Note that apex is nearly level with apertural plane. Same collection as figures 16, 17 above. USNM 265936.
    29. Dorsal view of silicified specimen; slightly curved beak probably caused by diagenetic distortion ( $\times 3$ ). Same collection as figures 16, 17 above. USNM 265935.
    - 30, 31. Dorsal and ventral views of bryozoan-encrusted silicified specimen ( $\times 3$ ). Same collection as figures 18–20 above. USNM 265933.



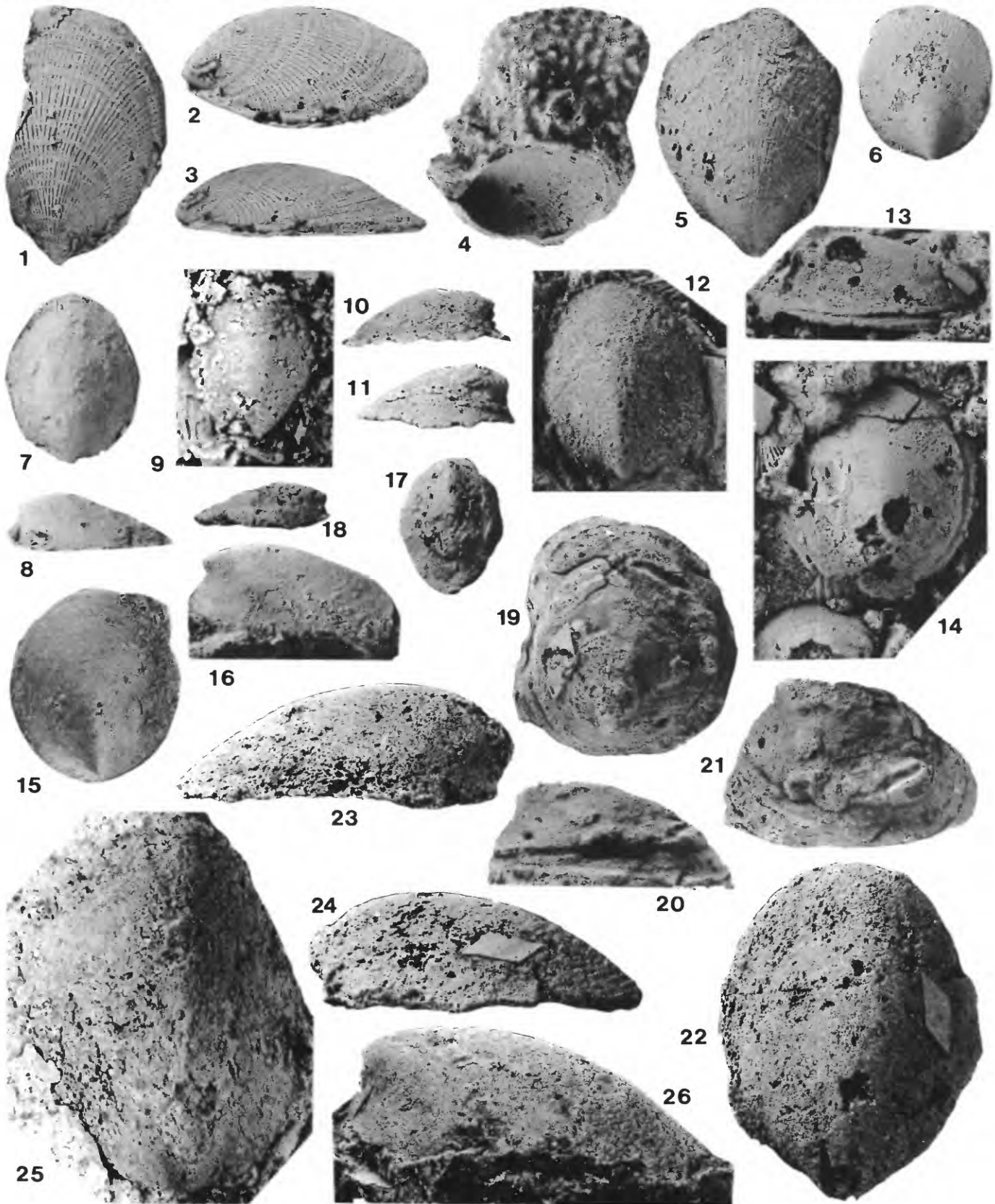
*MICROPILEUS AND VALLATOTHECA*

## PLATE 2

[All dorsal and ventral views, except fig. 17, have anterior end down]

- FIGURES 1–6. *Helcionopsis striata* Ulrich and Scofield, 1897 (p. 066).
- 1–3. Dorsal, oblique left-lateral, and left-lateral views of latex mold of holotype, which is an external mold in the base of a bryozoan colony ( $\times 2$ ). Museum label gives horizon and locality as “Richmond Group, Marion County, Kentucky.” USNM 45827.
  - 4, 5. Ventrolateral view of external mold in the base of a bryozoan colony ( $\times 2$ ), and dorsal view of latex mold of same ( $\times 3.25$ ). Bellevue biofacies, Grant Lake Limestone (Maysvillian), Cincinnati, Ohio. USNM 47494.
  6. Dorsal view of calcitic cast showing thin shell of species as well as small cone-shaped protoconch ( $\times 2$ ). Arnheim Formation (Maysvillian-Richmondian), Clifton, Tenn. USNM 263785.
- 7–12. *Archinacella simulatrix* Ulrich and Scofield, 1897 (p. 076).
- 7, 8. Dorsal and left-lateral views of latex mold of holotype, which is an external mold in the base of a bryozoan colony ( $\times 3$ ). Decorah Formation (Rocklandian-Kirkfieldian), St. Paul, Minn. USNM 45695.
  9. Dorsal view of silicified specimen embedded in matrix ( $\times 3$ ). Grier Limestone Member (Shermanian), Lexington Limestone, USGS 5094-CO. USNM 265941.
  10. Right-lateral view of silicified specimen ( $\times 2.5$ ). Grier Limestone Member (Shermanian), Lexington Limestone, USGS 4073-CO. USNM 265945.
  11. Right-lateral view of silicified specimen ( $\times 2.5$ ). Same collection as figure 10 above. USNM 265944.
  12. Dorsal view of silicified specimen embedded in matrix ( $\times 2.5$ ). Museum label gives horizon and locality as “Trenton (Hermitage), Frankfort, Kentucky” (Kirkfieldian). USNM 47471.
- 13, 14. *Archinacella* cf. *A. depressa* Ulrich and Scofield, 1897 (p. 079). Slightly oblique left-lateral and dorsal views of silicified specimen ( $\times 2.5$ ). Museum label gives horizon and locality as “Mohawkian (Cannon), Hartsville, Tennessee” (Kirkfieldian-Shermanian). USNM 59295.
- 15, 16. *Archinacella valida* (Sardeson, 1892) (p. 078). Dorsal and dorsolateral views of calcitic specimen ( $\times 2$ ). Museum label gives horizon and locality as “Trenton (*Ctenodonta* horizon), Mt. Pamassus, Columbia, Tennessee” (Kirkfieldian). USNM 47467.
- 17, 18. *Archinacella* cf. *A. pulaskiensis* Foerste, 1914b (p. 081) Dorsal and right-lateral views of fragmentary calcitic cast ( $\times 3$ ). Museum label gives only the horizon, as “Maysville,” but specimen most likely is from Cincinnati, Ohio, area. UCGM 19640.
- 19–21. *Archinacella rugatina* Ulrich, 1897 (p. 081). Dorsal, left-lateral, and dorsolateral views of holotype ( $\times 2$ ). Arnheim biofacies, Bull Fork Formation (Richmondian), Middleton, Ohio. USNM 45963.
- 22–26. *Archinacella cingulata* Ulrich, 1897 (p. 079).
- 22–24. Dorsal and right- and left-lateral views of holotype, a weathered silicified specimen ( $\times 2$ ). Curdsville Limestone Member (Kirkfieldian), Lexington Limestone, Mercer Co., Ky. USNM 45686.
  - 25, 26. Dorsal and left-lateral views of internal mold ( $\times 1.5$ ). Clays Ferry Formation (Edenian), Owenton, Ky. MU 249T.



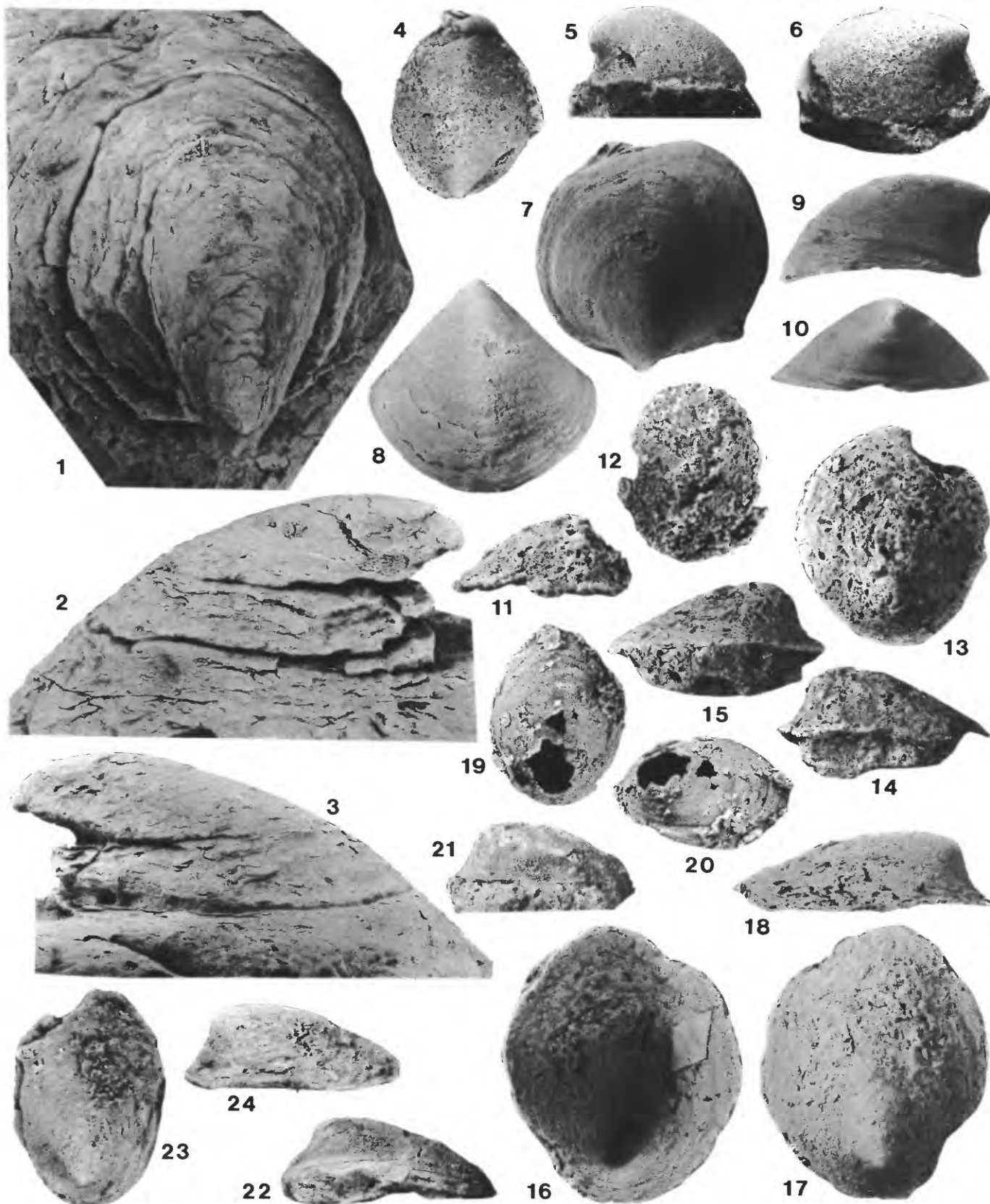


*HELCIONOPSIS* AND *ARCHINACELLA*

### PLATE 3

[All dorsal and ventral views have anterior end down]

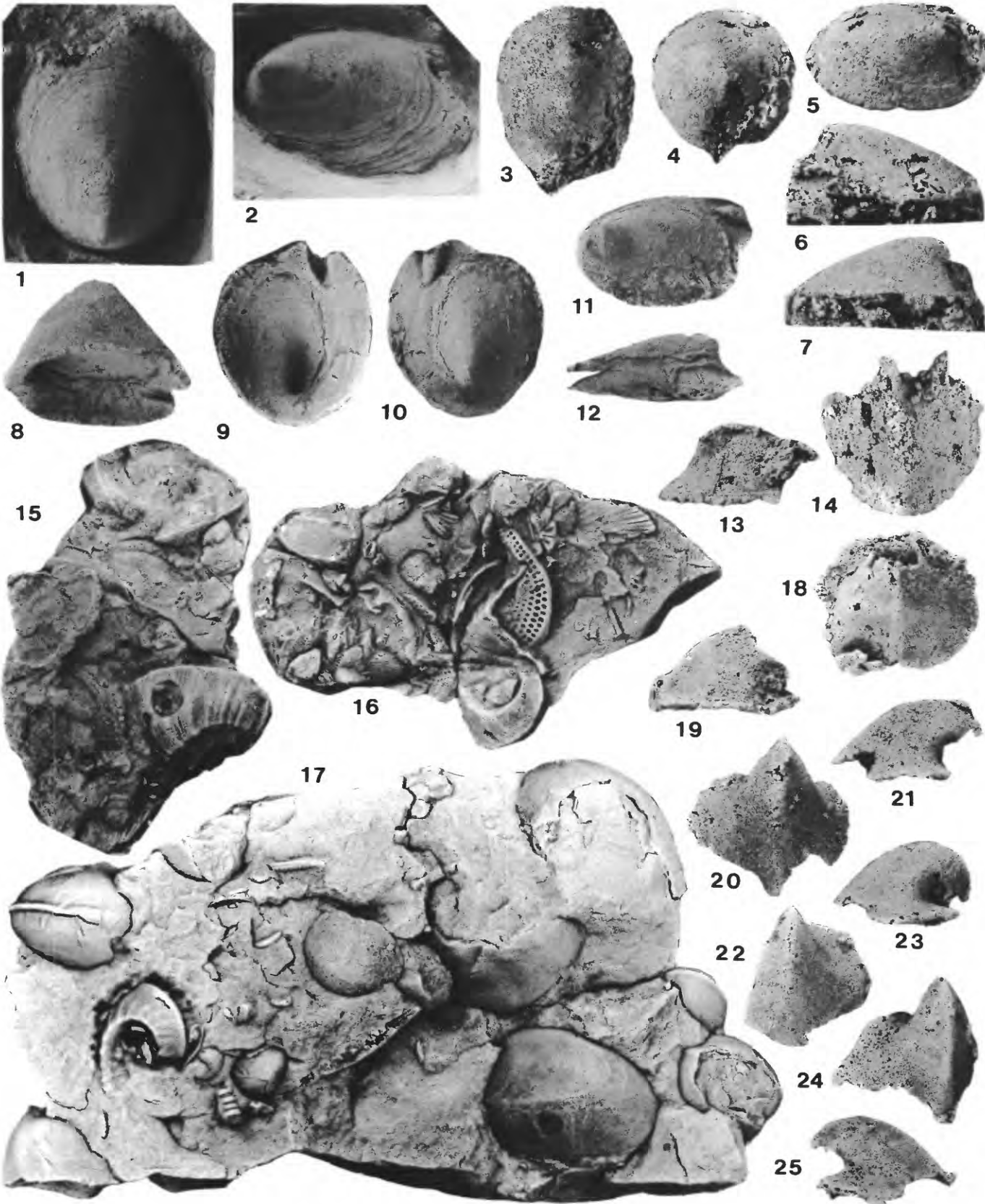
- FIGURES 1–3. *Archinacella? davisii* new species (p. O80). Dorsal and right- and left-lateral views of holotype, an internal mold ( $\times 1.0$ ). Kope Formation(?) (Edenian?), near Glencoe, Ky. CMNH P2.
- 4–6. *Archinacella alta* new species (p. O80). Dorsal, left-lateral, and oblique right-lateral views of holotype ( $\times 2$ ). Clays Ferry Formation (Edenian), northern Kentucky. MU 248T.
- 7–10. *Archinacella arca* new species (p. O82). Dorsal, posterior, right-lateral, and anterior views of holotype ( $\times 2$ ). Waynesville biofacies, Bull Fork Formation (Richmondian), Waynesville, Ohio. USNM 40615.
- 11, 12. *Archinacella* sp. (p. O75). Right-lateral and dorsal views of coarsely silicified specimen ( $\times 2$ ). Grier Limestone Member (Shermanian), Lexington Limestone, USGS 4073-CO. USNM 265955.
- 13–24. *Archinacella indianensis* (Miller, 1892) (p. O83).
- 13–15. Dorsal and left- and right-lateral views of holotype, a highly weathered internal mold ( $\times 1.5$ ). Museum label gives horizon and locality as “Richmond, Fayette County, Indiana.” UC 6065.
- 16–18. Ventral view of external mold in the base of a bryozoan colony, and dorsal and right-lateral views of latex mold ( $\times 2$ ). Holotype of *Archinacella richmondensis* Ulrich (1897). Whitewater Formation (Richmondian), Richmond, Ind. USNM 45691.
- 19, 20. Dorsal and oblique dorsal views of silicified specimen ( $\times 2$ ). Liberty biofacies, Dillsboro Formation (Richmondian), Ind. USGS 6139-CO. USNM 265946.
21. Left-lateral view of calcitic cast ( $\times 2$ ). Elkhorn biofacies, Drakes Formation, from creek just south of Morning Sun, Ohio. MU 246T.
22. Left-lateral view of calcitic cast ( $\times 1.5$ ). Note arched lateral apertural margin. Same horizon and locality as figure 21 above. MU 250T.
- 23, 24. Dorsal and left-lateral views of calcitic cast ( $\times 2$ ). No data with specimen; probably from Richmondian strata of southwestern Ohio or southeastern Indiana. MU 247T.



ARCHINACELLA

## PLATE 4

- FIGURES 1-14. *Archinacella indianensis* (Miller, 1892) (p. O83). (Dorsal and ventral views have anterior end down.)
- 1, 2. Dorsal and left-dorsolateral views of calcitic cast showing rather irregular growth lines ( $\times 2$ ). White water biofacies, Drakes Formation (Richmondian), Oakland, Ohio. USNM 70467.
  - 3-7. Dorsal, anterodorsal, oblique right-lateral, and left- and right-lateral views of silicified specimen ( $\times 2$ ). Liberty biofacies, Dillsboro Formation, (Richmondian), Ind. USGS 6139-CO. USNM 265951.
  - 8-12. Ventrolateral and ventral views of external mold in the base of a bryozoan colony, and dorsal, left-dorsolateral, and right-lateral views of latex mold made from specimen ( $\times 2$ ). Waynesville biofacies, Bull Fork Formation (Richmondian), Oregonia, Ohio. USNM 47468.
  - 13, 14. Left-lateral and dorsal views of anterior portion of fragmentary silicified specimen ( $\times 2$ ). Same collection as figures 3-7 above. USNM 265949.
  - 15-17. *Cyrtolites* (*Cyrtolites*) *claysferryensis* new species (p. O100).
  - 15, 16. Both sides of small slab from a mollusk bed ( $\times 2$ ) containing a paratype of *C. (C.) claysferryensis*, gastropods, pelecypods, some cephalopods, small unidentifiable bellerophonaceans, the trilobite *Cryptolithus*, and brachiopod fragments. Note circular hole in dorsal slope of paratype (lower right) in figure 15, which may be a boring. Kope Formation (Edenian), from northern end of bench in roadcut on northwestern side of Carrollton, Ky., exit from Interstate I- 71 (locality KY-1). USNM 265959.
  17. Lower side of slab from lenticular mollusk bed containing *Sinuities*, *Sphenosphaera*, *Tetranota*, a paratype of *Cyrtolites (C.) claysferryensis* (middle left), small conispiral gastropods, and cephalopods, in that order of abundance ( $\times 1.5$ ). Lower Kope Formation (Edenian), about 10 ft above contact with Point Pleasant Tongue, Clays Ferry Formation, Bear Creek Quarry, just north of Ohio River between Neville and Chilo, Ohio (locality OH-1). USNM 315609.
  - 18-25. *Carinaropsis acuta* Ulrich and Scofield, 1897 (p. O177).
  - 18, 19. Dorsal and left-lateral views of silicified specimen ( $\times 2$ ). Note subcircular outline and rather wide selenizone in figure 18. Basal 2 ft of Curdsville Limestone Member (Kirkfieldian), Lexington Limestone, USGS 7784- CO. USNM 265992.
  - 20, 21. Dorsal and left-lateral views of silicified specimen ( $\times 2$ ). Curdsville Limestone Member (Kirkfieldian), Lexington Limestone, USGS 7784-CO. USNM 265993.
  - 22, 23. Dorsal and left-lateral views of silicified specimen ( $\times 3$ ). Curdsville Limestone Member (Kirkfieldian), Lexington Limestone, USGS 5100-CO. USNM 265994.
  - 24, 25. Dorsal and right-lateral views of silicified specimen ( $\times 3$ ). Curdsville Limestone Member (Kirkfieldian), Lexington Limestone, USGS 5023-CO. USNM 265995.



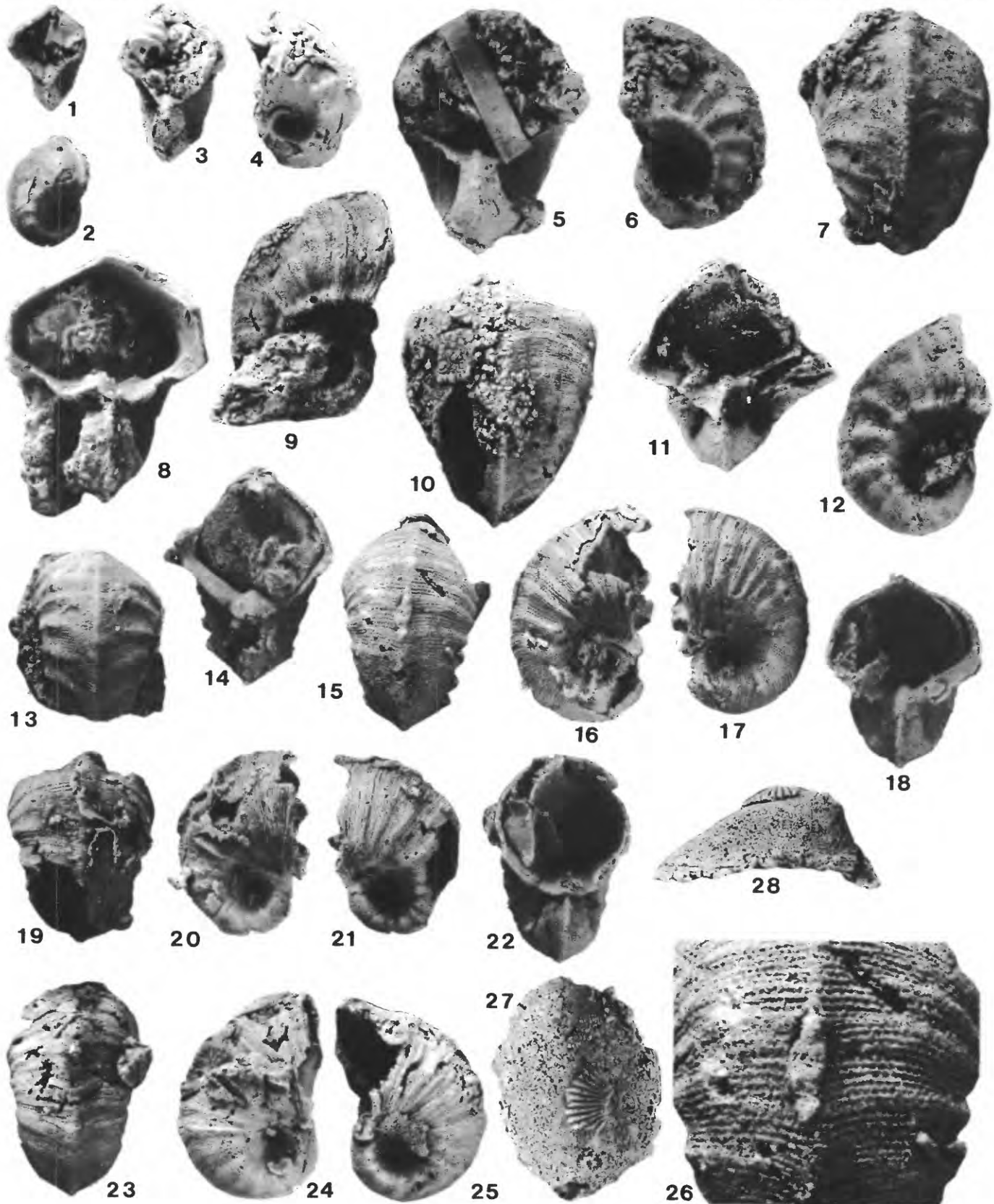
ARCHINACELLA, CYRTOLITES, AND CARINAROPSIS



## PLATE 5

FIGURES 1–26. *Cyrtolites* (*Cyrtolites*) *retrorsus* Ulrich, 1897 (p. 094).

- 1, 2. Apertural and left-lateral views of a paralectotype ( $\times 2$ ). Lexington Limestone, about 1 mi south of Burgin, Ky. USNM 265938.
- 3, 4. Apertural and right-lateral views of a paralectotype ( $\times 2$ ). Lexington Limestone, about 1 mi south of Burgin, Ky. USNM 265899.
- 5–7. Apertural, right-lateral, and dorsal views of lectotype ( $\times 2$ ). Museum label reads “Trenton [Kirkfieldian-Shermanian] near Nashville, Tennessee.” USNM 45789.
- 8–10. Apertural, left-lateral, and dorsal views of a paralectotype ( $\times 2$ ). Museum label reads “Trenton [Kirkfieldian-Shermanian], near Nashville, Tennessee.” USNM 265901.
- 11, 12. Apertural and left-lateral views of a paralectotype ( $\times 2$ ). Museum label reads “Trenton [Kirkfieldian-Shermanian], near Nashville, Tennessee.” USNM 265902.
13. Dorsal view of a paralectotype ( $\times 2$ ). Lexington Limestone, about 1 mi south of Burgin, Ky. USNM 265900.
- 14–17. Apertural, dorsal, and left- and right-lateral views ( $\times 2$ ). Lower Logana Member (Kirkfieldian), Lexington Limestone, USGS 6419- CO. USNM 265903.
- 18–21. Apertural, dorsal, and left- and right-lateral views ( $\times 2$ ). Same collection as figures 14–17 above. USNM 265904.
- 22–25. Apertural, dorsal, and left- and right-lateral views ( $\times 2$ ). Same collection as figures 14–17 above. USNM 265905.
26. Dorsal view illustrating shell sculpturing; enlargement of specimen shown in figures 14–17 above ( $\times 5$ ).
- 27, 28. *Archinacella indianensis* (Miller, 1892) (p. 083). Dorsal and right-lateral views ( $\times 3$ ). Liberty biofacies, Dillsboro Formation (Richmondian), USGS 6139- CO. USNM 265950.



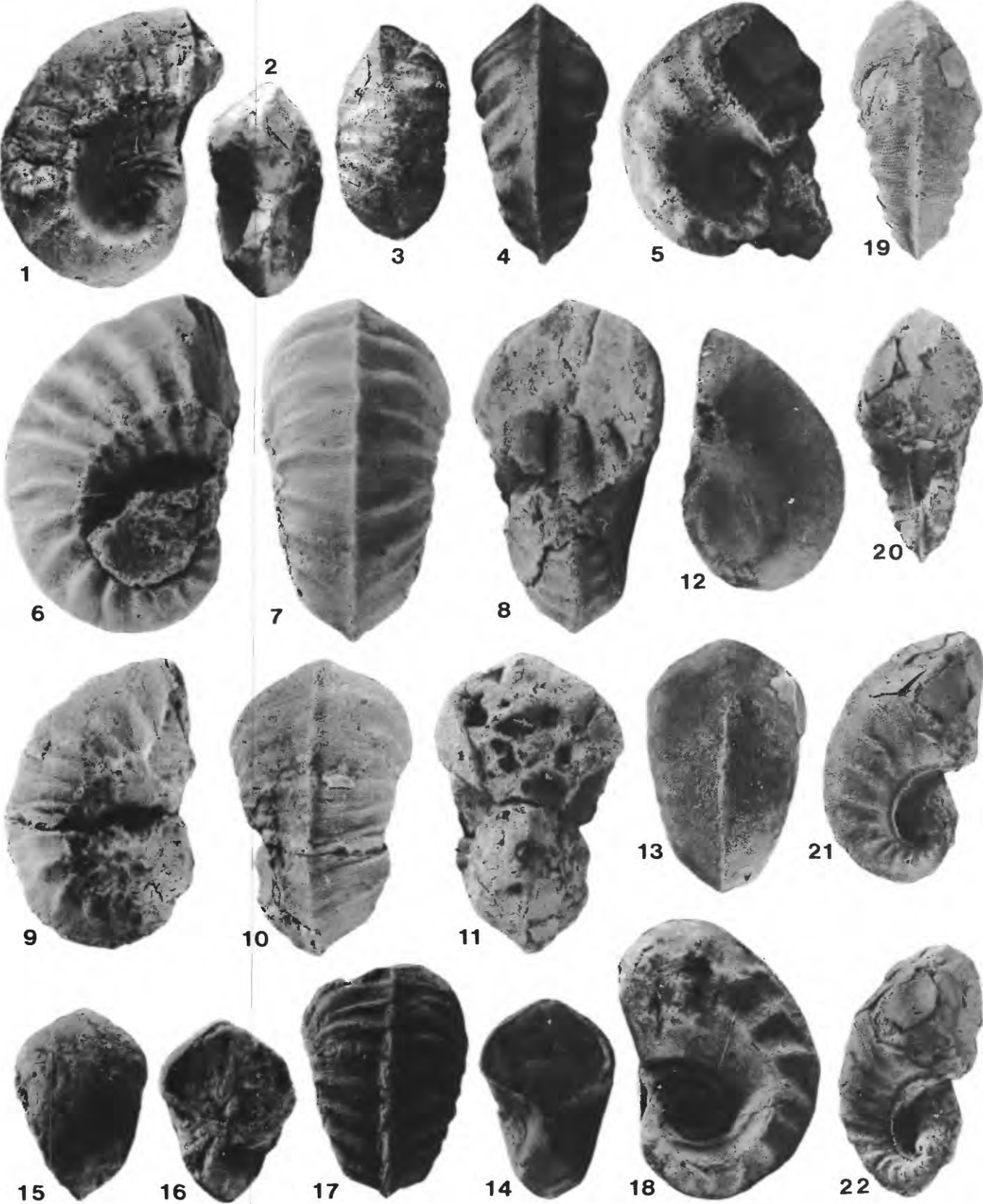
CYRTOLITES AND ARCHINACELLA



## PLATE 6

FIGURES 1–18. *Cyrtolites* (*Cyrtolites*) *ornatus* Conrad, 1838 (p. O91).

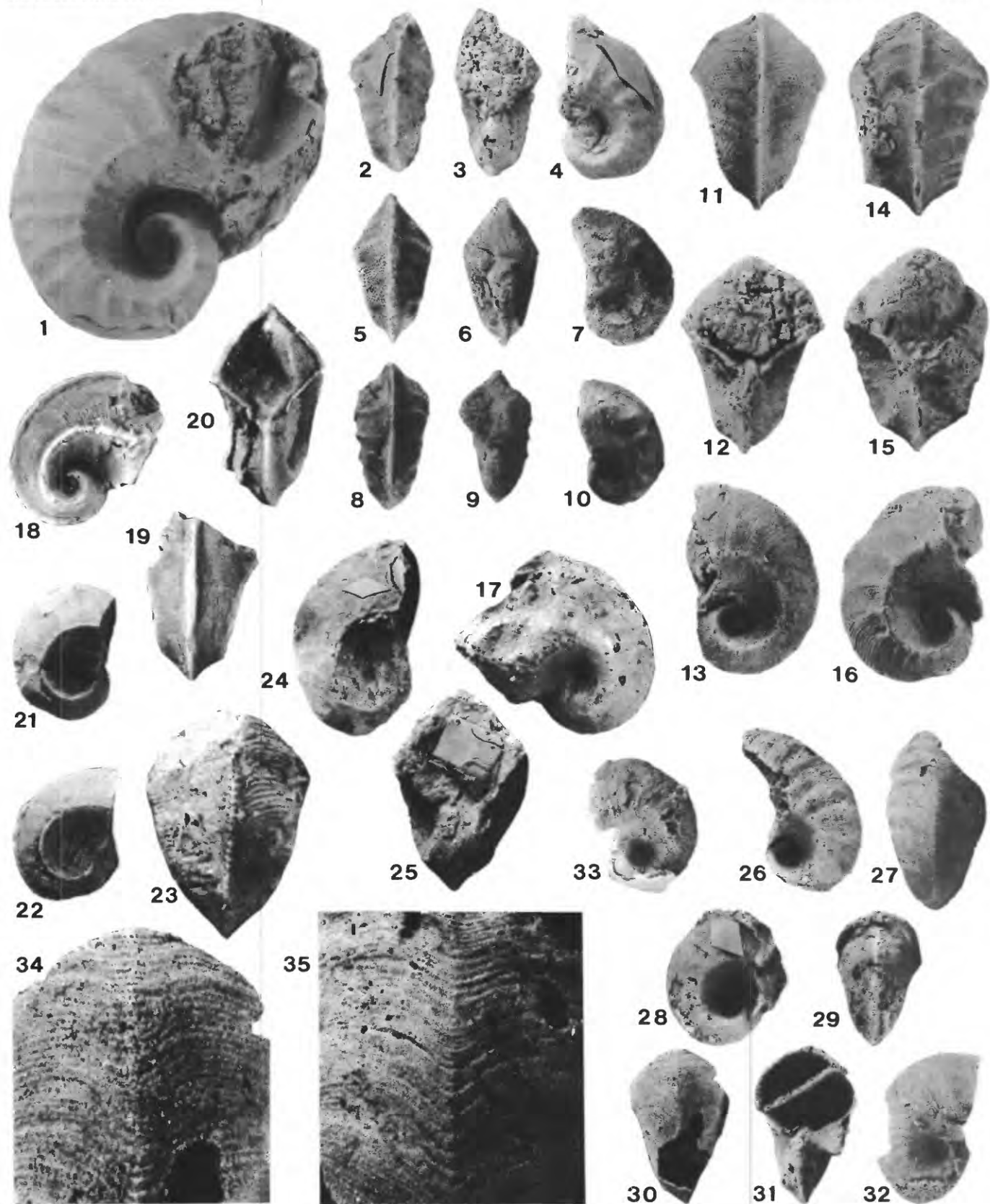
- 1–3. Left-lateral ( $\times 2$ ), apertural ( $\times 1.5$ ), and dorsal ( $\times 1.5$ ) views of an Ulrich and Scofield (1897) hypotype. Corryville biofacies, Grant Lake Limestone or Bull Fork Formation (Maysvillian), Cincinnati, Ohio. USNM 45786.
- 4, 5. Dorsal and left-lateral views of internal mold ( $\times 2$ ). Museum label gives locality and horizon as “Hudson River Group [Upper Ordovician], northern New York.” UCGM 44270.
- 6–8. Left-lateral, dorsal, and apertural views of composite mold ( $\times 2$ ). Same locality and horizon as figures 1–3 above. USNM 265906.
- 9–11. Left-lateral, dorsal, and apertural views of composite mold ( $\times 2$ ). Same locality and horizon as figures 1–3 above. USNM 265907.
- 12–14. Right-lateral ( $\times 2$ ), dorsal ( $\times 2$ ) and apertural ( $\times 1.5$ ) views of bryozoan-encrusted specimen. Museum label gives horizon as “Maysville”; locality not given, but the vicinity of Cincinnati, Ohio, seems likely. UCGM 44273.
- 15, 16. Dorsal and apertural views of bryozoan-encrusted specimen ( $\times 1.5$ ). Museum label gives horizon as “Richmond”; locality not given, but southwestern Ohio is likely. UCGM 44272.
17. Dorsal view of vertically compressed specimen preserving calcitic shell ( $\times 1.5$ ). Same sample as figures 15, 16 above. UCGM 44271.
18. Right-lateral view of disjunct internal mold ( $\times 2$ ). Waynesville biofacies, Rowland Member, Drakes Formation (Richmondian), southwestern Ohio. UCGM 44274.
- 19–22. *Cyrtolites* (*Cyrtolites*) *disjunctus* Ulrich and Scofield, 1897 (p. O106). Dorsal, apertural, left-lateral, and oblique left-lateral views of holotype, which is a calcitic specimen ( $\times 2$ ). Museum label gives horizon and locality as “Richmond Group, near Spring Valley, Minnesota.” USNM 45785.



CYRTOLITES

## PLATE 7

- FIGURES
1. *Cyrtolites (Cyrtolites) ornatus* Conrad, 1838 (p. 091). Right-lateral view of disjunct internal mold ( $\times 2$ ). Same sample and locality as on plate 6, figures 1–3. USNM 265908.
  - 2–10. *Cyrtolites (Cyrtolites) minor* Ulrich, 1897 (p. 0102).
    - 2–4. Dorsal, apertural, and right-lateral views of holotype ( $\times 3$ ). Museum label gives horizon and locality as “*Clitambonites* bed, Trenton (Prosser), Cannon Falls, Minnesota.” USNM 45787.
    - 5–7. Dorsal, apertural, and right-lateral views of bryozoan-encrusted specimen ( $\times 2.5$ ). McMicken biofacies, Kope Formation (Edenian); no locality given, but probably from the Cincinnati, Ohio, area. UCGM 19668.
    - 8–10. Dorsal, apertural, and right-lateral views of calcitic cast ( $\times 2$ ). Contact of Fairview Formation and Miamitown Shale (Maysvillian). Hamilton-Butler Co. line, Ohio. USNM 44275.
  - 11–16. *Cyrtolites (Cyrtolites) retrorsus* Ulrich, 1897 (p. 094).
    - 11–13. Dorsal, apertural, and right-lateral views of calcitic cast ( $\times 3$ ). Kope Formation (Edenian), Covington, Ky. USNM 265909.
    - 14–16. Dorsal, apertural, and left-lateral views of calcitic cast ( $\times 3$ ). Same collection and locality as figures 11–13 above. USNM 265910.
  17. *Cyrtolites (Paracyrtolites) parvus* Ulrich, 1897 (p. 0109). Right-lateral view of holotype ( $\times 4$ ). A museum label gives horizon and locality as “Upper Trenton [Shermanian], Covington, Kentucky.” USNM 45788.
  - 18–25. *Cyrtolites (Paracyrtolites) carinatus* Miller, 1874 (p. 0108).
    - 18, 19. Left-lateral and dorsal views of holotype ( $\times 3$ ). Kope Formation (Edenian); locality given on museum label as “within two hundred feet of low water-mark, at Bold Face Creek, opposite Fifth Street, and at the excavation for Columbia Avenue.” Note that Columbia Avenue is now named Columbia Parkway in Cincinnati, Ohio. UC 8895.
    20. Apertural view of calcitic cast ( $\times 3$ ). Kope Formation (Edenian), from mollusk bed in lower part of large exposure just southeast of Carrollton, Ky. Collected by Steven Felton. UCGM 44277.
    21. Left-lateral view of composite mold, which is an Ulrich and Scofield (1897) hypotype ( $\times 2$ ). Southgate biofacies, Kope Formation (Edenian), Newport, Ky. USNM 265912.
    22. Left-lateral view of another Ulrich and Scofield (1897) hypotype ( $\times 2$ ). Same collection as figure 21 above. USNM 47499.
    23. Dorsal view of another Ulrich and Scofield (1897) hypotype, which retains the shell and its fine growth lines ( $\times 3$ ). Same collection as figure 21 above. USNM 265911.
    - 24, 25. Left-lateral and apertural views of another Ulrich and Scofield (1897) hypotype showing fine growth lines ( $\times 3$ ). Same collection as figure 21 above. USNM 265913.
  - 26–32, 34, 35. *Cyrtolites (Paracyrtolites) subplanus* Ulrich, 1897 (p. 0107).
    - 26, 27, 35. Right-lateral ( $\times 1.5$ ), dorsal ( $\times 1.5$ ), and dorsal closeup (about  $\times 4.5$ ) views of lectotype, a slightly weathered silicified cast. Note strong deflection of growth lines, reflecting a relatively deep sinus, and the faint trace of revolving threads along some growth lines. Cannon facies, Bigby- Cannon Limestone (Kirkfieldian-Shermanian), Snow’s Hill, 4 mi east of Liberty, Tenn. USNM 45792.
    - 28, 29. Left-lateral and dorsal views of a paralectotype ( $\times 2$ ). Same collection as figures 26, 27 above. USNM 265914.
    - 30–32, 34. Dorsal, apertural, and left-lateral views (all  $\times 2$ ) and dorsal closeup view showing detail of shell sculpturing (about  $\times 5$ ). Note weak revolving threads, which give surface a faintly pitted appearance. Logana Member, Lexington Limestone (Kirkfieldian), USGS D-1196-CO. USNM 265915.
  33. *Cyrtolites (Paracyrtolites) cf. C. (P.) subplanus* Ulrich, 1897 (p. 0107). Right-lateral view of silicified specimen ( $\times 2$ ). Grier Limestone Member, Lexington Limestone (Shermanian), USGS 4852-CO. USNM 265918.

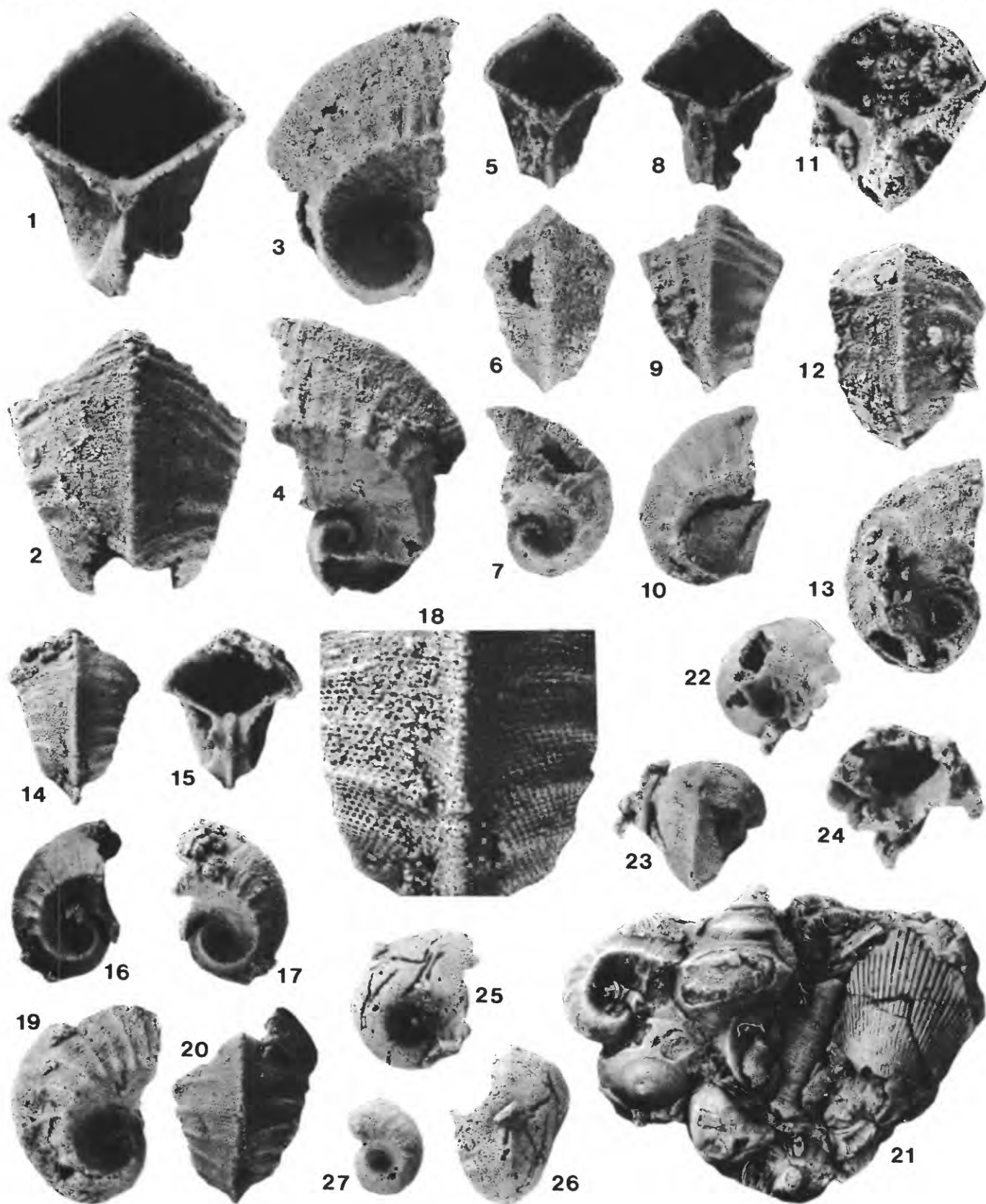


CYRTOLITES

## PLATE 8

- FIGURES 1–10. *Cyrtolites* (*Cyrtolites*) *hornyi* new species (p. O104).  
 1–4. Apertural, dorsal, and left- and right-lateral views of holotype ( $\times 2$ ). Liberty biofacies, Dillsboro Formation (Richmondian), USGS 6139-CO. USNM 265920.  
 5–7. Apertural, dorsal, and right-lateral views of a paratype ( $\times 1$ ). Same collection as figures 1–4 above. USNM 265921.  
 8–10. Apertural, dorsal, and left-lateral views of another paratype ( $\times 1$ ). Same collection as figures 1–4 above. USNM 265922.
- 11–20. *Cyrtolites* (*Cyrtolites*) *claysferryensis* new species (p. O100).  
 11–13. Apertural, dorsal, and left-lateral views of a paratype ( $\times 2$ ). Clays Ferry Formation (Edenian), USGS 6990-CO. USNM 265925.  
 14–18. Dorsal, apertural, and left- and right-lateral views of holotype (all  $\times 2$ ) and dorsal closeup view of shell sculpturing (about  $\times 6$ ). Upper tongue of Clays Ferry Formation, USGS 6143-CO. USNM 265924.  
 19, 20. Left-lateral and dorsal views of a paratype ( $\times 2$ ). Same collection as figures 14–18 above. USNM 265923.
21. *Cyrtolites* (*Paracyrtolites*) *carinatus* Miller, 1874 (p. O108). Small slab from mollusk bed. Same horizon and locality as plate 7, figure 20, Kope Formation (Edenian), near Carrollton, Ky ( $\times 2$ ). Also shows the univalves *Lophospira*, *Liospira*, and *Sinuities*, the pelecypod *Ambonychia*, and cephalopod fragments. Collected by Steven Felton. UCGM 44279.
- 22–26. *Cyrtolites* (*Paracyrtolites*) cf. *C. (P.) subplanus* Ulrich, 1897 (p. O107).  
 22–24. Left-lateral, dorsal, and apertural views of silicified specimen ( $\times 2$ ). Grier Limestone Member, Lexington Limestone, USGS 4852-CO. USNM 265916.  
 25, 26. Left-lateral and dorsal views of worn silicified specimen, which has been bored ( $\times 2$ ). Same collection as figures 22–24 above. USNM 265919.
27. *Cyrtolites* (*Paracyrtolites*) *subplanus* Ulrich, 1897 (p. O107). Right-lateral view of small silicified specimen ( $\times 2$ ). Logana Member, Lexington Limestone. USGS D-1196-CO. USNM 265917.





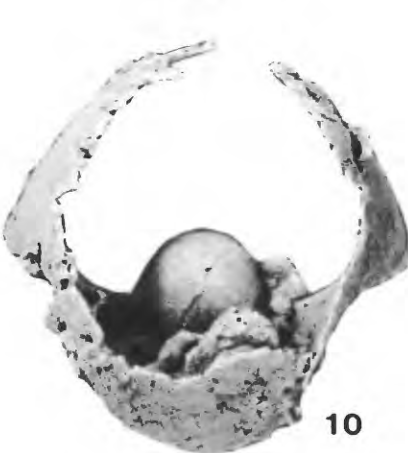
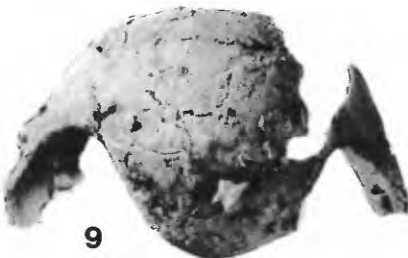
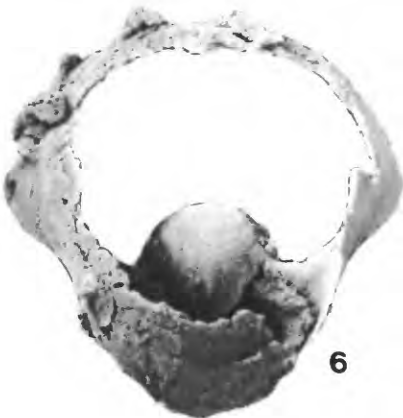
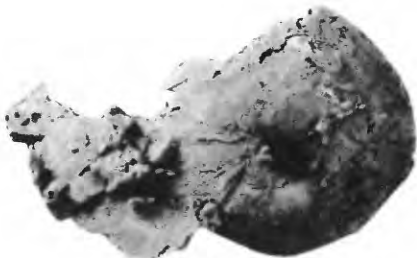
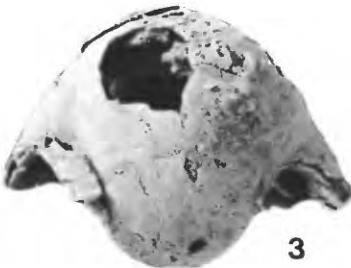
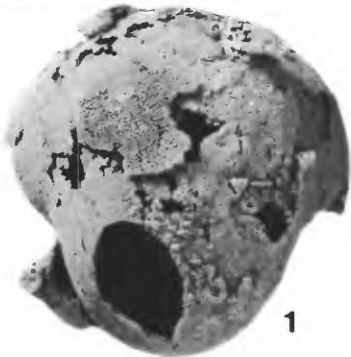
CYRTOLITES

## PLATE 9

FIGURES 1-12. *Simuities obesus* (Ulrich), 1897 (p. 0112).

- 1-4. Dorsal, ventral, anterior, and left-lateral views of silicified specimen ( $\times 1.5$ ). Curdsville Limestone Member (Kirkfieldian), Lexington Limestone, USGS 5022-CO. USNM 315634.
5. Dorsal view of silicified specimen preserving trace of growth lines ( $\times 1.5$ ). Logana Member (Kirkfieldian), Lexington Limestone, USGS 5092-CO. USNM 315636.
- 6-9. Dorsal, ventral, right-lateral, and anterior views of fragmentary silicified specimen ( $\times 1.5$ ). Same collection as figure 5 above. USNM 315635.
- 10-12. Dorsal, ventral, and posterior views of fragmentary silicified specimen ( $\times 2$ ). Same collection as figure 5 above. USNM 315637.



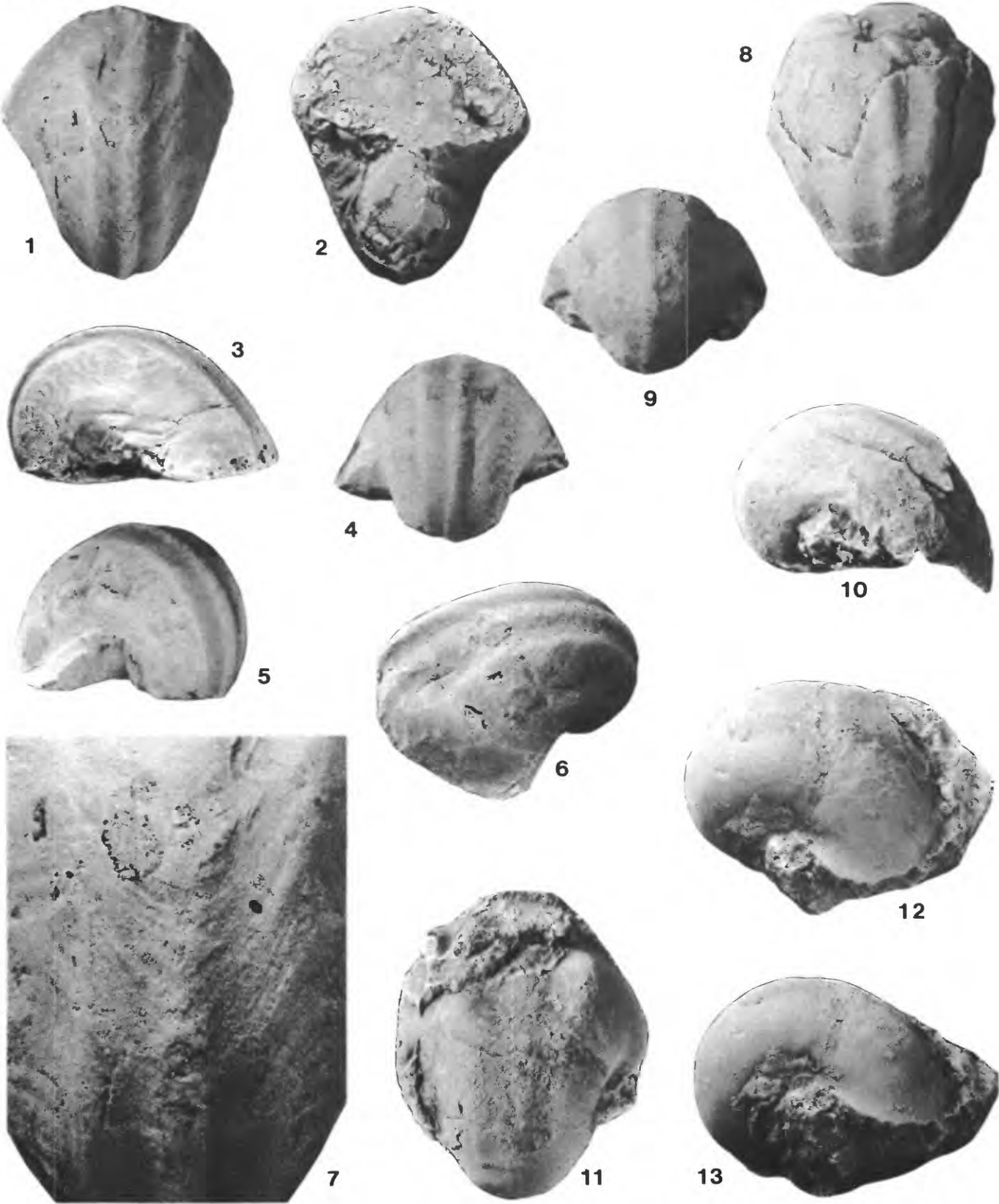


*SINUITES*

## PLATE 10

FIGURES 1–13. *Sinuities globularis* (Miller and Faber), 1894 (p. 0114).

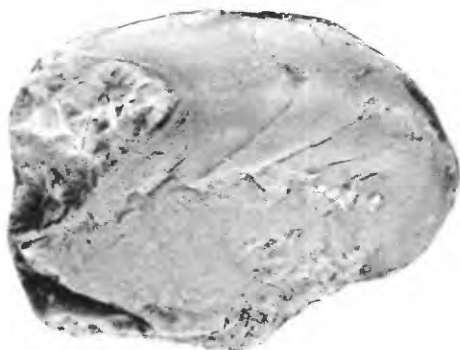
- 1–7. Dorsal, ventral, left-lateral, anterior, right- anterolateral, and right-dorsolateral views ( $\times 2.5$ ) and closeup dorsal view ( $\times 6.75$ ) of calcitic lectotype. Kope Formation (Edenian), Cincinnati, Ohio. UC 8811a.
- 8–10. Dorsal, anterior, and left-lateral views of another calcitic specimen ( $\times 3$ ). Kope Formation (Edenian), Carrollton, Ky. UCGM 44305.
- 11–13. Dorsal, left-dorsolateral, and left-lateral views of calcitic paralectotype ( $\times 2.5$ ). Same locality as figures 1–7 above. UC 8811b.



SINUITES

PLATE 11

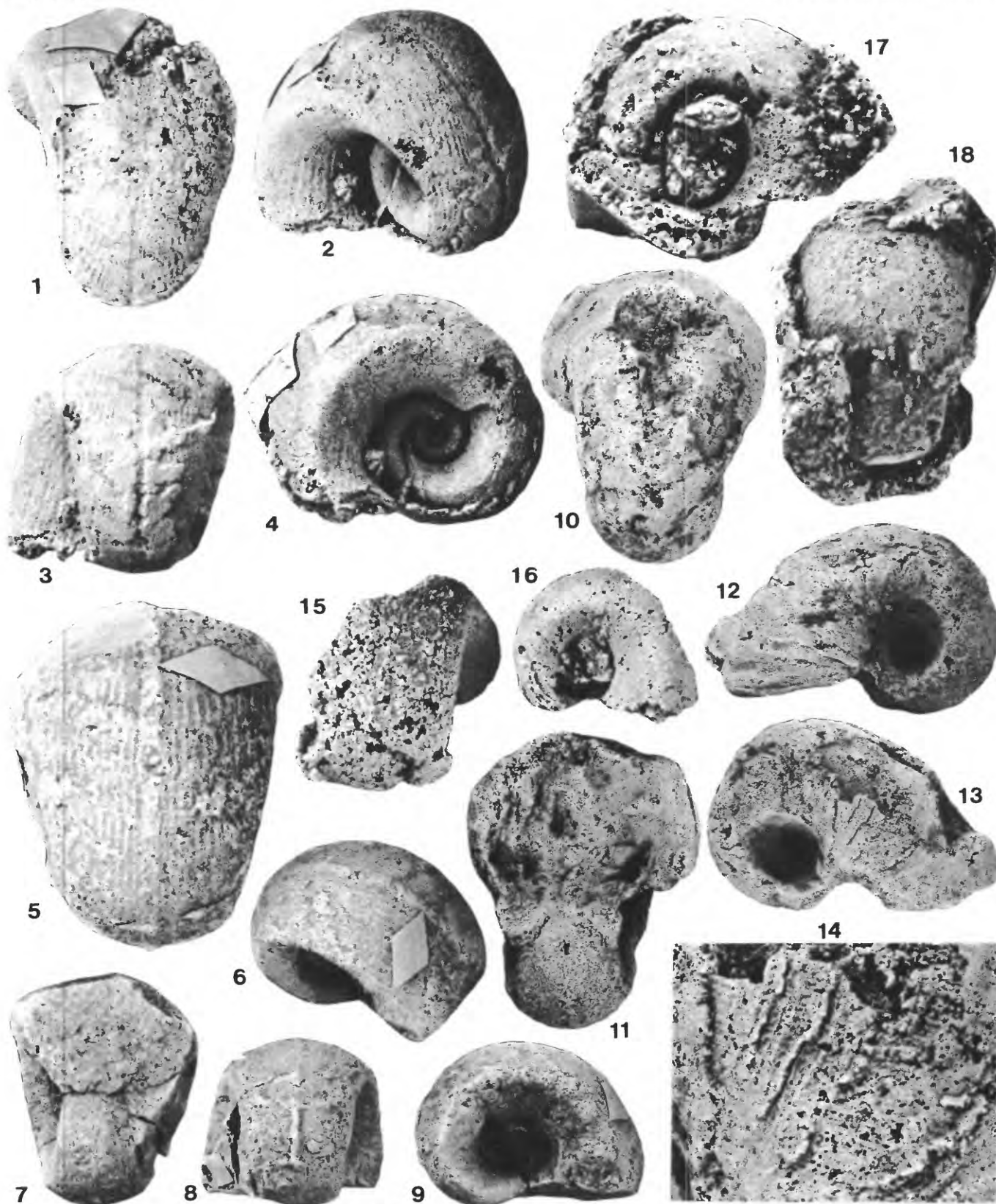
- FIGURES 1–5. *Sinuities granistriatus* (Ulrich), 1897 (p. O113). Dorsal, right-dorsolateral, right-lateral, and ventral views ( $\times 2$ ) and closeup dorsal view ( $\times 4.5$ ) of calcitic specimen preserving the growth lines. Kope Formation, Chilo, Ohio (locality OH-1). UCGM 44295.
- 6–12. *Sinuities cancellatus* (Hall), 1847 (p. O111).
- 6–9. Dorsal, anterior, right-lateral, and left- anterolateral views of calcitic specimen with shell weathered away dorsally ( $\times 2$ ). Museum label reads only “Cincinnatian, Cincinnati, Ohio.” UCGM 44304.
- 10–12. Dorsal, posterior, and left-lateral views of calcitic specimen ( $\times 2$ ). Kope Formation (Edenian), Cincinnati, Ohio. UCGM 44307.



*SINUITES*

## PLATE 12

- FIGURES 1–4. *Bucania emmonsii* Ulrich and Scofield, 1897 (p. 0128). Dorsal, left-posterolateral, posterior, and left-lateral views of silicified lectotype ( $\times 3$ ). Murfreesboro Limestone (Blackriveran), Tenn. USNM 46049.
- 5–16. *Bucania halli* Ulrich and Scofield, 1897 (p. 0129).
- 5–9. Dorsal ( $\times 3$ ) and right-anterodorsal, ventral, posterior, and right-lateral ( $\times 2$ ) views of lectotype. Museum label reads “Black River Group Decorah Formation [Rocklandian], Cannon Falls, Minnesota.” USNM 45717.
- 10–14. Dorsal, ventral, left-lateral, and right-lateral views of a paralectotype ( $\times 1.5$ ) and right-lateral closeup view ( $\times 6$ ) showing shell markings. Curdsville Limestone Member (Kirkfieldian), Lexington Limestone, Mercer Co., Ky. USNM 315582.
- 15, 16. Anterior and right-lateral views of fragmentary silicified specimen ( $\times 3$ ). Grier Limestone Member (Shermanian), Lexington Limestone, USGS 4073-CO. USNM 315544.
- 17, 18. *Bucania* cf. *B. halli* Ulrich and Scofield. Right-lateral and dorsal views of silicified specimen ( $\times 2$ ). Lower Curdsville Limestone Member (Kirkfieldian), Lexington Limestone, USGS 5100-CO. USNM 315545.

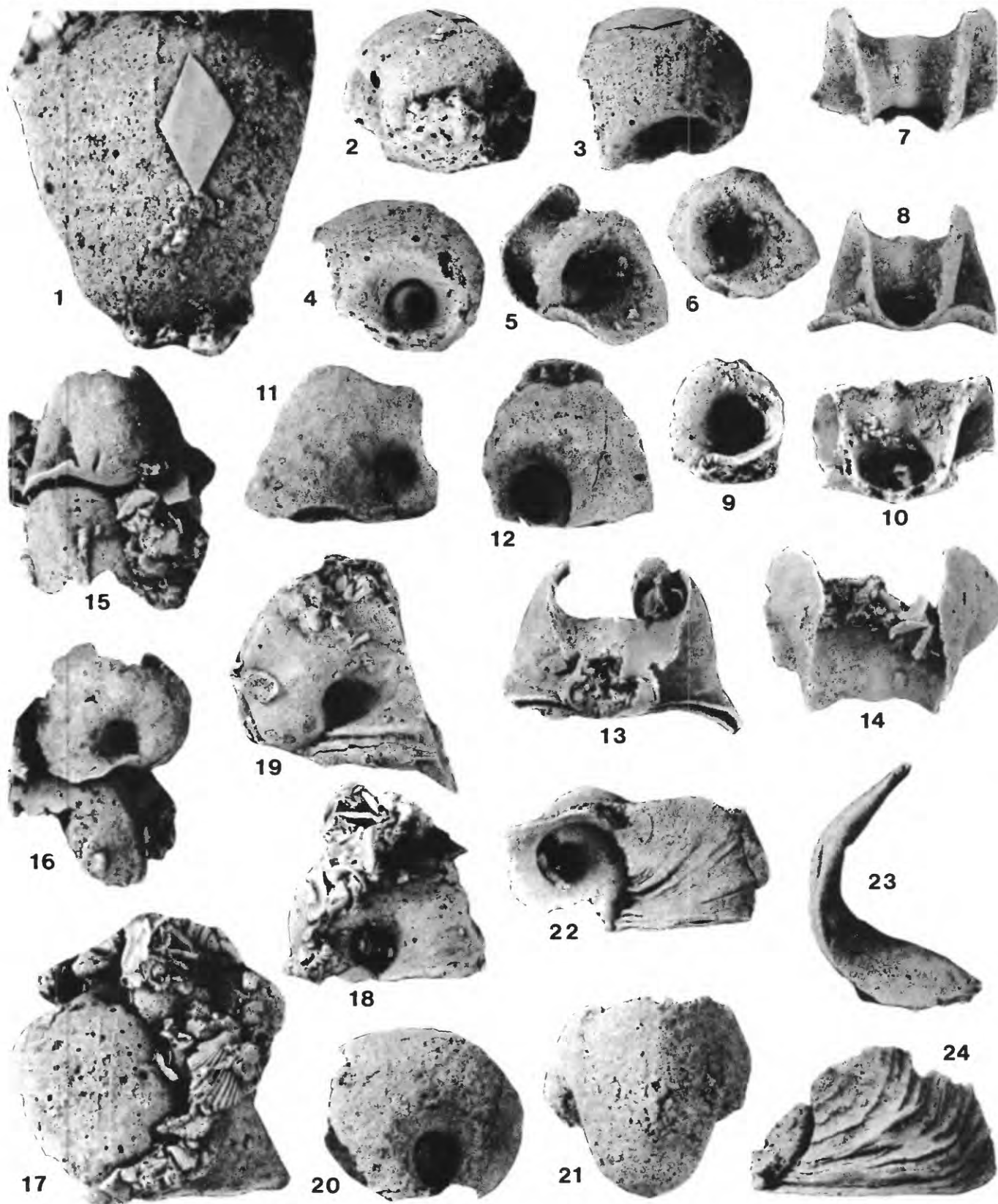


*BUCANIA*



## PLATE 13

- FIGURES 1–8. *Bucania sublata* Ulrich and Scofield, 1897 (p. O135).
- 1–4. Dorsal ( $\times 5$ ) and posterior, left- dorsolateral, and left-lateral ( $\times 3$ ) views of silicified lectotype. Lexington Limestone, near Burgin, Ky. USNM 315561.
  - 5–8. Right-posterolateral, right-lateral, dorsal, and posterior views of silicified fragment showing large umbilicus, reflexed parietal lip, and broad median parietal ridge ( $\times 2$ ). Same collection as figures 1–4 above. Paralectotype, USNM 315562.
- 9–14. *Bucania* cf. *B. sublata* Ulrich and Scofield, 1897 (p. O135).
- 9, 10. Right-lateral and dorsal views of silicified fragment ( $\times 3$ ). Grier Limestone Member, Lexington Limestone, USGS 4879-CO. USNM 315563.
  - 11. Left-lateral view of silicified fragment ( $\times 2$ ). Faulconer Bed, Perryville Limestone Member, Lexington Limestone, USGS 6136-CO. USNM 315564.
  - 12–14. Right-lateral, posterior, and dorsal views of large silicified fragment ( $\times 1.5$ ). Devils Hollow Member, Lexington Limestone, USGS 5095- CO. USNM 315565.
- 15–21. *Bucania nashvillensis* Ulrich, 1897 (p. O132).
- 15, 16. Two views of two silicified specimens cemented together with other skeletal debris showing characteristic small umbilicus and narrowly rounded dorsum ( $\times 2$ ). Salvisa Bed, Perryville Limestone Member, Lexington Limestone, USGS 5015-CO. USNM 315566.
  - 17, 18. Posterior ( $\times 3$ ) and right-lateral ( $\times 2$ ) views of incomplete specimen. Same collection as figures 15, 16 above. USNM 315567.
  - 19. Right-posterolateral view of silicified fragment showing small umbilicus, angular dorsum, and thickened parietal lip ( $\times 2$ ). Same collection as figures 15, 16 above. USNM 315568.
  - 20, 21. Left-lateral and dorsal views of silicified specimen ( $\times 2$ ). Salvisa Bed, Perryville Limestone Member, Lexington Limestone, USGS 6916-CO. USNM 315569.
- 22–24. *Bucania frankfortensis* Ulrich, 1897 (p. O133).
- 22. Right-lateral view of silicified fragment showing characteristic wrinkled lateral apertural slope ( $\times 2$ ). Devils Hollow Member, Lexington Limestone, USGS 5036-CO. USNM 315571.
  - 23, 24. Ventral and right-lateral views of silicified fragment showing subtriangular apertural outline and wrinkled lateral apertural slope ( $\times 2$ ). Same collection as figure 22 above. USNM 315570.



*BUCANIA*

## PLATE 14

FIGURES 1–14. *Bucania nashvillensis* Ulrich, 1897 (p. O132).

1–5. Anterior, posterior, left-lateral, dorsal, and ventral views of a silicified paralectotype ( $\times 1.5$ ). Cannon facies, Bigby-Cannon Limestone, Nashville, Tenn. USNM 45724.

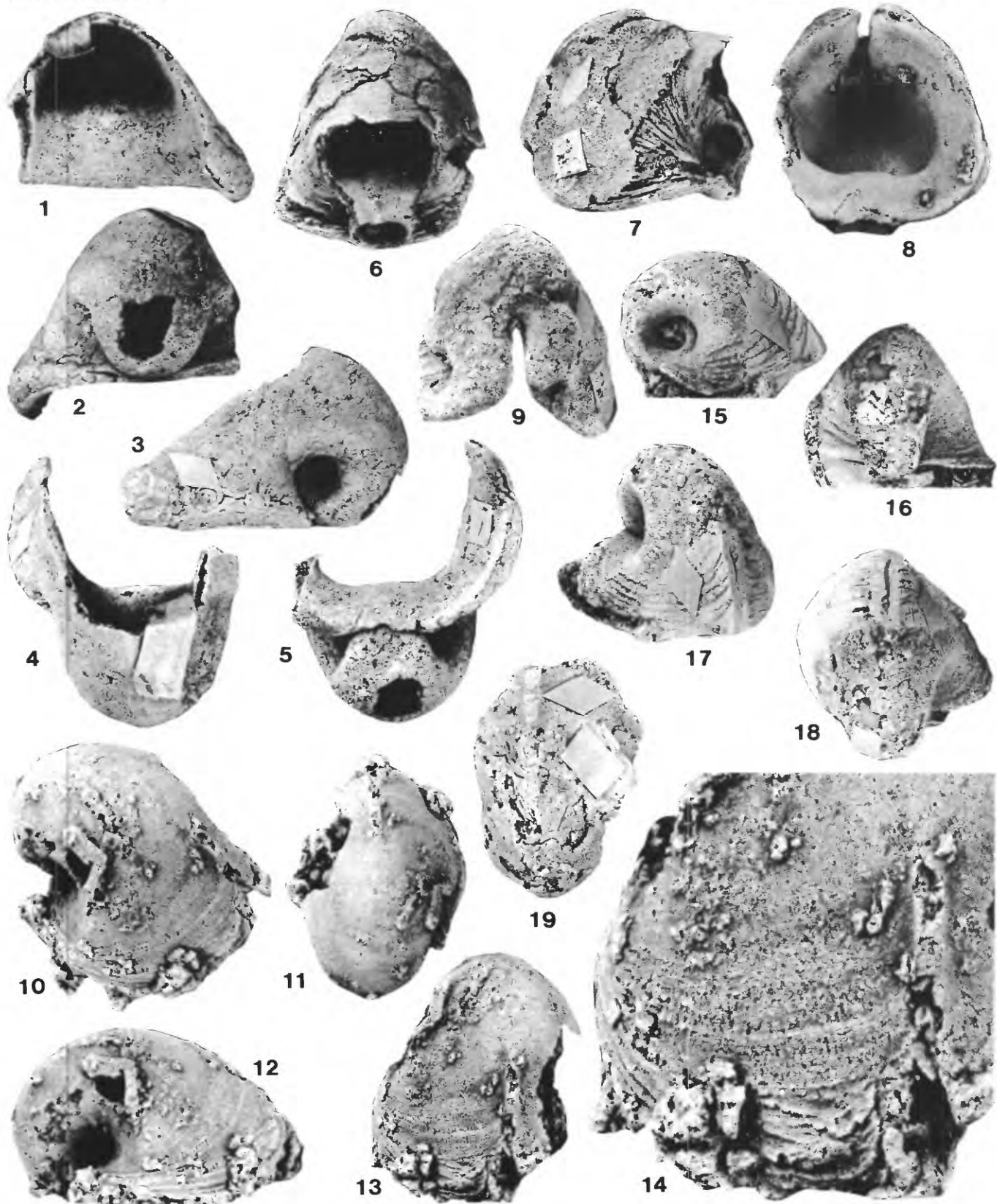
6–9. Posterodorsal, left-lateral, ventral, and anterior views of a bryozoan-encrusted, silicified paralectotype showing deep slit and mature lamellose growth lines ( $\times 1.5$ ). Cannon facies, Bigby-Cannon Limestone, Dekalb Co., Tenn. USNM 315558.

10–14. Oblique anterolateral, dorsal, right-lateral, and anterodorsal views of lectotype ( $\times 2$ ) and closeup view of slit and shell ornament ( $\times 5$ ). Same collection as figures 6–9 above. USNM 315557.

15–19. *Bucania subangulata* Ulrich, 1897 (p. O130).

15–18. Right-lateral, posterior, antero-right-lateral, and posterodorsal views of silicified lectotype, in which anterodorsal shell area has been reconstructed with plaster (lighter colored area) ( $\times 1.5$ ). Lexington Limestone, 1.5 mi south of Burgin, Ky. USNM 315559.

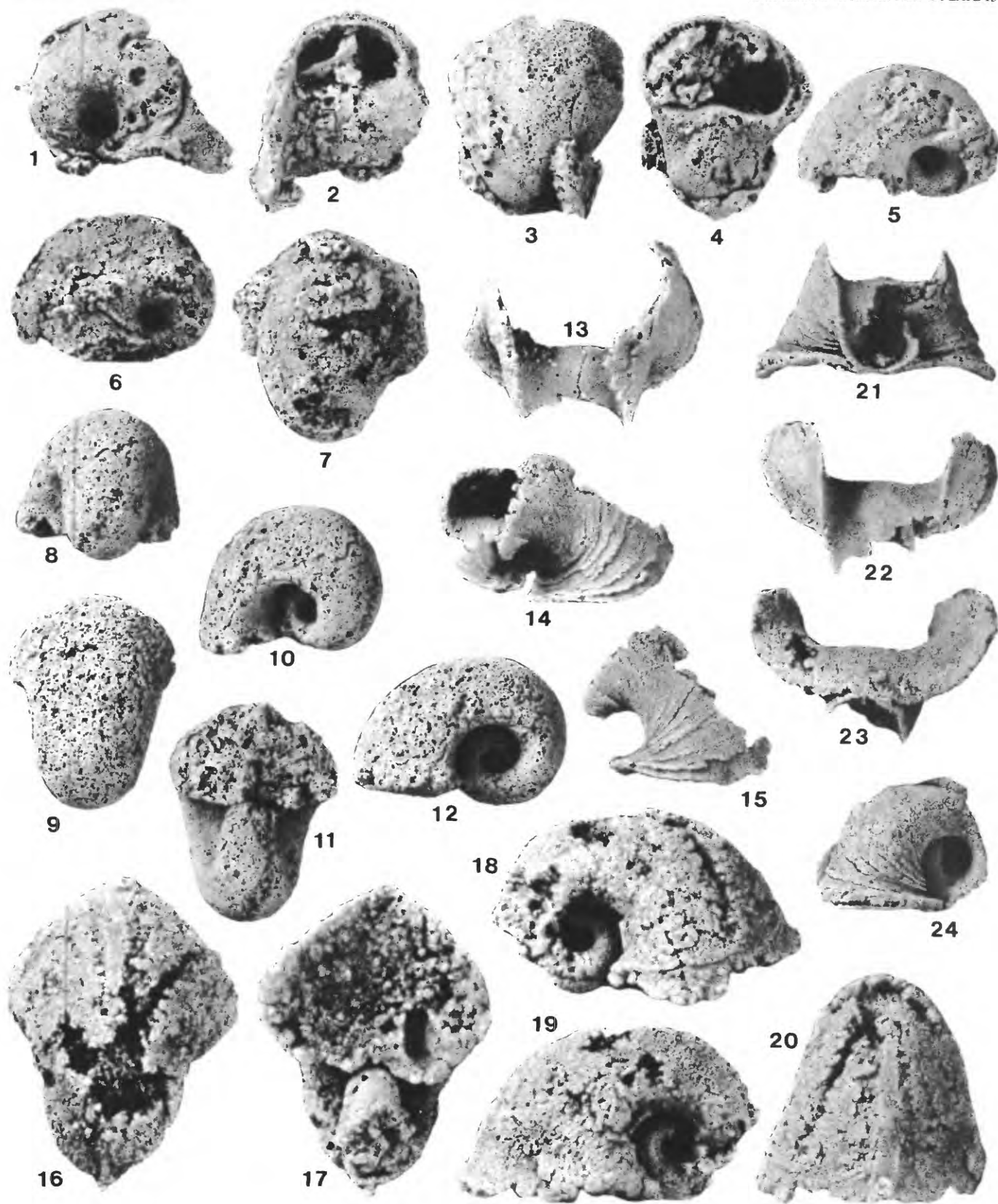
19. Dorsal view of a silicified paralectotype showing lunulae of selenizone and shell markings ( $\times 2$ ). Same collection as figures 15–18 above. USNM 315560.



*BUCANIA*

## PLATE 15

- FIGURES 1–7. *Bucania nashvillensis* Ulrich, 1897 (p. O132).
- 1, 2. Right-lateral and anterior views of fragmentary silicified specimen ( $\times 2$ ). Grier Limestone Member, Lexington Limestone, USGS 4959-CO. USNM 315572.
  - 3–5. Dorsal, ventral, and left-lateral views of fragmentary specimen ( $\times 3$ ). Same collection as figures 1, 2 above. USNM 315573.
  - 6, 7. Left-lateral and dorsal views of silicified specimen ( $\times 2.5$ ). Grier Limestone Member, Lexington Limestone, USGS 4073-CO. USNM 315574.
- 8–24. *Bucania subangulata* Ulrich, 1897 (p. O130).
- 8–12. Posterior, dorsal, left-posterior, ventral, and left-lateral views of silicified internal mold ( $\times 3$ ). Curdsville Limestone Member, Lexington Limestone, USGS 7785-CO. USNM 315575. (For a similar specimen from the Grier Limestone Member, USGS 5094-CO, see pl. 38, figs. 11, 12.)
  - 13–15. Dorsal, right-posterior, and right-lateral views of relatively large fragment of silicified specimen ( $\times 2.5$ ). Grier Limestone Member, Lexington Limestone, USGS 5094-CO. USNM 315576.
  - 16–20. Dorsal, ventral, right-lateral, left-lateral, and anterior views of small silicified specimen preserving selenizone ( $\times 4$ ). Same collection as figures 13–15 above. USNM 315577.
  - 21–24. Posterior, dorsal, ventral, and left-lateral views of fragment of silicified specimen ( $\times 2$ ). Grier Limestone Member, Lexington Limestone, USGS 5096-CO. USNM 315578.



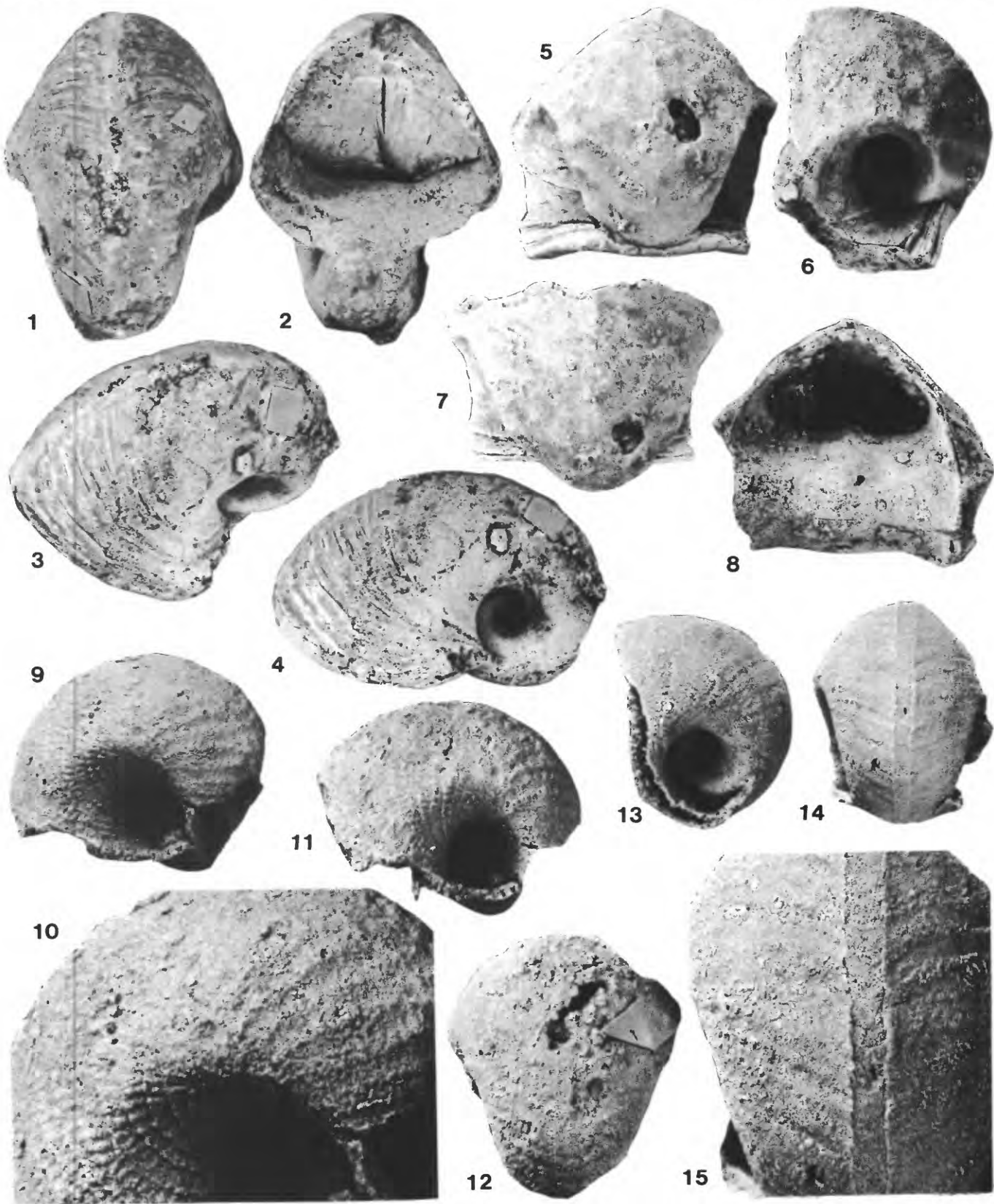
*BUCANIA*



## PLATE 16

- FIGURES 1-4. *Bucania frankfortensis* Ulrich, 1897 (p. O133). Dorsal, ventral, left-dorsolateral, and left-lateral views of silicified holotype ( $\times 1.5$ ), in which much of the dorsum and essentially all of the anteromedian shell have been reconstructed with plaster (the smoother, less granular surfaces). Probably Devils Hollow Member, Lexington Limestone, Frankfort, Ky. USNM 45716.
- 5-8. *Bucania peracuta* Ulrich, 1897 (p. O134). Posterior, left-lateral, dorsal, and cross-sectional views of silicified holotype ( $\times 1.5$ ), in which the anterior portion of the shell has been broken away. Cannon facies, Bigby-Cannon Limestone, Dekalb Co., Tenn. USNM 45726.
- 9-15. *Bucania rugatina* Ulrich, 1897 (p. O136).  
 9-12. Left-posterolateral view ( $\times 3$ ), closeup view of shell markings ( $\times 6$ ), and left-lateral and dorsal views ( $\times 3$ ) of lectotype. Lexington Limestone, 1.5 mi south of Burgin, Ky. USNM 315555.  
 13-15. Left-lateral and dorsal views ( $\times 3$ ) of a silicified paralectotype and closeup view of selenizone and growth lines (approximately  $\times 6$ ). Same collection as figures 9-12 above. USNM 315556.



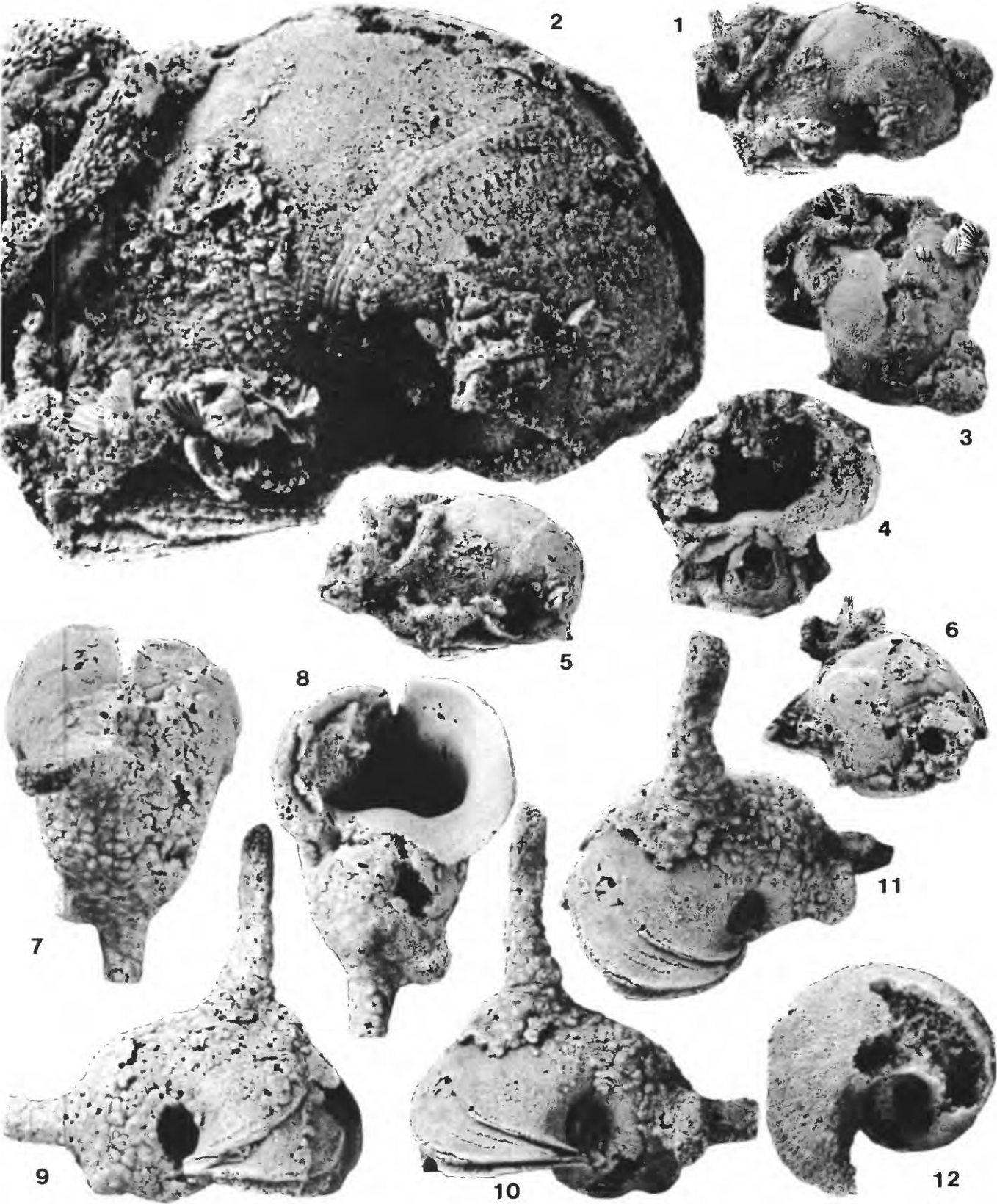


*BUCANIA*

## PLATE 17

FIGURES 1–12. *Bucania rugatina* Ulrich, 1897 (p. 0136).

- 1–6. Left-posterolateral view ( $\times 2$ ), enlarged left-posterolateral view ( $\times 6$ ), and dorsal, ventral, left-lateral, and posterior views ( $\times 2$ ) of silicified specimen preserving shell markings. Upper tongue, Clays Ferry Formation, USGS 6143-CO. USNM 315579.
- 7–11. Dorsal, ventral, right-lateral, left-lateral, and left-anterodorsal views of silicified specimen encrusted by a bryozoan colony ( $\times 2.5$ ). The chimneylike growths of the bryozoan colony in two directions may have resulted from partial burial of the shell, exhumation, and reburial in a different orientation. Tongue of Clays Ferry Formation between tongues of the underlying Millersburg Member and overlying Tanglewood Member of the Lexington Limestone, USGS 7348-CO. USNM 315580.
12. Left-lateral view of worn fragment showing characteristic shell markings of species ( $\times 3$ ). Same collection as figures 7–11 above. USNM 315581.



*BUCANIA*

## PLATE 18

FIGURES 1–9. *Bucania lindsleyi* (Safford), 1869 (p. O131).

1–6. Dorsal, ventral, left-lateral, and left- dorsolateral views of silicified lectotype ( $\times 1.5$ ) and closeup views of selenizone and of shell markings on left-anterior aperture ( $\times 5$ ). Cannon facies, Bigby-Cannon Limestone. Dekalb Co., Tenn. USNM 315550.

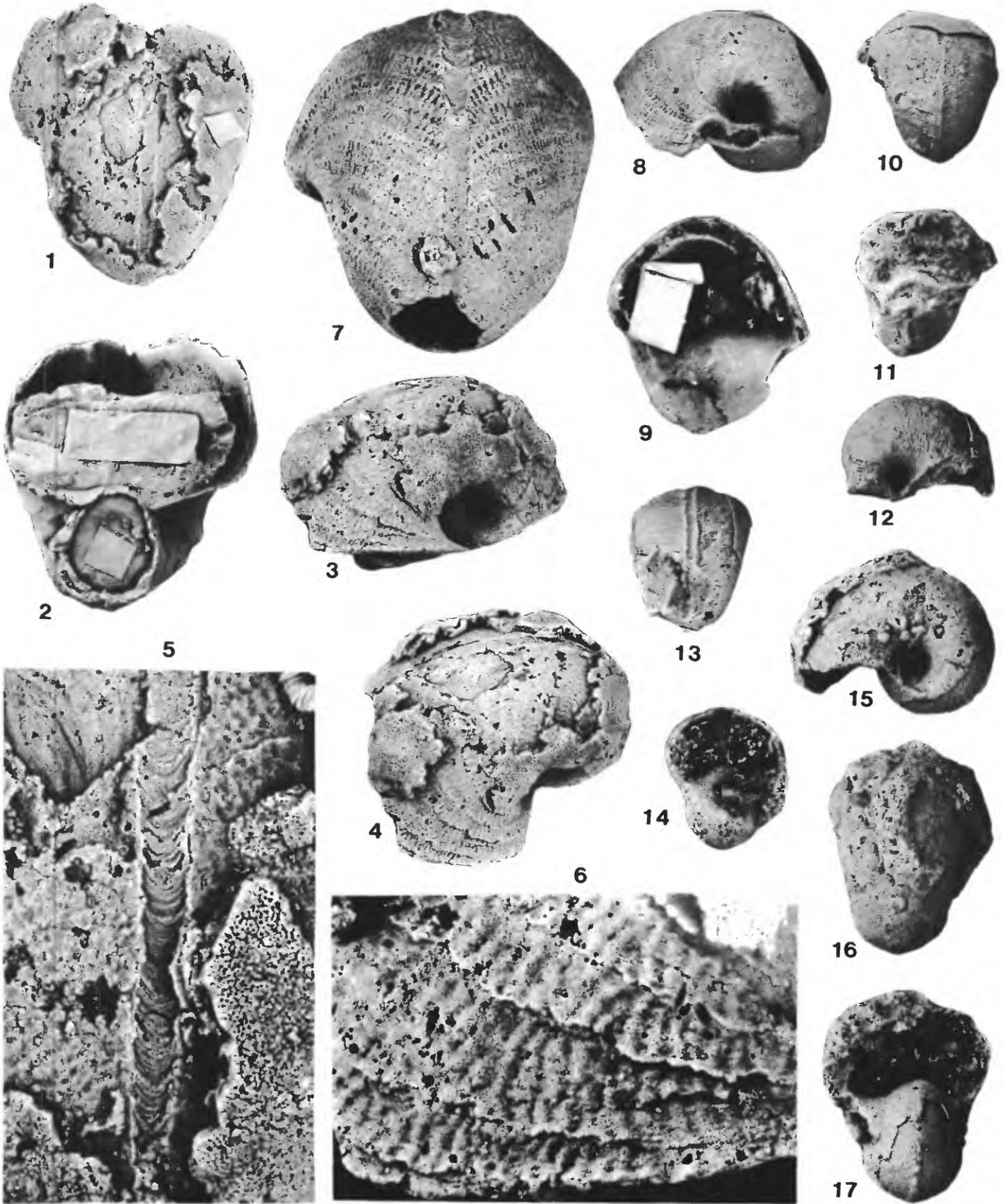
7–9. Dorsal view ( $\times 3.5$ ) and left-lateral and ventral views ( $\times 2$ ) of a silicified paralectotype. Note that this specimen is smaller than that in figures 1–6 above, and has not yet developed the lamellose growth lines. Same collection as figures 1–6 above. USNM 315551.

10–12. *Bellerophon* (*B.*) *subpatula* (Ulrich), 1897 (p. O161). Dorsal, ventral, and right-lateral views of silicified lectotype ( $\times 4$ ). Lexington Limestone, 1.5 mi south of Burgin, Ky. USNM 315552.

13–17. *Bellerophon* (*B.*) *nana* (Ulrich), 1897 (p. O160).

13, 14. Dorsal and ventral views of silicified lectotype ( $\times 4$ ). Upper Lexington Limestone, 1.5 mi south of Burgin, Ky. USNM 315553.

15–17. Left-lateral, dorsal, and ventral views of a silicified paralectotype ( $\times 4$ ). Same collection as figures 13, 14 above. USNM 315554.

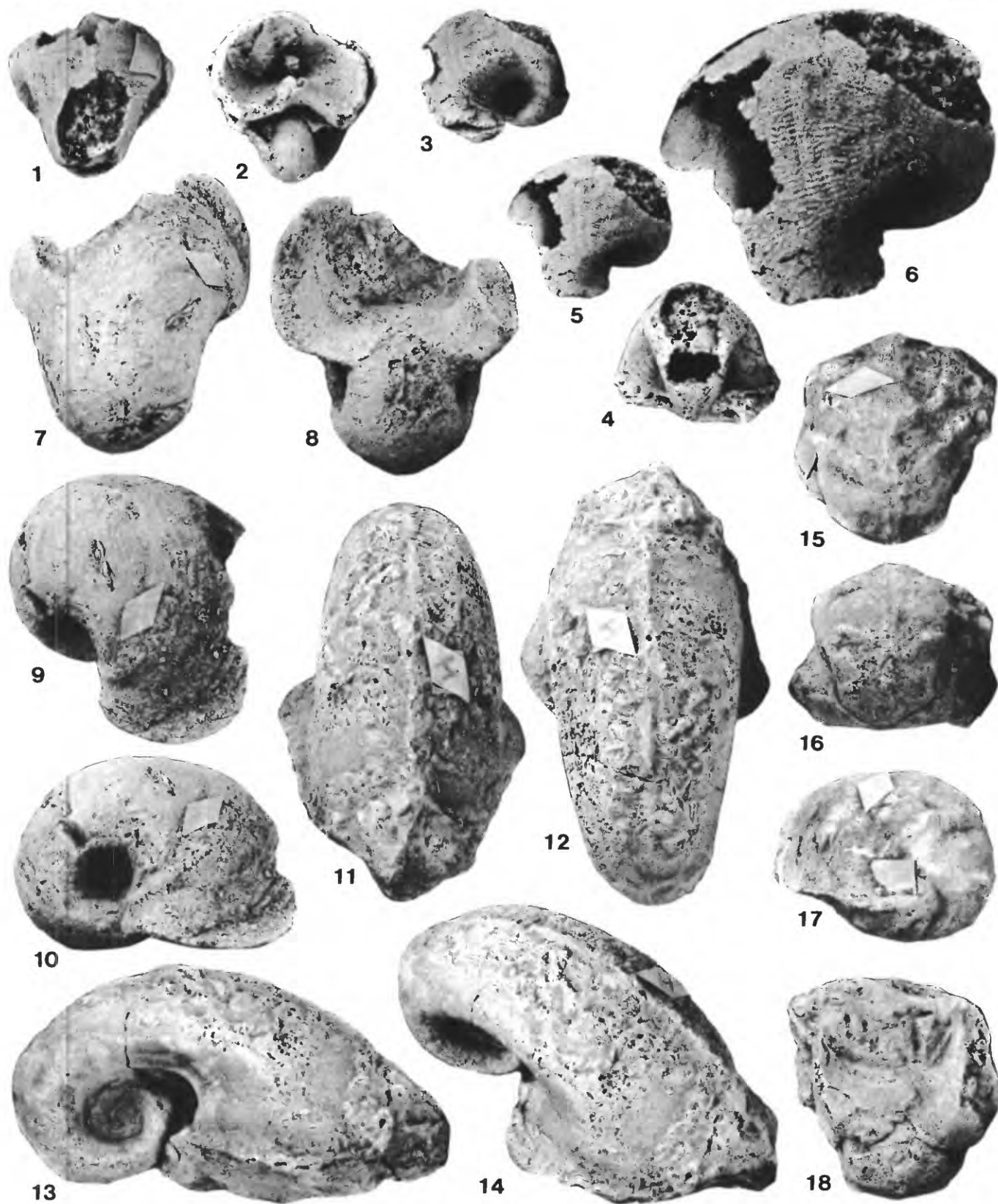


*BUCANIA AND BELLEROPHON*

## PLATE 19

- FIGURES 1–6. *Bucania micronema* Ulrich, 1897 (p. 0136). Dorsal, ventral, left-lateral, posterior, and left- anterodorsal views of silicified holotype ( $\times 3$ ), and closeup view of the last showing shell markings ( $\times 6$ ). Note that in figure 2 there is an extraneous shell fragment blocking the apertural opening. Upper Lexington Limestone, Danville, Ky. USNM 45720.
- 7–10. *Bucania crassa* Ulrich, 1897 (p. 0139). Dorsal, ventral, right-anterolateral, and right-lateral views of calcitic lectotype ( $\times 1.5$ ). Museum label reads “Richmond (Elkhorn Formation), near Richmond, Indiana.” USNM 315547.
- 11–14. *Bucania simulatrix* Ulrich, 1897 (p. 0139). Anterodorsal, dorsal, right-lateral, and right- anterolateral views of calcitic lectotype ( $\times 1.5$ ). Whitewater Formation, Richmond, Ind. USNM 315548.
- 15–18. *Bucania singularis* Ulrich, 1897 (p. 0137). Dorsal, posterior, left-lateral, and ventral views of lectotype ( $\times 1.5$ ). Catheys Formation, Nashville, Tenn. USNM 315549.





*BUCANIA*



## PLATE 20

FIGURES 1–8. *Bucania pojetai* new species (p. 0138).

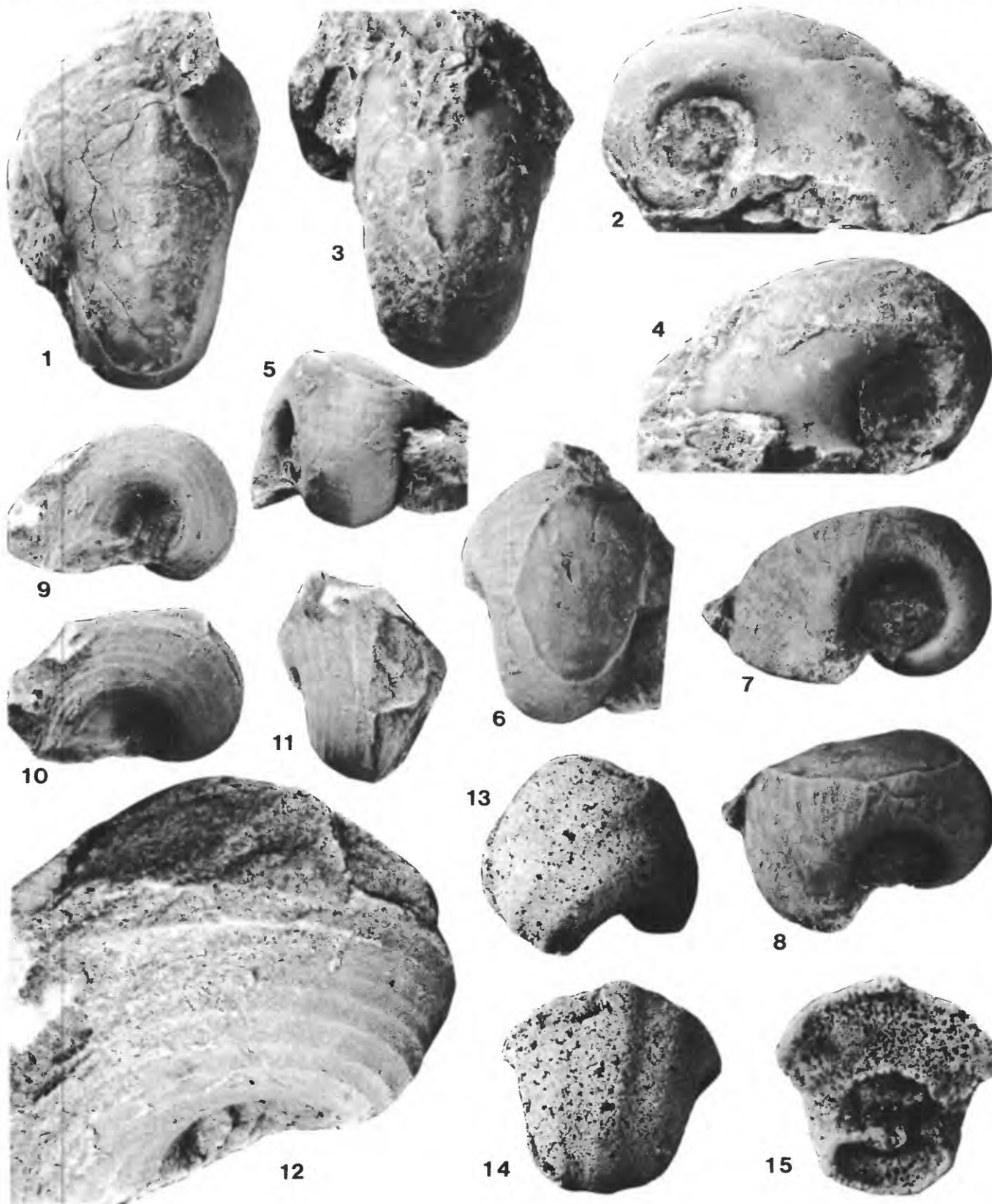
1, 2. Dorsal and right-lateral views of calcitic specimen ( $\times 1.5$ ) preserving some remnants of the shell, and showing the internal mold of the dorsum as lacking the ridgelike slit filling that would be expected in species of *Salpingostoma*, which has a similar shell form. Leipers Limestone, Rowena Ferry, Russell Co., Ky. Paratype, UCGM 44286.

3, 4. Dorsal and left-lateral views of calcitic specimen having apparently highly recrystallized shell, showing the selenizone as a low, rounded ridge ( $\times 1.5$ ). Same collection as figures 1, 2 above. Holotype. UCGM 44285.

5–8. Posterior, dorsal, left-lateral, and oblique dorsal views of a calcitic paratype showing wrinklelike growth lines ( $\times 1.5$ ). Same collection as figures 1, 2 above. UCGM 44287.

9–12. *Kokenospira costalis* (Ulrich and Scofield), 1897 (p. 0140). Left-lateral, left-posterolateral, and dorsal views ( $\times 2.5$ ) and dorsolateral closeup view of calcitic specimen ( $\times 6$ ). Southgate biofacies, Kope Formation, Cincinnati, Ohio. UCGM 26519.

13–15. *Tetranota* cf. *T. obsoleta* Ulrich and Scofield, 1897 (p. 0146). Right-posterodorsal, dorsal, and ventral views of small silicified specimen ( $\times 4$ ). Upper Curdsville Member, Lexington Limestone, USGS 6131-CO. USNM 315541.

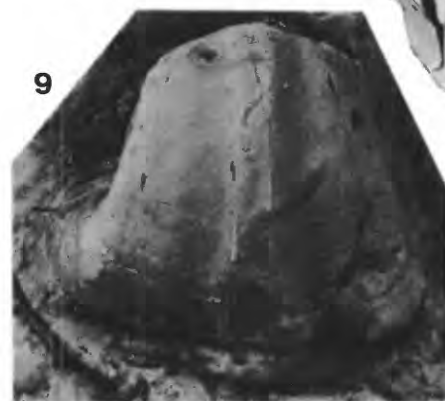
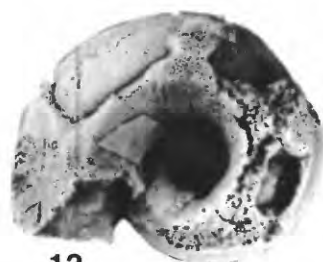
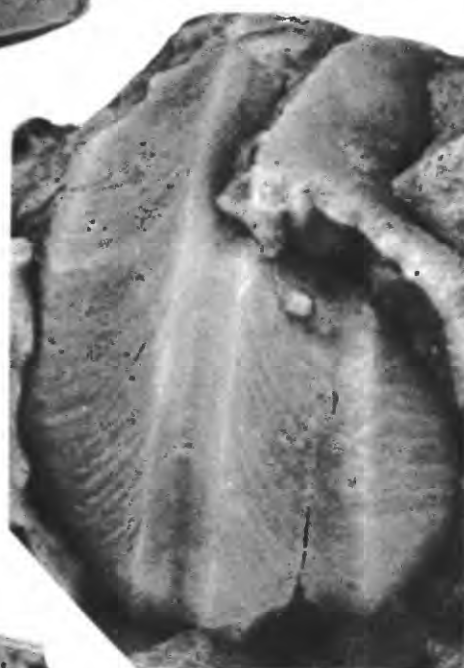
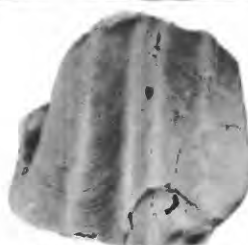


*BUCANIA, KOKENOSPIRA, AND TETRANOTA*

## PLATE 21

FIGURES 1–14. *Tetranota bidorsata* (Hall), 1847 (p. O145).

- 1–4. *Tetranota bidorsata* and *Simuities granistriatus* (Ulrich) in small slab of limestone ( $\times 1.5$ ), two closeup views ( $\times 3$  and  $\times 6$ ) emphasizing lateral ridges and selenizone of specimen in upper center, and closeup view ( $\times 3$ ) of specimen in lower left showing growth lines. From lenslike mollusk bed in Economy biofacies, lower Kope Formation, Chilo, Ohio (locality OH-1). UCGM 44291.
- 5–7. Posterior, anterior, and right-dorsolateral views of calcitic specimen ( $\times 2$ ). Same collection as figures 1–4 above. UCGM 44292.
8. Dorsal view of specimen in association with fragments of a crinoid column and the trilobite *Cryptolithus* sp., a typical assemblage of the Kope Formation ( $\times 2$ ). Note that the gastropod is somewhat crushed. Same collection as figures 1–4 above. UCGM 44293.
- 9–11. Anterodorsal, right-lateral, and right- anterodorsal views of calcitic specimen preserving the lateral apertural expansion of maturity ( $\times 2$ ). Economy biofacies, Kope Formation, Bloody Run, Cincinnati, Ohio. USNM 47545.
- 12, 13. Left-lateral and ventral views of lectotype ( $\times 2$ ). Trenton Group, Watertown, N.Y. AMNH F1 29592 (James Hall collection).
14. Dorsal view of a paralectotype ( $\times 2$ ). Trenton Group, Middleville, N.Y. AMNH F1 787 (James Hall collection).

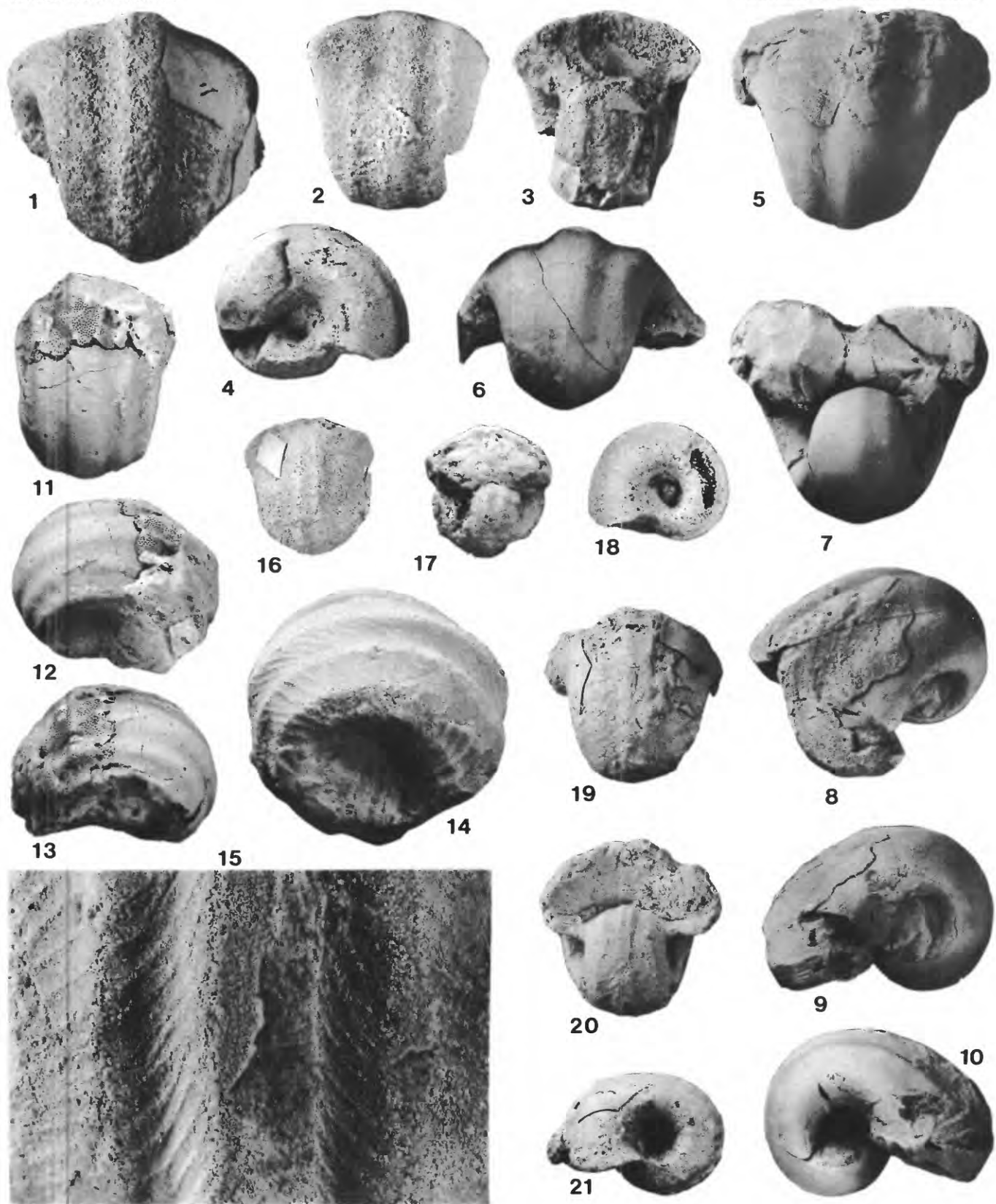


*TETRANOTA*

PLATE 22

FIGURES 1–10. *Tetranota bidorsata* (Hall), 1847 (p. 0145).

1. Dorsal view of large internal mold ( $\times 2$ ). Trenton Group, Watertown, Jefferson Co., N.Y. Paralectotype. AMNH F1 29593.
- 2–4. Dorsal, ventral, and right-lateral views of internal mold ( $\times 2$ ). Trenton Group, Watertown, N.Y. Paralectotype. AMNH F1 29594.
- 5–10. Dorsal, posterior, ventral, left-anterodorsal, left-lateral and right-lateral views of internal mold with some shell preserved dorsally ( $\times 2$ ). Pogonip Group, White Pine District, Nev. USNM 17301.
- 11–15. *Tetranota sexcarinata* Ulrich and Scofield, 1897 (p. 0147).
  - 11–13. Dorsal and left- and right-dorsolateral views of internal mold ( $\times 2$ ). Lebanon Formation, Lavergne, Tenn. USNM 47712.
  - 14, 15. Right dorsolateral ( $\times 2$ ) and dorsal closeup ( $\times 6$ ) views of selenizone, growth lines, and first lateral ridges. *Fusispira* bed, Prosser Formation, Wykoff, Minn. Lectotype. USNM 46018.
- 16–21. *Tetranota obsoleta* Ulrich and Scofield, 1897 (p. 0146).
  - 16–18. Dorsal, ventral, and left-lateral views of small silicified specimen ( $\times 2$ ). Hypotype of Butts (1926). Little Oak Formation, north of Pelham, Ala. USNM 71496.
  - 19–21. Dorsal, ventral, and left-lateral views of silicified lectotype ( $\times 2$ ). *Ctenodonta* bed, Decorah Formation, Chatfield, Minn. USNM 46014.



*TETRANOTA*

## PLATE 23

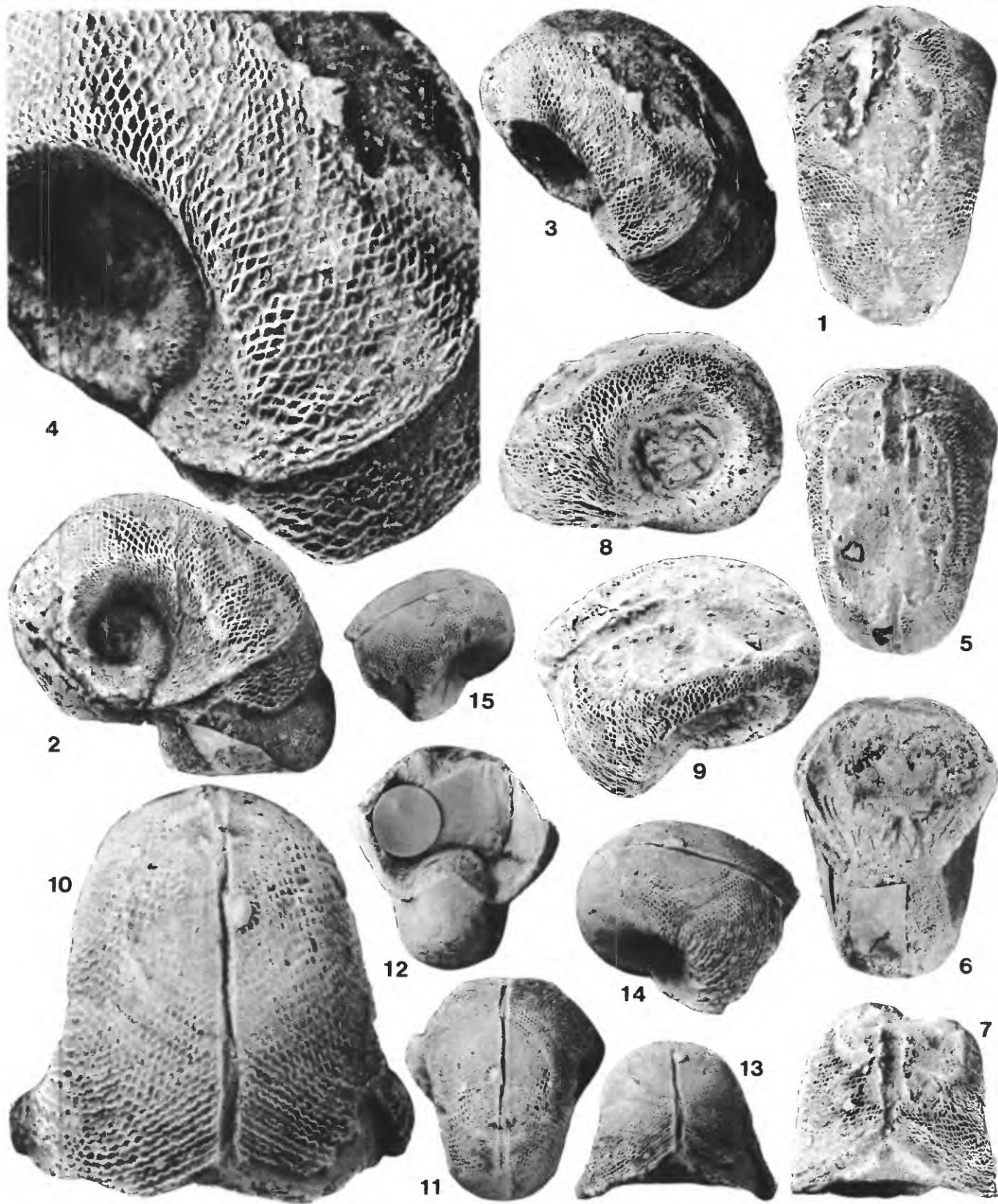
FIGURES 1-9. *Undulabucania punctifrons* (Emmons), 1842 (p. O142).

1-4. Dorsal, right-lateral, and right-anterodorsal views of calcitic specimen ( $\times 3$ ) and closeup view of the last showing shell sculpturing ( $\times 6$ ). Base of Hermitage Formation, Nashville, Tenn. USNM 45727.

5-9. Dorsal, ventral, anterior, left-lateral, and left-anterodorsal views of another calcitic specimen ( $\times 3$ ). Same collection as figures 1-4 above. USNM 315546.

10-15. *Undulabucania gorbyi* (Miller), 1892 (p. O142). Anterodorsal ( $\times 4$ ), dorsal, ventral, anterior, right-anterodorsal ( $\times 2$ ), and left-anterodorsal ( $\times 1.5$ ) views of calcitic holotype. Maysvillian-age strata, Dearborn Co., Ind. UC 6138.





*UNDULABUCANIA*

## PLATE 24

FIGURES 1–9. *Salpingostoma buelli* (Whitfield, 1878) (p. 0150).

1–5. Left- and right-anterolateral, dorsal, and left- and right-lateral views of an Ulrich and Scofield (1897) hypotype ( $\times 1.5$ ), which is a composite mold dorsally but retains some dolomitized shell material around expanded aperture. Platteville Formation (Blackriveran), Beloit, Wis. USNM 265960.

6–8. Dorsal, apertural, and right-lateral views of dolomitized internal mold of submature specimen ( $\times 2$ ). Same horizon and locality as figures 1–5 above. USNM 265957.

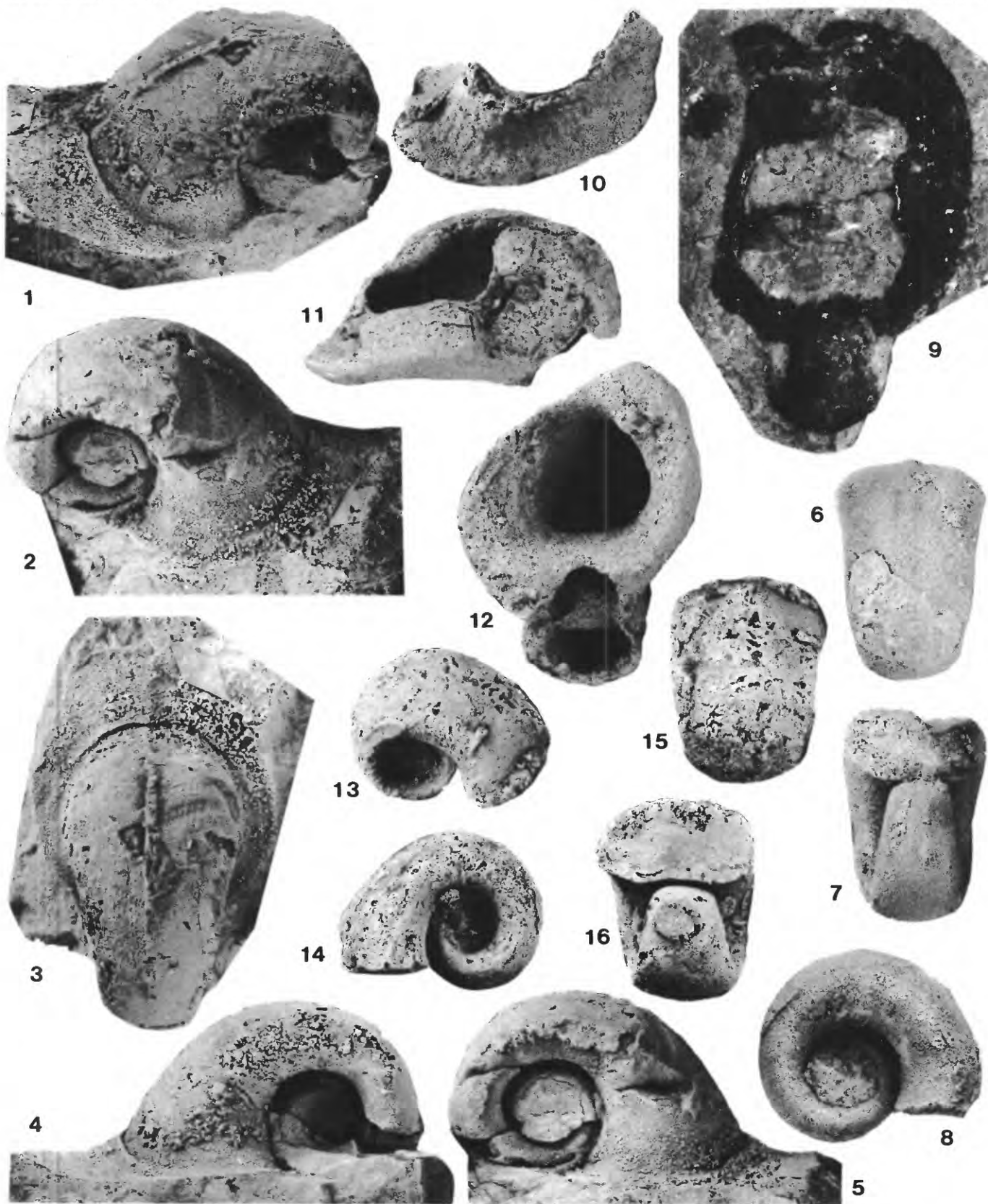
9. Apertural view of dark-gray calcitic cast showing outline of aperture and its anterior sinus ( $\times 1.5$ ). Specimen not whitened for photograph. Platteville Formation (Blackriveran), Old Concord, Minn. USNM 47590.

10–12. *Salpingostoma kentuckyense* Ulrich and Scofield, 1897 (p. 0151).

10. Dorsolateral view of weathered silicified fragment of expanded, thickened aperture rim showing trace of coarse radiating ribs ( $\times 1.5$ ). Paralectotype. Curdsville Member, Lexington Limestone (Kirkfieldian), Mercer Co., Ky. USNM 265962.

11, 12. Left-lateral and ventral views of weathered silicified lectotype ( $\times 1.5$ ). USNM 265961.

13–16. *Salpingostoma richmondensis* Ulrich, 1897 (p. 0154). Right-dorsolateral, left-lateral, dorsal, and apertural views of internal mold of immature specimen ( $\times 1.5$ ). Museum label gives horizon and locality as “Richmond Group, Richmond, Indiana.” UCGM 44280.

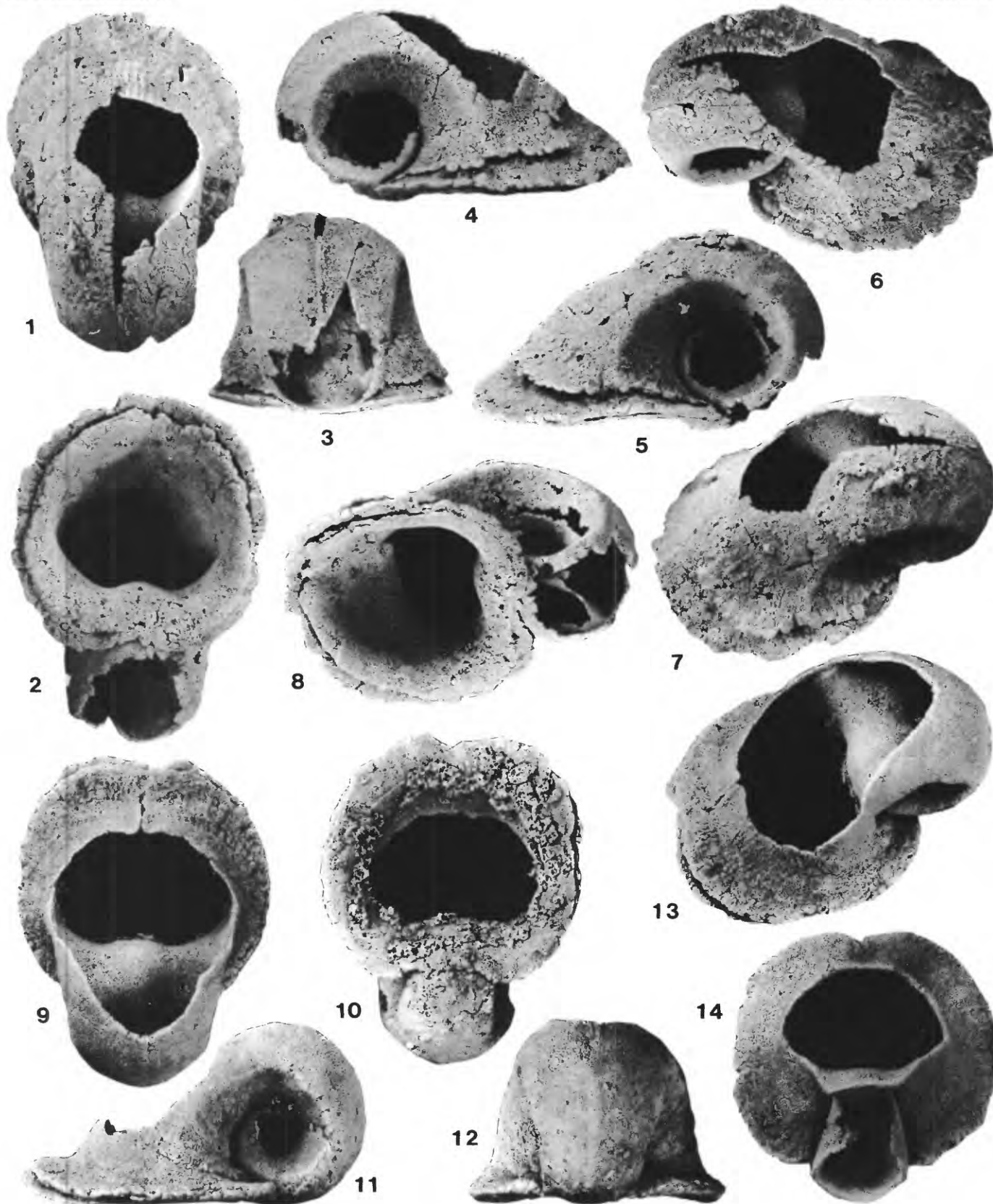


*SALPINGOSTOMA*

PLATE 25

FIGURES 1-14. *Salpingostoma kentuckyense* Ulrich and Scofield, 1897 (p. O151).

- 1-8. Dorsal, apertural, posterior, right-lateral, left-lateral, right oblique and left oblique dorsolateral, and left-ventrolateral views of silicified specimen ( $\times 1.5$ ). Tyrone Limestone (Rocklandian), USGS 6034-CO. USNM 265964.
- 9-13. Dorsal, ventral, left-lateral, posterior, and left oblique dorsolateral views of silicified specimen ( $\times 1.5$ ). Same collection as figures 1-8 above. USNM 265965.
- 14. Dorsal view of silicified specimen showing chevron wrinkling beneath coil ( $\times 1.5$ ). Same collection as figures 1-8 above. USNM 265979.



*SALPINGOSTOMA*

PLATE 26

FIGURES 1-8. *Salpingostoma richmondensis* Ulrich, 1897 (p. O154).

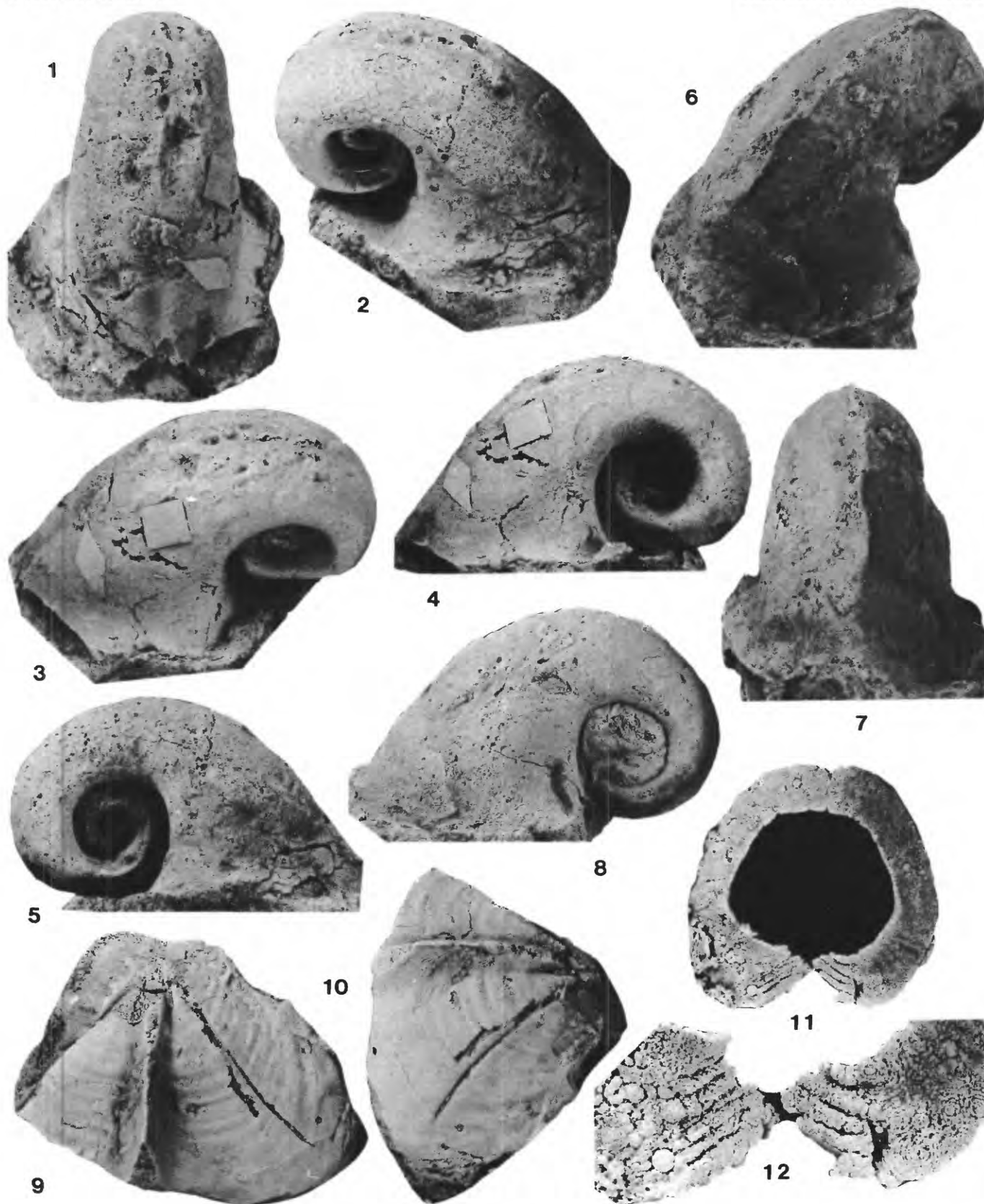
1-5. Anterodorsal, right oblique, left oblique, and left- and right-lateral views of internal mold preserving some shell around expanded apertural rim ( $\times 1.5$ ). Holotype. Whitewater Formation (Richmondian), Richmond, Ind. USNM 45988.

6-8. Oblique anterodorsal, anterior, and left-lateral views of internal mold ( $\times 1.5$ ). Museum label gives horizon and locality as "Whitewater Formation, Camden, Ohio." UCGM 44281.

9, 10. *Pterotheca harviei* Foerste, 1924 (p. O186). Dorsal and left-dorsolateral views of composite mold ( $\times 1.5$ ). Southgate biofacies, Kope Formation (Edenian), Covington, Ky. USNM 50092.

11, 12. *Salpingostoma kentuckyense* Ulrich and Scofield, 1897 (p. O151). Dorsal ( $\times 1.5$ ) and closeup ( $\times 3$ ) views of posterior area of silicified apertural rim showing chevron wrinkling beneath coil. Same collection as plate 25, figures 1-8. USNM 265966.





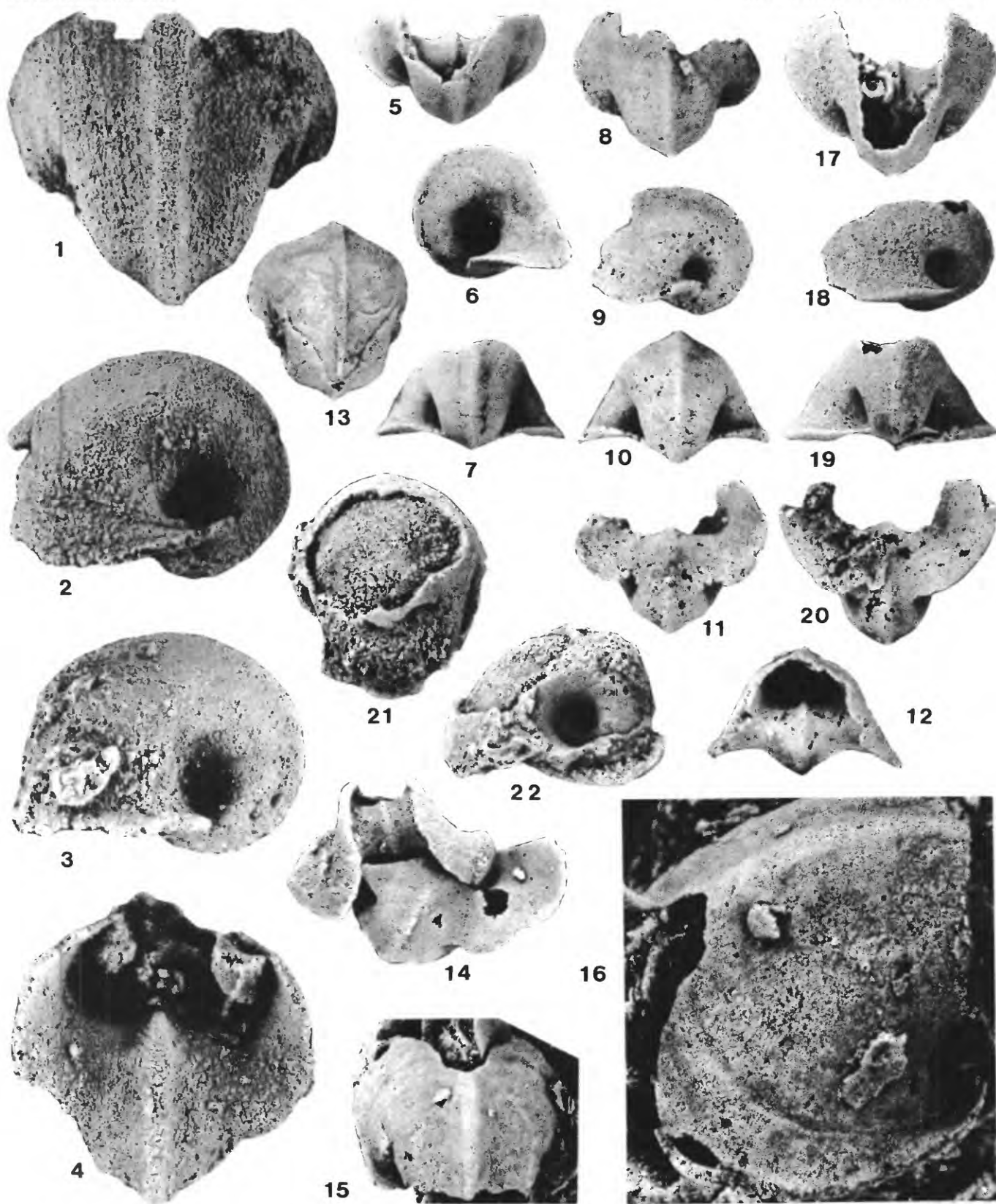
*SALPINGOSTOMA AND PTEROTHECA*



## PLATE 27

FIGURES 1–16. *Bucanopsis carinifera* Ulrich, 1897 (p. O163).

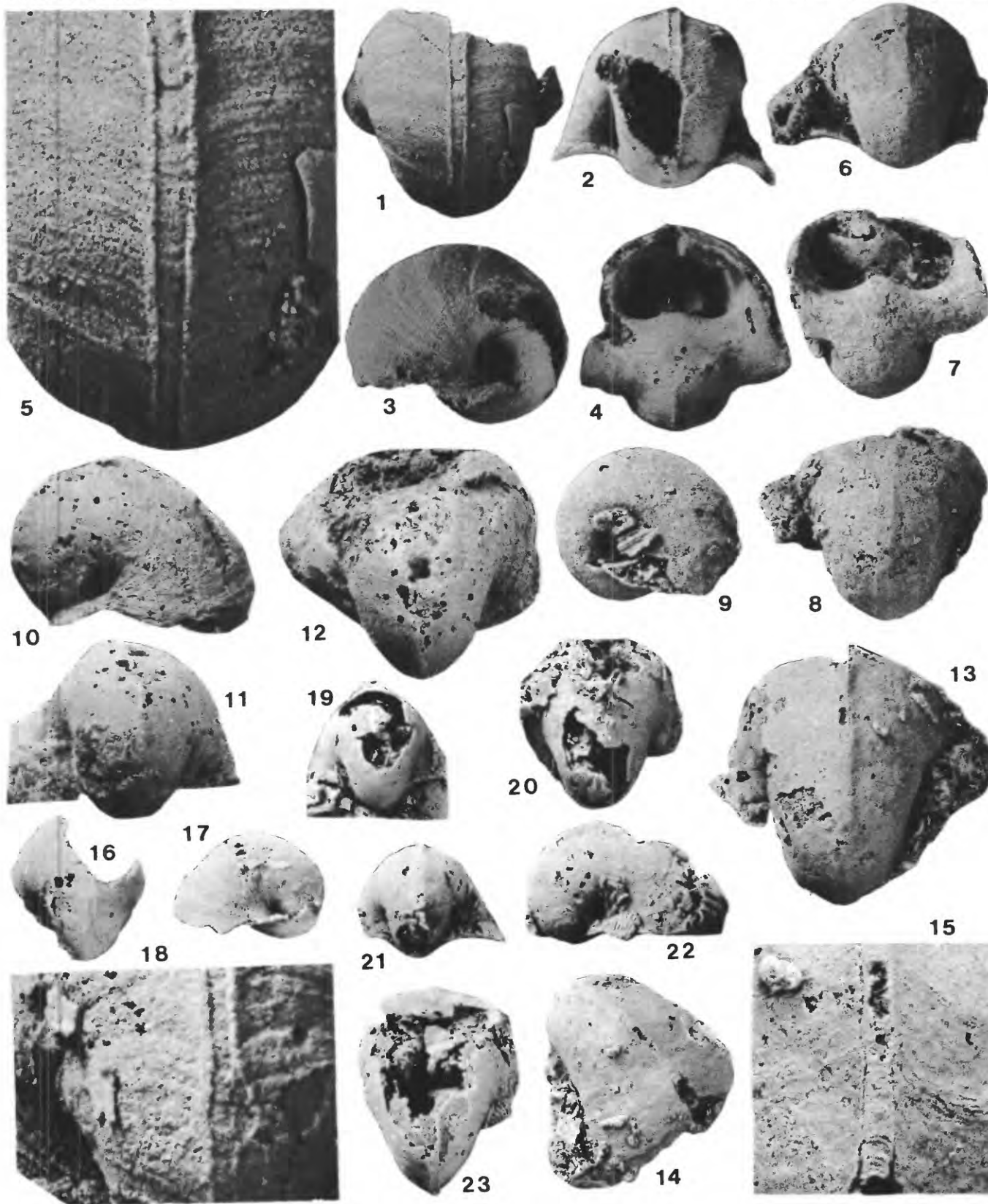
- 1, 2. Dorsal and left-lateral views of silicified lectotype showing revolving threads ( $\times 6$ ). Museum label reads "Trenton (Flanagan), near Danville, Kentucky." USNM 315583.
3. Left-lateral view of a silicified paralectotype ( $\times 6$ ). Same collection as figures 1, 2 above. USNM 315584.
4. Ventral view of another silicified paralectotype showing sharp whorl floor keel ( $\times 6$ ). Same collection as figures 1, 2 above. USNM 315585.
- 5–7. Dorsal, right-lateral, and posterior views of silicified specimen ( $\times 3$ ). Cannon facies, Bigby-Cannon Limestone, "Hill north of Well No. 1, Smith County, Tennessee." UCGM 44283.
- 8–12. Dorsal, left-lateral, posterior, ventral, and anterior views of silicified specimen ( $\times 2.5$ ). Grier Limestone Member, Lexington Limestone, USGS 4928-CO. USNM 315586.
13. Dorsal view of small silicified specimen showing outer shell layers peeling away ( $\times 3$ ). Faulconer Bed, Perryville Limestone Member, Lexington Limestone, USGS 6136-CO. USNM 315589.
14. Two silicified specimens cemented together showing aperture form and whorl floor keel ( $\times 3$ ). Salvisa Bed, Perryville Limestone Member, Lexington Limestone, USGS 5015-CO. USNM 315587.
- 15, 16. Dorsal ( $\times 3$ ) and left anterodorsal closeup ( $\times 9$ ) views showing faint revolving threads on weathered silicified specimen. Salvisa Bed, Perryville Limestone Member, Lexington Limestone, USGS 5015-CO. USNM 315588.
- 17–20. *Bucanopsis diabloensis* new species (p. O165). Dorsal, left-lateral, posterior, and ventral views of silicified holotype ( $\times 2.5$ ). Note narrower coil and relatively wider and more rounded aperture compared with *Bucanopsis carinifera*. Devils Hollow Member, Lexington Limestone, USGS 5095-CO. USNM 315590.
- 21, 22. *Bucania nashvillensis* Ulrich, 1897 (p. O132). Dorsal and left-lateral views of fragmentary silicified specimen ( $\times 2.5$ ). Cannon facies, Bigby-Cannon Limestone, "Hill north of Well No. 1, Smith Co., Tennessee." UCGM 44284.



*BUCANOPSIS AND BUCANIA*

## PLATE 28

- FIGURES 1–5. *Bellerophon (Bellerophon) bilineatus* Ulrich, 1897 (p. O160). Dorsal, posterior, left-lateral, and ventral views of silicified holotype ( $\times 3$ ) and dorsal closeup view ( $\times 6.5$ ) of selenizone and growth lines. Labeled as coming from “Upper portion of the Trenton Group, near Danville, Kentucky.” USNM 45697.
- 6–9. *Bellerophon (Bellerophon) cf. B. (B.) bilineatus* Ulrich, 1897 (p. O160). Posterior, ventral, dorsal, and right-lateral views of silicified specimen ( $\times 2.5$ ). Faulconer Bed, Perryville Limestone Member, Lexington Limestone, USGS 6136-CO. USNM 315612.
- 10–23. *Sphenosphaera burginensis* (Ulrich), 1897 (p. O170).
- 10–12. Right-lateral, posterior, and dorsal views of silicified holotype ( $\times 2$ ). Upper Lexington Limestone, 3 mi north of Burgin, Ky. USNM 45712.
- 13–15. Dorsal ( $\times 2.5$ ) and right-anterodorsal ( $\times 2$ ) views of a silicified paratype and anterodorsal closeup view of selenizone ( $\times 6$ ). Upper Lexington Limestone, 1.5 mi south of Burgin, Ky. USNM 47595.
- 16–18. Dorsal and left-lateral ( $\times 2$ ) views of silicified specimen and dorsal closeup view of selenizone ( $\times 10$ ). Grier Limestone Member, Lexington Limestone, USGS 5096-CO. USNM 315167.
- 19, 20. Posterior and dorsal views of silicified specimen ( $\times 2$ ). Grier Limestone Member, Lexington Limestone, USGS 4883-CO. USNM 315615.
- 21–23. Posterior, right-lateral, and dorsal views of silicified specimen ( $\times 2$ ). Same collection as figures 16–18 above. USNM 315616.

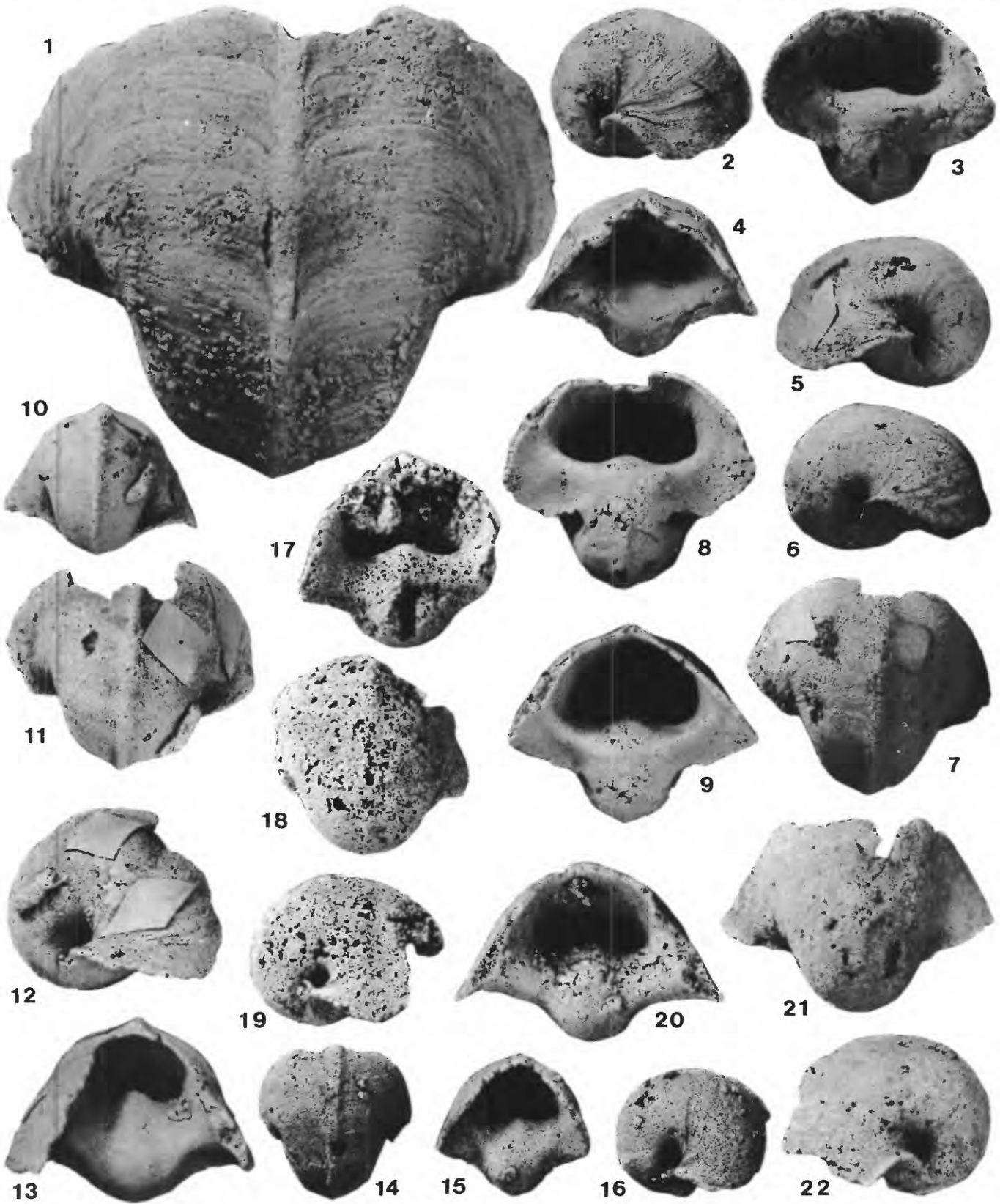


*BELLEROPHON AND SPHENOSPHERA*

## PLATE 29

FIGURES 1–22. *Sphenosphaera troosti* (d'Orbigny), 1840 (p. O168).

- 1–4. Dorsal closeup view ( $\times 5$ ) and right-lateral, ventral, and anteroventral views ( $\times 2$ ) of silicified neotype. Cannon facies, Bigby-Cannon Limestone, Nashville, Tenn. USNM 315602.
- 5–9. Left-lateral, right-lateral, dorsal, ventral, and anterior views of silicified paraneotype figured by Ulrich and Scofield (1897) ( $\times 2$ ). Same horizon and locality as figures 1–4 above. USNM 315665.
- 10–13. Posterior view ( $\times 2$ ) and dorsal, right-lateral, and anterior views ( $\times 2.5$ ) of silicified hypotype from Ulrich and Scofield (1897) collection. Labeled as coming from “Flanagan chert” (Lexington Limestone), near Danville, Ky. USNM 315603.
- 14–16. Dorsal, anterior, and right-lateral views of another Ulrich and Scofield (1897) silicified hypotype ( $\times 3$ ). Same collection as figures 10–13 above. USNM 315604.
- 17–19. Apertural, dorsal, and right-lateral views of coarsely silicified specimen ( $\times 3$ ). Grier Limestone Member, Lexington Limestone, USGS 4073-CO. USNM 315614.
- 20–22. Anterior, dorsal, and left-lateral views of silicified specimen ( $\times 3$ ). Grier Limestone Member, Lexington Limestone, USGS 4959-CO. USNM 315613.



*SPHENOSPHERA*



PLATE 30

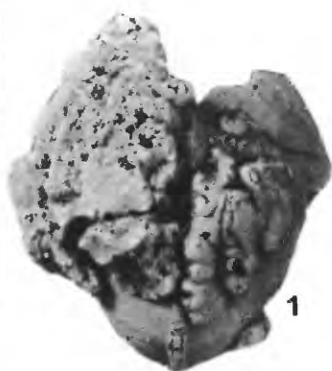
FIGURES 1–23. *Sphenosphaera clausus* (Ulrich), 1897 (p. 0167).

- 1–6. Dorsal, anterior, ventral, right-lateral, and left-posterolateral views of silicified holotype ( $\times 2$ ) and posterodorsal closeup ( $\times 6$ ) view. Cannon facies, Bigby-Cannon Limestone, central Tennessee. USNM 45701.
- 7, 8. Dorsal and left-lateral views of a slightly compressed calcitic paratype ( $\times 2$ ). Lexington Limestone, Frankfort, Ky. USNM 45700.
- 9, 10. Anteroventral and ventral views of silicified specimen ( $\times 3$ ). Salvisa Bed, Perryville Limestone Member, Lexington Limestone, USGS 5015-CO. USNM 315621.
- 11–14. Dorsal, right-lateral, ventral, and anteroventral views of silicified specimen ( $\times 2$ ). Same collection as figures 9, 10 above. USNM 315620.
- 15, 16. Posterodorsal and right-lateral views of silicified specimen showing an outer shell layer peeling away ( $\times 2$ ). Salvisa Bed, Perryville Limestone Member, Lexington Limestone, USGS 6916-CO. USNM 315619.
- 17, 18. Anterior and left-lateral views of silicified specimen ( $\times 2$ ). Clays Ferry Formation, USGS 7812-CO. USNM 315628.
19. Right-lateral view of silicified specimen encrusted by a digitate bryozoan colony ( $\times 2$ ). Same collection as figures 17, 18 above. USNM 315626.
- 20, 21. Dorsal and left-lateral views of silicified specimen ( $\times 2$ ). Same collection as figures 17, 18 above. USNM 315627.
- 22, 23. Dorsal and left-lateral views of silicified specimen ( $\times 3$ ). Devils Hollow Member, Lexington Limestone, USGS 5087-CO. USNM 315622.

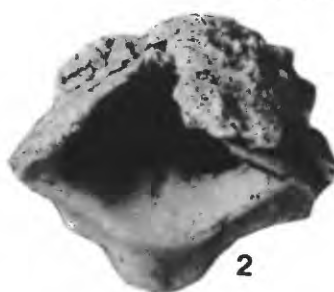




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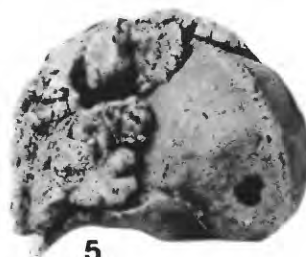
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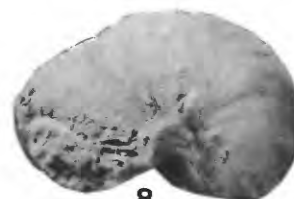
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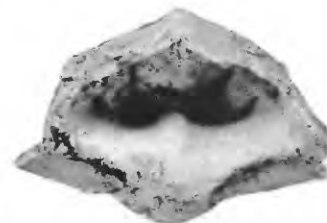
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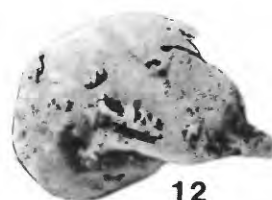
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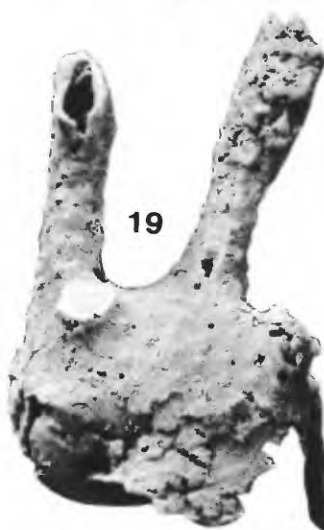
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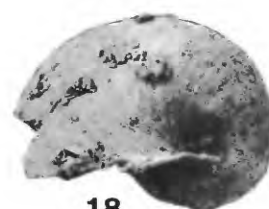
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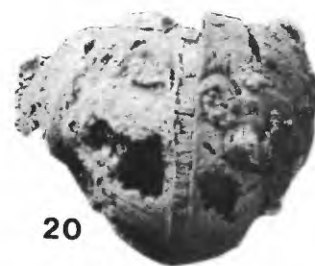
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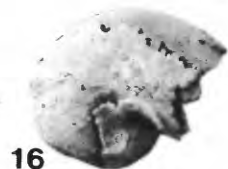
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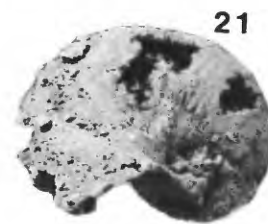
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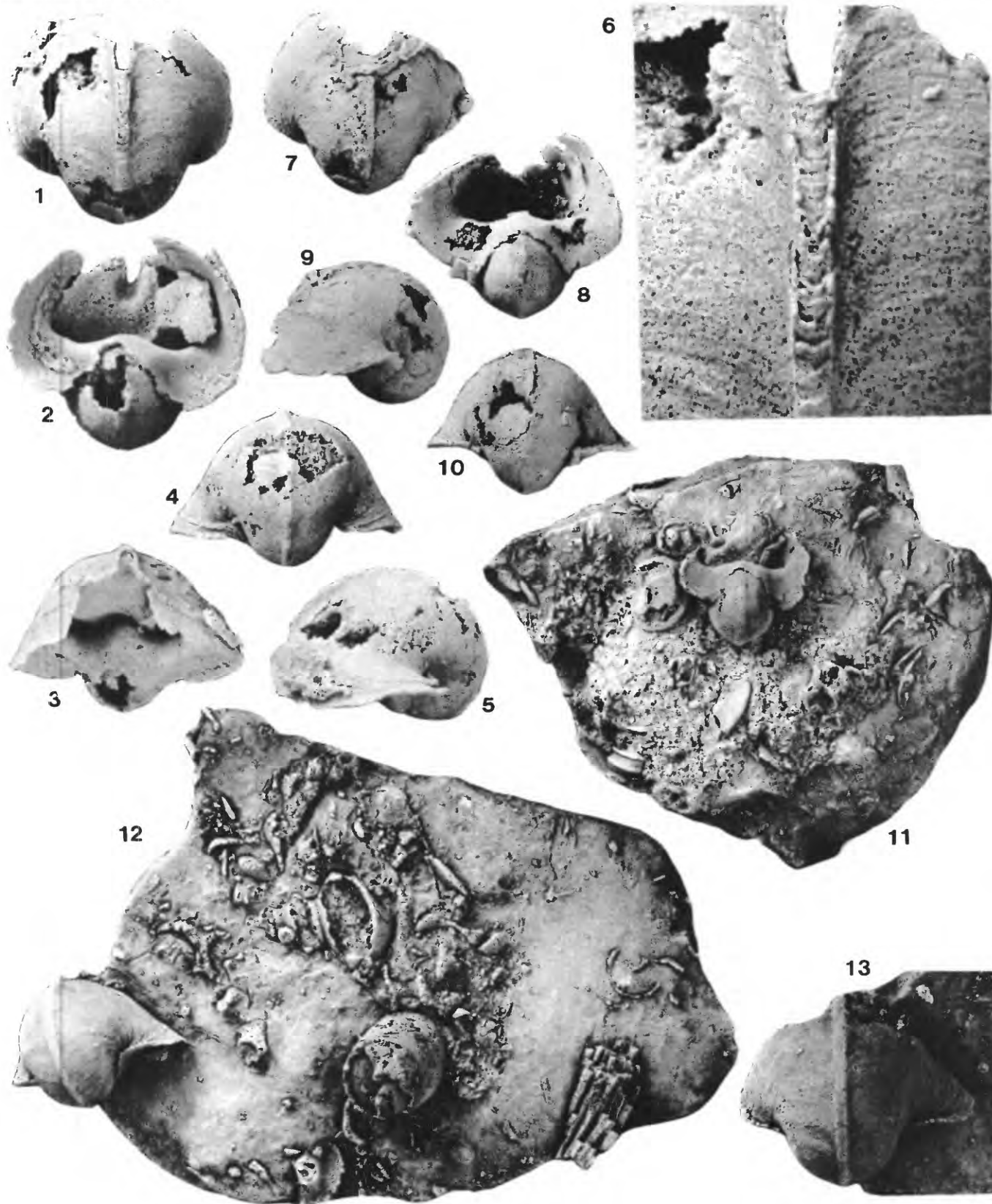
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*SPHENOSPHERA*

## PLATE 31

FIGURES 1–13. *Sphenosphaera clausus* (Ulrich), 1897 (p. 0167).

- 1–6. Dorsal, ventral, anteroventral, posterior, and left-lateral views of silicified specimen ( $\times 2$ ) and dorsal closeup view of selenizone ( $\times 8$ ). Millersburg Member, Lexington Limestone, USGS 7353-CO. USNM 315624.
- 7–10. Dorsal, ventral, left-lateral, and posterior views of silicified specimen ( $\times 2$ ). Grier Limestone Member, Lexington Limestone, USGS 4879-CO. USNM 315618.
- 11. Small slab showing ventral view of specimen associated with other silicified skeletal debris in gray, dense wackestone-packstone ( $\times 1$ ). Cannon facies, Bigby-Cannon Limestone, “Hill north of Well No. 1, Smith Co., Tennessee.” UCGM 44301.
- 12, 13. Small slab showing right-posterolateral view of silicified specimen ( $\times 1.5$ ) and dorsal view of same specimen ( $\times 2$ ). Other silicified skeletal material includes lophospirid gastropod and nautiloid cephalopod fragments, and a portion of a tabulate coral colony. Same collection as figure 11 above. UCGM 44302.

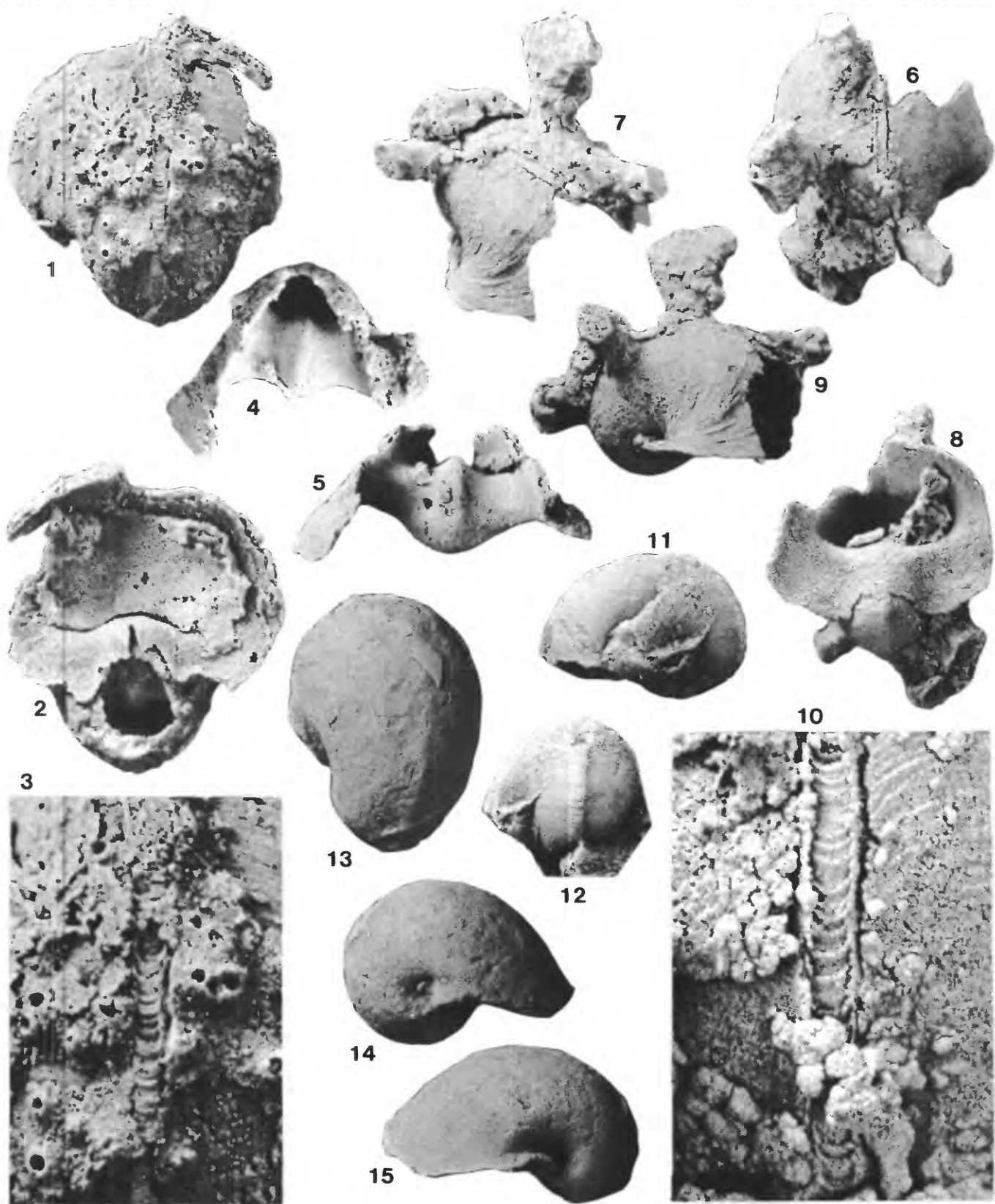


*SPHENOSPHAERA*

## PLATE 32

FIGURES 1–15. *Sphenosphaera clausus* (Ulrich), 1897 (p. O167).

- 1–3. Dorsal and ventral views ( $\times 2$ ) and closeup view of selenizone ( $\times 6$ ) of silicified specimen encrusted by a bryozoan colony. Millersburg Limestone Member, Lexington Limestone, USGS 7353-CO. USNM 315665.
- 4, 5. Anterodorsal and anterior views of fragmentary silicified specimen showing the whorl floor ridge clearly ( $\times 2$ ). Same collection as figures 1–3 above. USNM 315625.
- 6–10. Dorsal, right-anterodorsal, ventral, and right-lateral views ( $\times 2$ ) and dorsal closeup view ( $\times 10$ ) of silicified specimen encrusted on one side by a digitate bryozoan colony. Millersburg Limestone Member, Lexington Limestone, USGS 7344-CO. USNM 315623.
- 11, 12. Left-lateral and posterior views of calcareous specimen ( $\times 2.5$ ). Museum label states that specimen came from “top of the Bromley Shale” (now included in Clays Ferry Formation), 1.5 mi east of Sadieville, Ky. MU 235T.
- 13–15. Dorsal, right-lateral, and left-lateral views of internal mold ( $\times 2$ ). Specimen is lectotype of *Bellerophon rogersensis* Foerste, which is here placed in synonymy with *S. clausus*. Note that the specimen is slightly compressed. Clays Ferry Formation, Rogers Gap, Ky. USNM 315601.

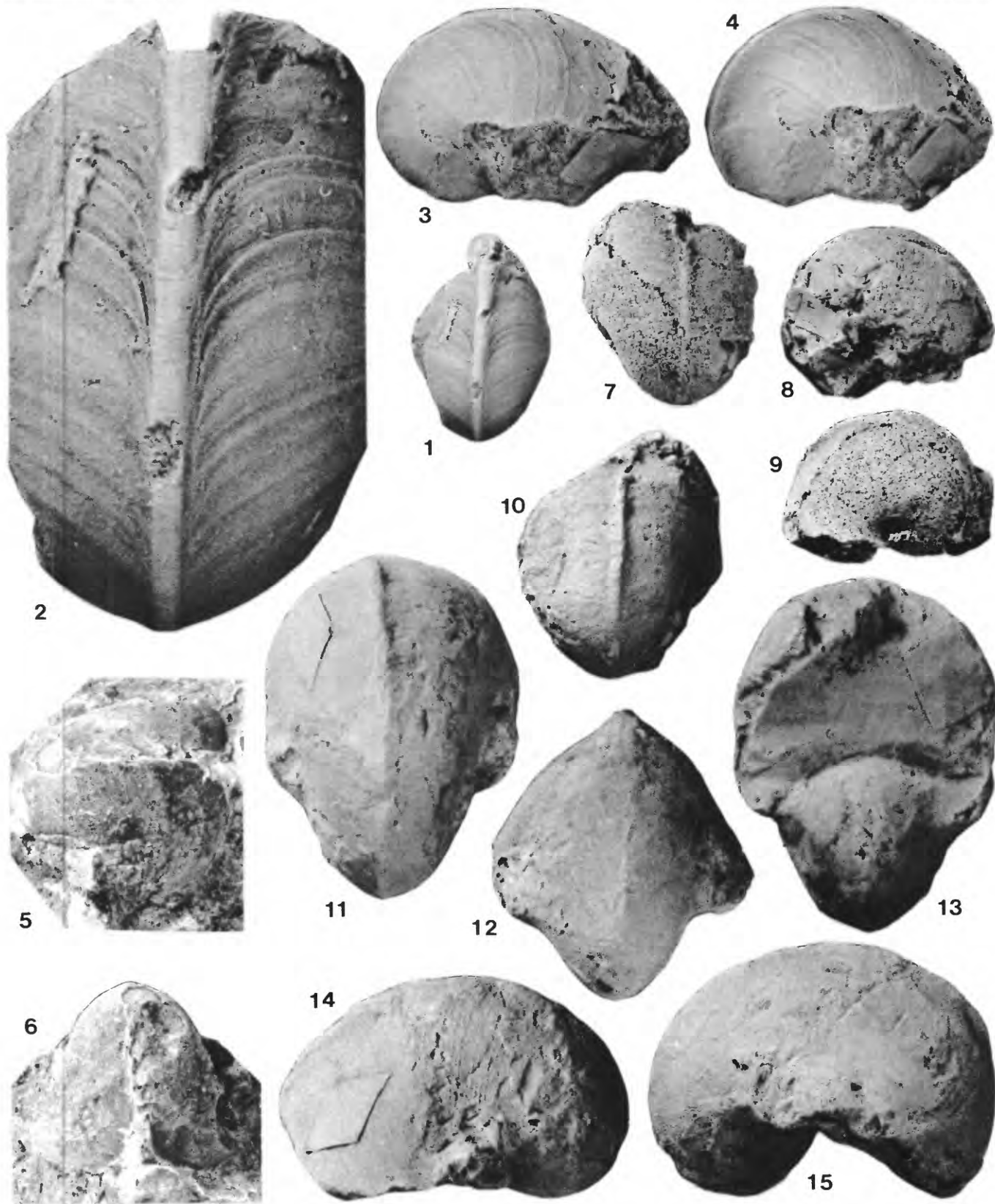


*SPHENOSPHERA*

# PLATE 33

- FIGURES 1–4. *Sphenosphaera recurvus* (Ulrich), 1897 (p. O171). Dorsal ( $\times 2$ ), dorsal closeup ( $\times 8$ ), and right-lateral and right posterolateral ( $\times 3$ ) views of calcareous holotype. Corryville biofacies, Grant Lake Limestone, Cincinnati, Ohio. USNM 45705.
- 5, 6. *Sphenosphaera* aff. *S. recurvus* (Ulrich), 1897 (p. O171). Right-dorsolateral and anterior views of highly recrystallized calcareous specimen partly embedded in limestone ( $\times 2$ ). Leipers Limestone, Rowena Ferry, Russell Co., Ky. UCGM 44282.
- 7–9. *Bellerophon* (*Bellerophon*) *subglobulus* Ulrich, 1897 (p. O159). Dorsal, right-lateral, and left-lateral views of silicified lectotype ( $\times 2$ ). Museum label reads “Black River Group, Mercer Co., Kentucky.” USNM 45709.
- 10–15. *Sphenosphaera subangularis* (Ulrich), 1897 (p. O171).
10. Dorsal view of a paralectotype ( $\times 3$ ). Museum label reads “Richmond Group, Richmond, Indiana.” USNM 315666.
- 11–15. Dorsal, posterior, ventral, left-lateral, and right-lateral views of calcareous lectotype ( $\times 3$ ). Same collection as figure 10 above. USNM 45708.





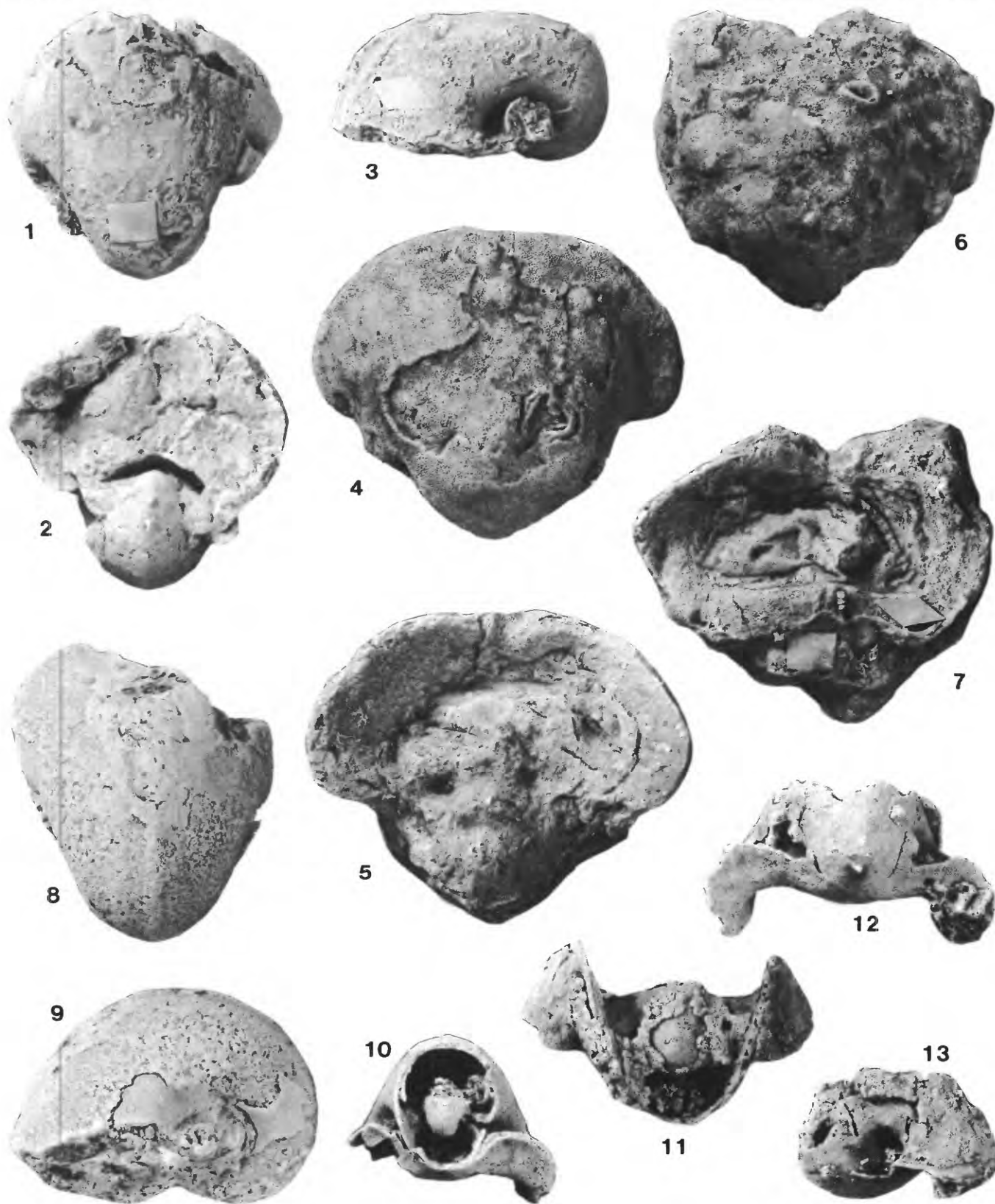
*SPHENOSPHAERA AND BELLEROPHON*



## PLATE 34

FIGURES 1–13. *Sphenosphaera capax* (Ulrich), 1897 (p. 0172).

- 1–3. Dorsal, left-lateral, and ventral views of calcareous lectotype ( $\times 1.5$ ). Fairmount biofacies, Fairview Formation, Covington, Ky. USNM 315606.
- 4, 5. Dorsal and ventral views of a bryozoan-encrusted, calcareous paralectotype ( $\times 2$ ). Note that specimen is vertically compressed. Same collection as figures 1–3 above. USNM 45699.
- 6, 7. Dorsal and ventral views of another bryozoan-encrusted, calcareous paralectotype ( $\times 1.5$ ). This specimen is also vertically compressed. Same collection as figures 1–3 above. USNM 315608.
- 8, 9. Dorsal and left-lateral views of a calcareous paralectotype ( $\times 1.5$ ). Same collection as figures 1–3 above. USNM 315607.
10. Posterior view of silicified specimen with shell broken away to expose whorl interior and whorl floor ridge ( $\times 1.5$ ). Gilbert Member, Ashlock Formation, USGS 6412-CO. USNM 387016.
- 11–13. Dorsal, posterior, and right-lateral views of silicified specimen with dorsal shell broken away showing whorl floor ridge ( $\times 1.5$ ). Same collection as figure 10 above. USNM 387017.

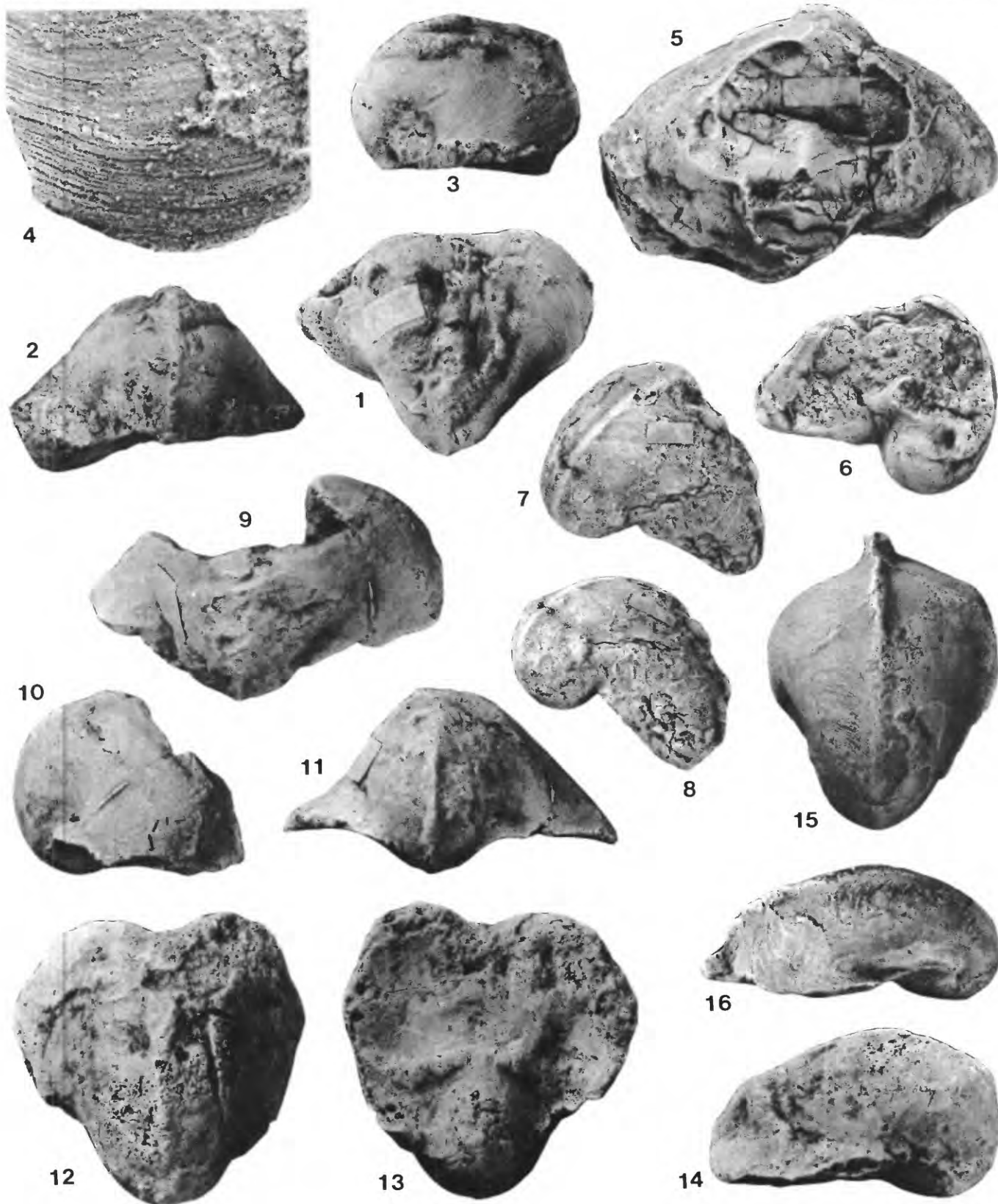


*SPHENOSPHAERA*

## PLATE 35

FIGURES 1–16. *Sphenosphaera mohri* (Miller), 1874 (p. O173).

- 1–4. Dorsal, posterior, and right-lateral views ( $\times 1.5$ ) and right-dorsolateral closeup view ( $\times 4$ ) of calcareous lectotype. Whitewater Formation, Richmond, Ind. UC 8793a.
5. Dorsal view of a large, broken, and vertically compressed, calcareous paralectotype ( $\times 1.5$ ). Same collection as figures 1–4 above. UC 8793b.
- 6–8. Ventral, right-dorsolateral, and right-lateral views of broken calcareous paralectotype that has been distorted by compression ( $\times 1.5$ ). Same collection as figures 1–4 above. UC 8793c.
- 9–11. Dorsal, right-lateral, and posterior views of calcareous specimen figured by Ulrich and Scofield (1897) ( $\times 2$ ). Whitewater Formation, Richmond, Ind. USNM 315611.
- 12–14. Dorsal, ventral, and left-lateral views of another calcareous specimen figured by Ulrich and Scofield (1897) ( $\times 2$ ). Same collection as figures 9–11 above. USNM 315610.
- 15, 16. Dorsal and left-lateral views of calcareous holotype of *Bellerophon cincinnatiensis* Miller and Faber, 1894, which is placed in synonymy with *S. mohri* ( $\times 1.5$ ). Museum label reads “Maysville, at quarries in Cincinnati, Ohio.” UC 8796.

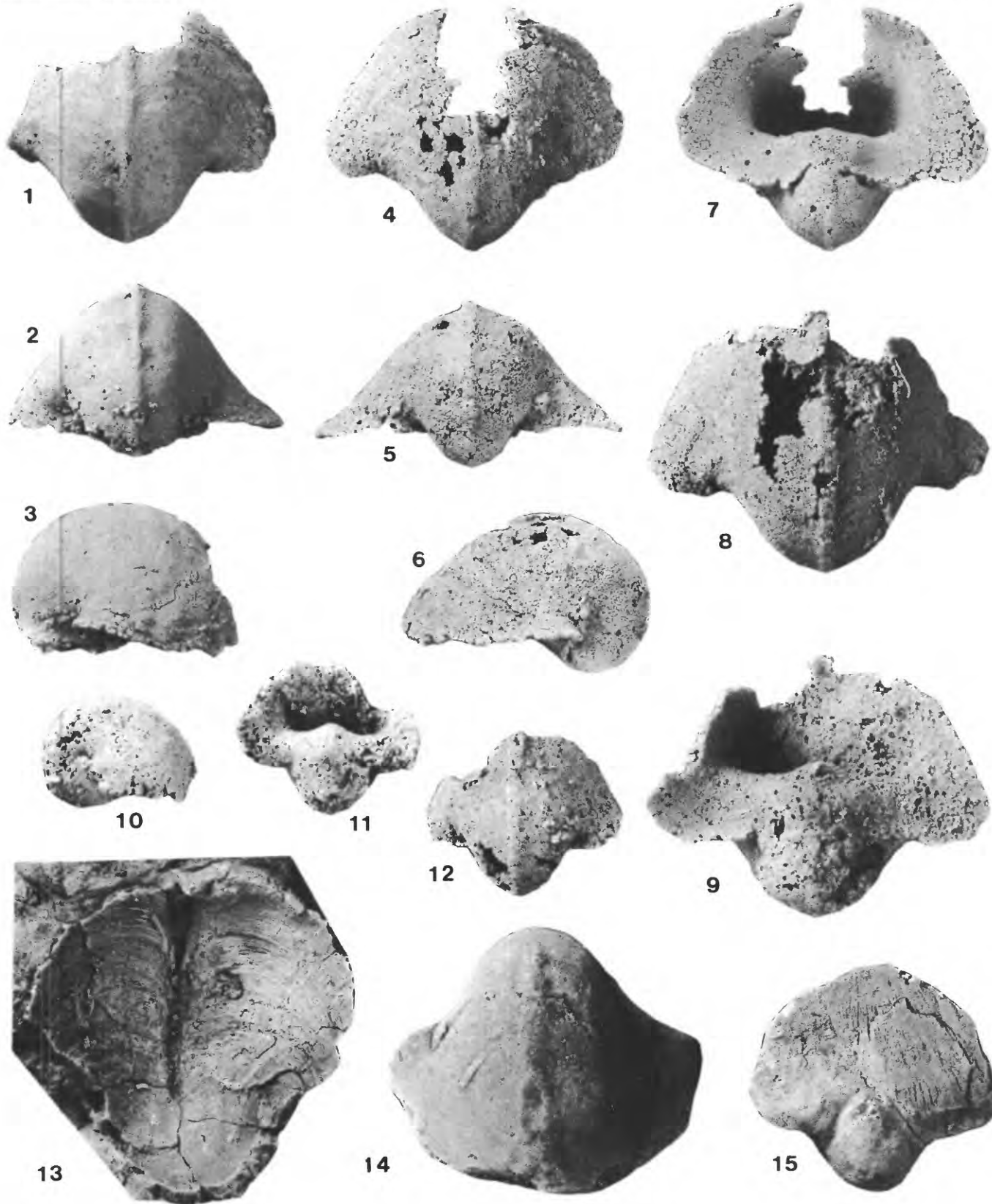


*SPHENOSPHAERA*

## PLATE 36

FIGURES 1–15. *Sphenosphaera mohri* (Miller), 1874. (p. O173).

- 1–3. Dorsal, posterior, and right-lateral views of silicified specimen ( $\times 1.5$ ). Liberty biofacies, upper Dillsboro Formation (Richmondian), USGS 6139-CO. USNM 315631.
- 4–7. Dorsal, posterior, left-lateral, and ventral views of silicified specimen ( $\times 1.5$ ). Same collection as figures 1–3 above. USNM 315629.
- 8, 9. Dorsal and ventral views of silicified specimen ( $\times 3$ ). Same collection as figures 1–3 above. USNM 315633.
- 10–12. Right-lateral, ventral, and dorsal views of juvenile silicified specimen ( $\times 3$ ). Same collection as figures 1–3 above. USNM 315632.
- 13. View of concave external impression of shell of fragmentary dorsum showing dorsal slit and growth lines ( $\times 1.5$ ). Whitewater Formation; locality unknown, but probably from southwestern Ohio or southeastern Indiana. MU 14539.
- 14, 15. Anterodorsal view ( $\times 2$ ) showing slit, and ventral view ( $\times 1.5$ ), of internal mold encrusted by bryozoans. Labeled as from Waynesville Formation; locality not given, but probably from same area cited for figure 13 above. UCGM 44303.



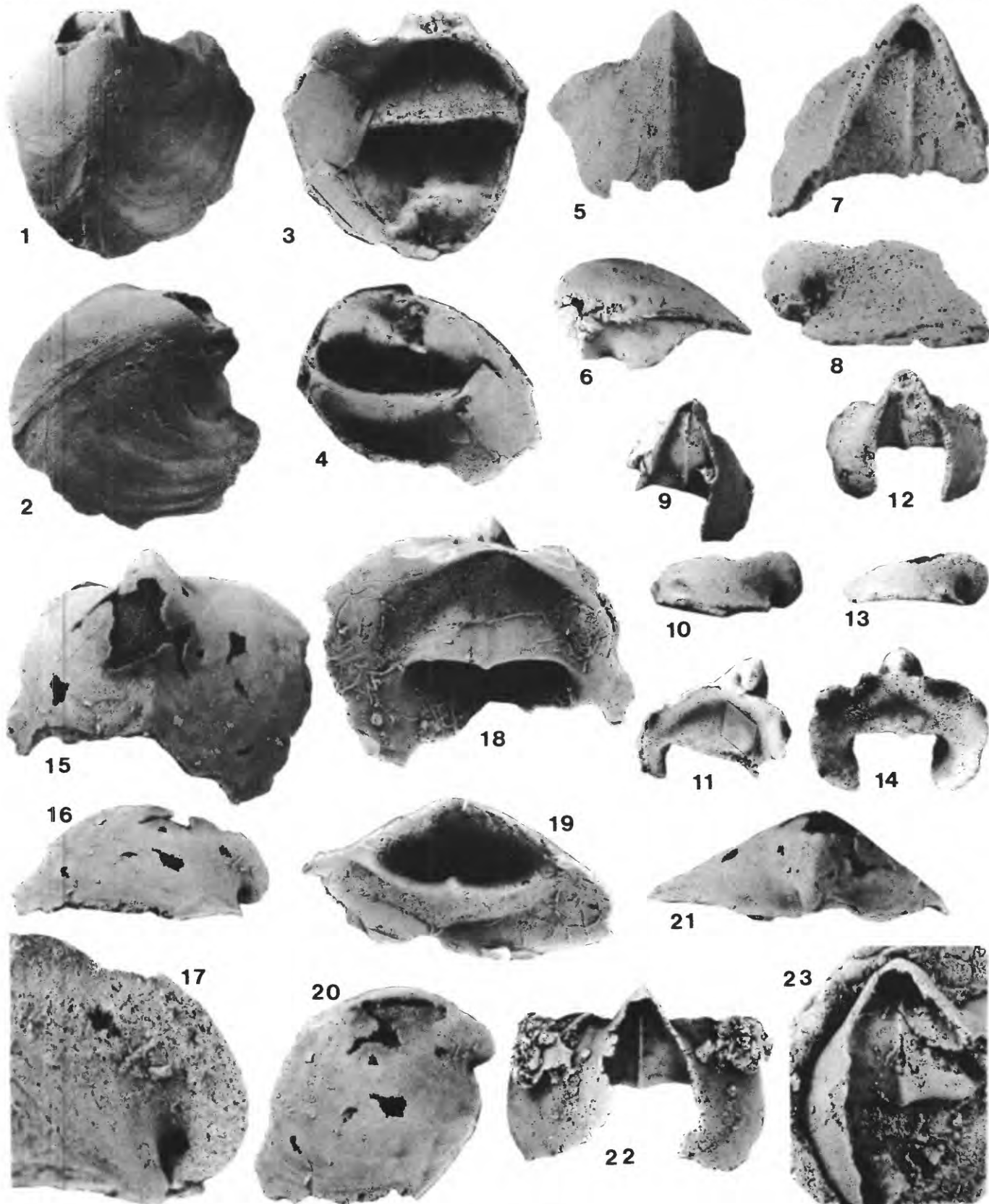
*SPHENOSPHERA*

## PLATE 37

FIGURES 1–11, 15–23. *Carinaropsis cymbula* (Hall, 1861) (p. O178).

- 1–4. Dorsal, left-anterodorsal, ventral, and anteroventral views of holotype ( $\times 2$ ). Note median groove in selenizone. Museum label gives horizon and locality as “Trenton Limestone, Allen’s Bluff, Tennessee.” AMNH 37725a.
- 5, 6. Dorsal and right-lateral views of a paratype ( $\times 2$ ). Same collection as figures 1–4 above. AMNH 37725b.
- 7, 8. Dorsal and right-lateral views of specimen from Ulrich and Scofield’s (1897) hypotypic suite, USNM 45739 ( $\times 3$ ). Museum label gives horizon and locality as “Trenton Group, near Danville, Kentucky.” USNM 265996.
- 9–11. Dorsal, left-lateral, and ventral views of another Ulrich and Scofield (1897) hypotype, USNM suite 45739 ( $\times 1.5$ ). Same collection as figures 7, 8 above. USNM 265997.
- 15–21. Dorsal and left-lateral views ( $\times 1.5$ ), left-lateral closeup view of coil ( $\times 4$ ), and ventral, anteroventral, left-dorsolateral, and posterior views ( $\times 1.5$ ) of silicified specimen. Grier Limestone Member, Lexington Limestone, USGS 5096-CO. USNM 265984.
22. Dorsal view of specimen showing dorsal septum ( $\times 1.5$ ). Grier Limestone Member, Lexington Limestone, USGS 4879-CO. USNM 265985.
23. Dorsal view of specimen showing dorsal septum ( $\times 2$ ). Museum label reads “Siliceous layer below Perryville bed, 2 miles north of Danville, Kentucky.” USNM 87778.
- 12–14. *Carinaropsis cumulae* (Hall, 1861) (p. O178). Dorsal, left-lateral, and ventral views of an Ulrich and Scofield (1897) hypotype from USNM suite 45738 ( $\times 1.5$ ). Museum label gives horizon and locality as “Trenton (Cannon Limestone), Nashville, Tennessee.” USNM 265998.





*CARINAROPSIS*

## PLATE 38

FIGURES 1–12. *Carinaropsis cymbula* (Hall, 1861) (p. 0178).

- 1, 2. Anterolateral view ( $\times 1.5$ ) and closeup view of same (about  $\times 6$ ) of broken silicified specimen showing structure of septum and parietal lip. Grier Limestone Member, Lexington Limestone, USGS 5096-CO. USNM 265986.
- 3–6. Dorsolateral, ventral, anteroventral, and right-lateral views of silicified specimen ( $\times 2$ ). Grier Limestone Member, Lexington Limestone, USGS 4879-CO. USNM 265988.
- 7, 8. Posterior and left-posterolateral views of silicified specimen, the latter view showing fine radial threads ( $\times 1.5$ ). Same collection as figures 1, 2 above. USNM 265991.
9. Dorsal view of silicified specimen showing coil and septum ( $\times 1.5$ ). Same collection as figures 3–6 above. USNM 265987.
10. Dorsal view of silicified specimen showing selenizone with median groove ( $\times 2$ ). Same collection as figures 3–6 above. USNM 265990.
- 11, 12. Dorsal and anteroventral views of silicified specimen with *Bucania subangulata* ( $\times 2$ ). Note that anterior margin of septum is nearly straight. Grier Limestone Member, Lexington Limestone, USGS 5094-CO. USNM 265989.

13–16. *Tetranota wisconsinensis* (Whitfield, 1878) (p. 0148).

- 13–15. Dorsal, right oblique anterodorsal, and posterior views of hypotype of Shrock and Raasch (1937) ( $\times 2$ ). Museum label gives horizon and locality as “Platteville Formation, Dir. 4–6, McCray Quarry, 3 miles east of Kentland, Indiana.” USNM 158279.
16. Anterior view of another dolomitized internal mold showing high median slit ( $\times 2$ ). No locality or horizon data with specimen, but based on mode of preservation, probably from Middle Ordovician rocks in the upper Midwest of the United States. MU 251T.

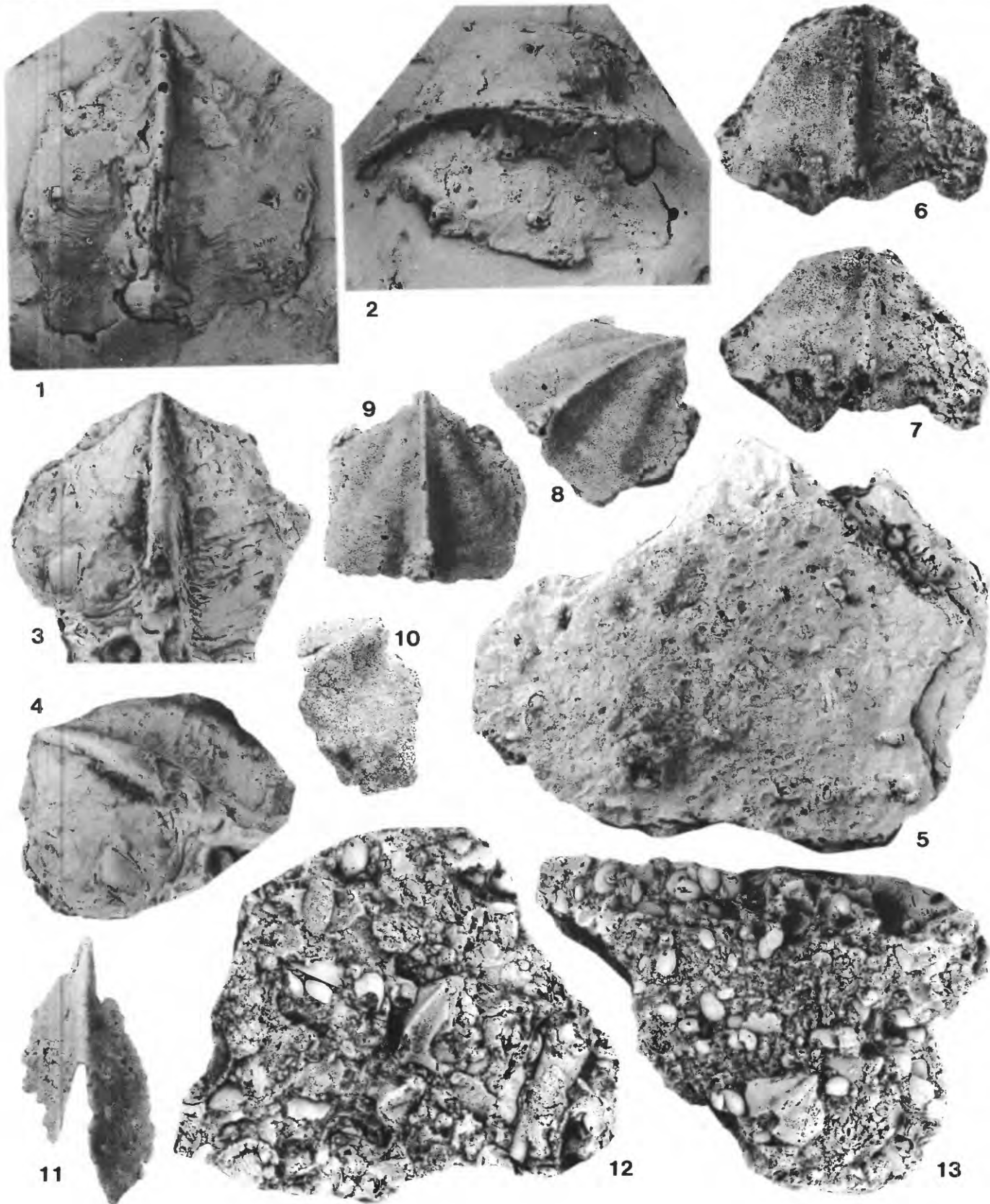


*CARINAROPSIS AND TETRANOTA*

## PLATE 39

FIGURES 1-5, 13. *Pterotheca saffordi* (Hall, 1861) (p. 0182).

- 1, 2. Dorsal and left-dorsolateral views of plastotype of holotype ( $\times 1.5$ ). Museum label gives horizon and locality as "Stones River (Lebanon Limestone), Lebanon, Tennessee." USNM 79262.
- 3-5. Dorsal and left-anterolateral views of calcitic specimen ( $\times 1$ ), and view of underside of small slab showing association with ostracodes ( $\times 1.5$ ). Tyrone Limestone (Rocklandian), High Bridge, Ky. USNM 79268.
13. Dorsal view of small specimen on lower part of slab with abundant leperditiid ostracodes ( $\times 1$ ). Museum label gives horizon and locality as "Top of Tyrone Limestone just beneath lower bentonite beds, High Bridge, Kentucky." USNM 50093.
- 6, 7, 12. *Pterotheca* cf. *P. expansa* (Emmons, 1842) (p. 0184).
  - 6, 7. Dorsal and anterodorsal views of weathered silicified specimen ( $\times 1.5$ ). Curdsville Limestone Member, Lexington Limestone, Curdsville, Ky. USNM 79283.
  12. Dorsal view of fragment in center of small slab with abundant leperditiid ostracodes ( $\times 1$ ). Murfreesboro Limestone (Blackriveran), Murfreesboro, Tenn. USNM 50100.
- 8, 9. *Pterotheca angusta* Raymond, 1921 (p. 0185). Dorsal and right-anterolateral oblique views of silicified specimen ( $\times 1.5$ ). Note narrow septal angle. Basal 2 ft of Curdsville Limestone Member, Lexington Limestone (Kirkfieldian), USGS 7784-CO. USNM 315538.
- 10, 11. *Pterotheca expansa* (Emmons, 1842) (p. 0183).
  10. Right-anterolateral oblique view of dorsal fragment showing high, narrowing keel ( $\times 2$ ). Lower part of Curdsville Limestone Member, Lexington Limestone, USGS 6134-CO. USNM 315535.
  11. Dorsal view of fragment of dorsal keel ( $\times 1.5$ ). Tyrone Limestone (Rocklandian), USGS 6034-CO. USNM 315533.

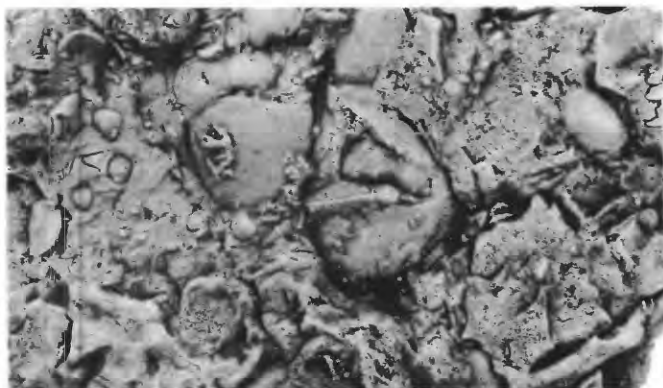
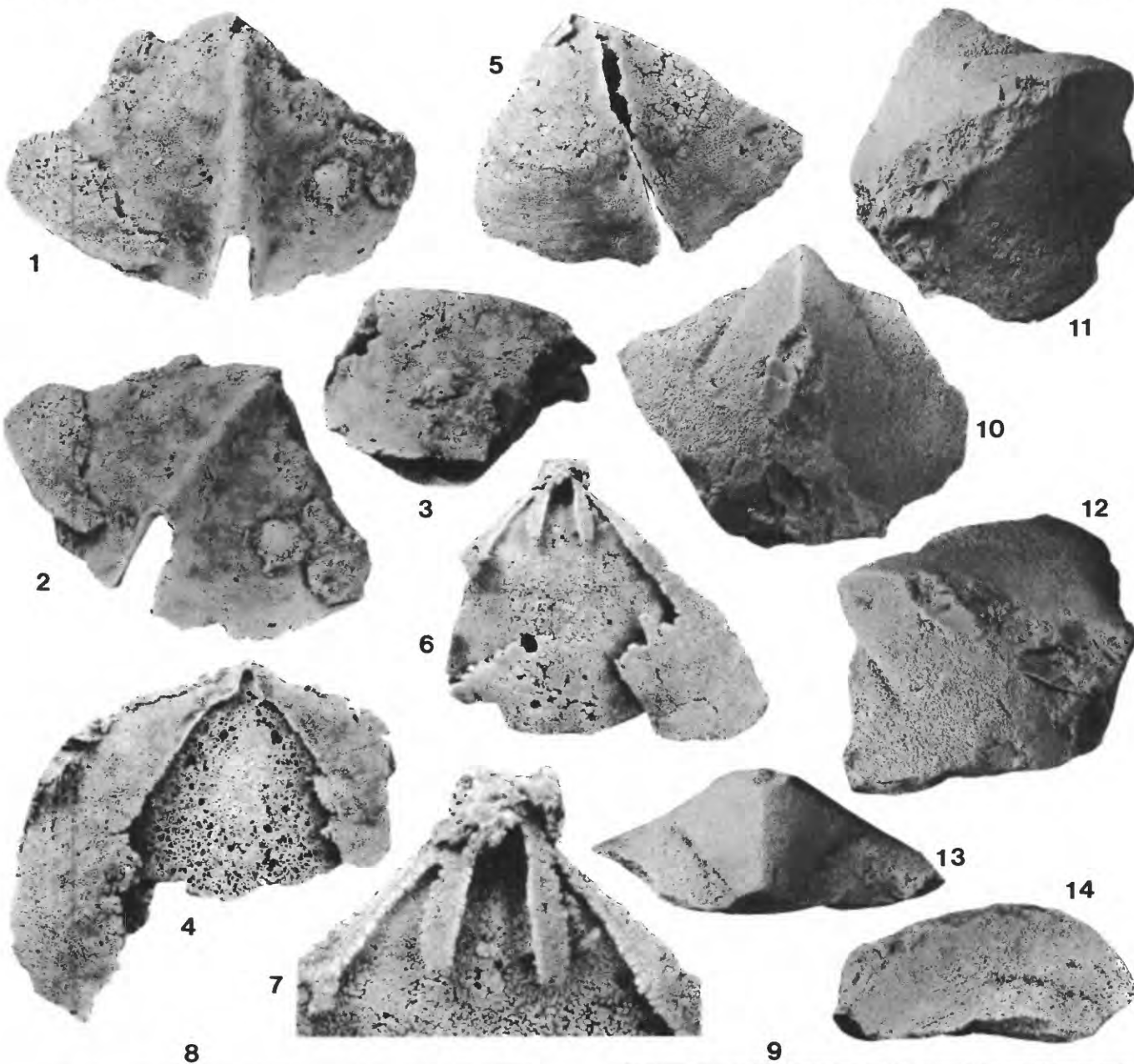


*PTEROTHECA*

## PLATE 40

- FIGURES 1-4. *Pterotheca* cf. *P. expansa* (Emmons, 1842) (p. 0184).  
 1-3. Dorsal, right-anterolateral, and left-lateral views of silicified specimen ( $\times 1$ ). Basal 2 ft of Curdsville Limestone Member, Lexington Limestone (Kirkfieldian), USGS 7784-CO. USNM 315536.  
 4. Dorsal view of silicified specimen showing septum ( $\times 1.5$ ). Note that there is no trace of divergent apical ridges in specimen. Same collection as figures 1-3 above. USNM 315537.
- 5-7. *Pterotheca expansa* (Emmons, 1842) (p. 0183).  
 5. Dorsolateral view of fragmentary silicified specimen showing fine, closely spaced growth lines ( $\times 1.5$ ). Tyrone Limestone (Rocklandian), USGS 6034-CO. USNM 315532.  
 6, 7. Dorsal view of fragmentary specimen ( $\times 2$ ), and closeup view of apical area ( $\times 5$ ), showing convex septum and divergent apical ridges. Same collection as figure 5 above. USNM 315534.
- 8, 9. *Pterotheca saffordi* (Hall, 1861) (p. 0182). Both sides of small slab showing *P. saffordi* in center in association with ostracodes ( $\times 1.5$ ). Tyrone Limestone (Rocklandian), High Bridge, Ky. USNM 50099.
- 10-14. *Carinaropsis explanata* Ulrich, 1897 (p. 0180). Dorsal, left- and right-anterolateral oblique, posterior, and left-lateral views of lectotype ( $\times 1.5$ ). Museum label gives horizon and locality as "Upper Trenton, Covington, Kentucky." USNM 45740.



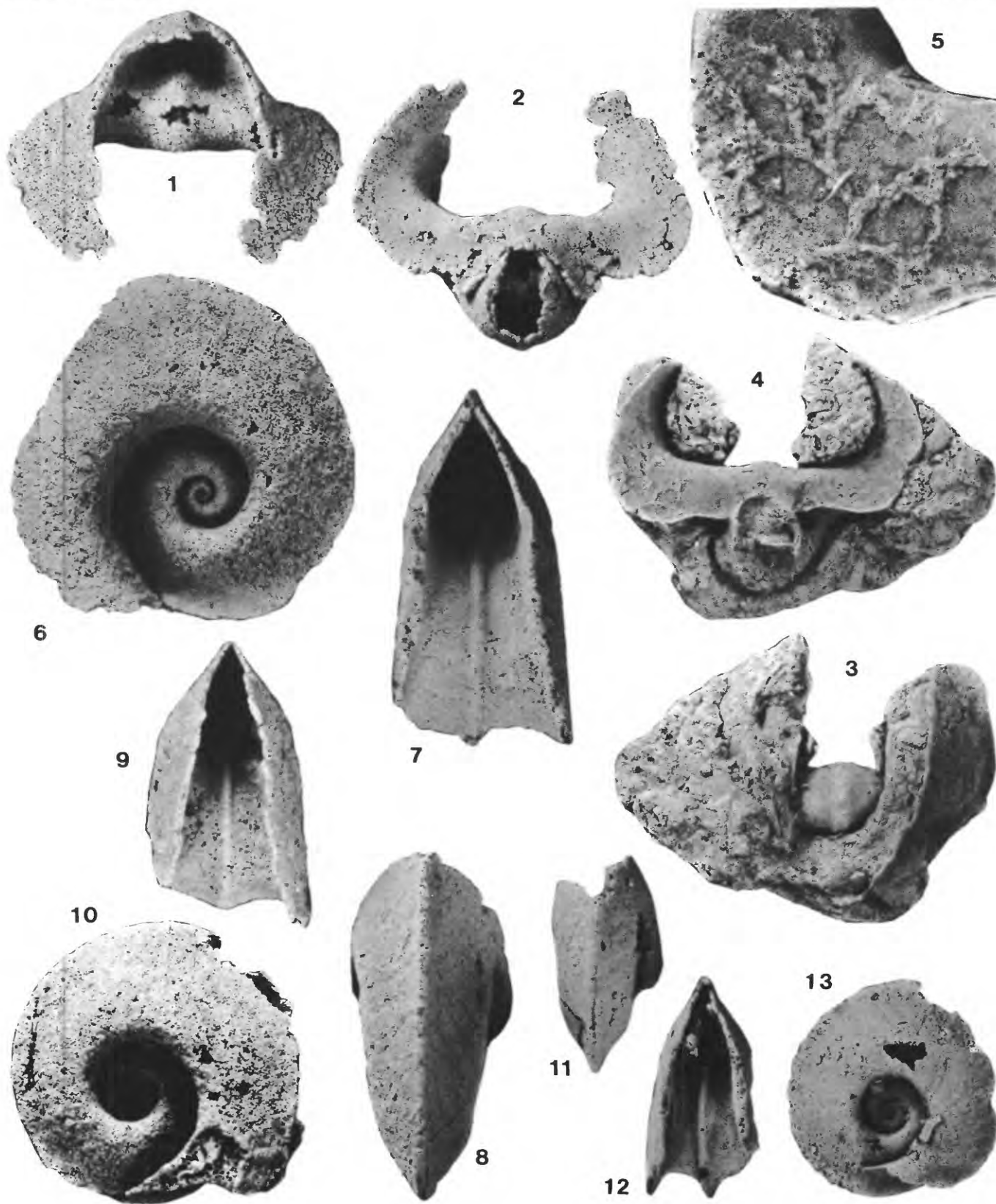


*PTEROTHECA AND CARINAROPSIS*



PLATE 41

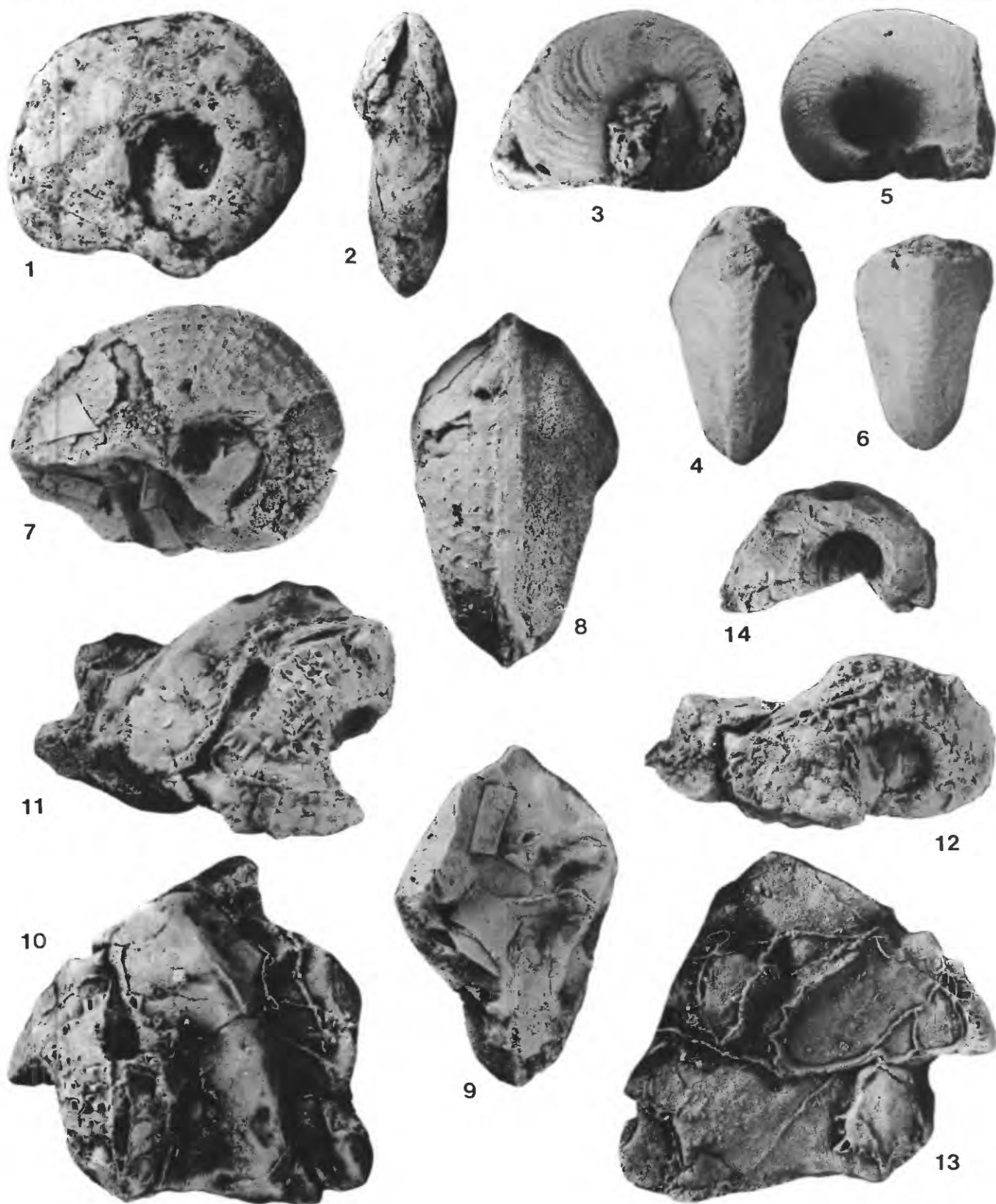
- FIGURES 1–5. *Sphenosphaera mohri* (Miller), 1874 (p. O173).  
1, 2. Anterodorsal and ventral views of silicified specimen with dorsum broken away to show whorl floor ridge ( $\times 1.5$ ). Liberty biofacies, Dillsboro Formation, USGS 6139-CO. USNM 315630.  
3–5. Dorsal and ventral views ( $\times 1.5$ ) and closeup view of parietal lip showing bryozoan encrustation (about  $\times 5$ ). Saluda Formation, “roadside exposure above upper part of Crooked Creek, Madison, Indiana.” MU 252T.
- 6–8. *Tropidodiscus cristatus* (Safford), 1869 (p. O119). Left-lateral, anterior, and dorsal views of silicified lectotype with anterodorsal portion of shell broken away ( $\times 3$ ). Cannon facies, Bigby-Cannon Limestone, Jackson Co., Tenn. USNM 45950.
- 9–13. *Tropidodiscus subacutus* (Ulrich), 1897 (p. O118).  
9, 10. Anterior and right-lateral views of silicified specimen with anterodorsal shell broken away ( $\times 3$ ). Salvisa Bed, Perryville Limestone Member, Lexington Limestone, USGS 6915-CO. USNM 315638.  
11–13. Dorsal, anterior, and right-lateral views of silicified lectotype with anterodorsal shell broken away ( $\times 3$ ). Upper Lexington Limestone, Danville, Ky. USNM 387021.



*SPHENOSPHAERA AND TROPIDODISCUS*

## PLATE 42

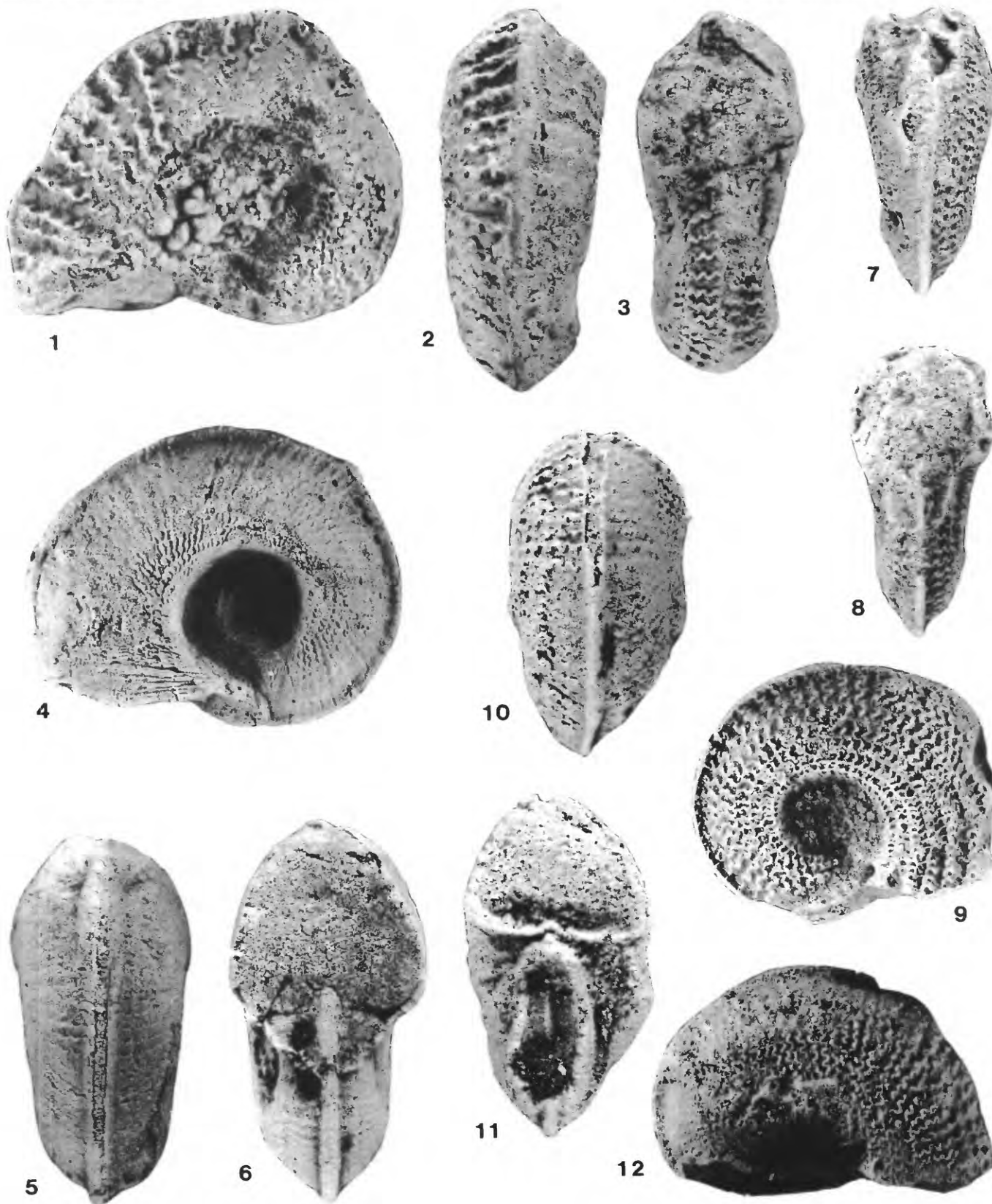
- FIGURES 1, 2. *Tropidodiscus magnus* (Miller), 1878 (p. 0119). Left-lateral and ventral views of calcitic holotype ( $\times 2$ ). "Richmond Group" (Richmondian), Richmond, Ind. UC 10838.
- 3-6. *Temnodiscus nitidula* (Ulrich), 1897 (p. 0125).
- 3, 4. Left-lateral and dorsal views of lectotype ( $\times 5$ ). "Upper Trenton" (Shermanian), Covington, Ky. USNM 315542.
- 5, 6. Right-lateral and dorsal views of a paralectotype ( $\times 5$ ). Same collection as figures 3, 4 above. USNM 315543.
- 7-13. *Phragmolites grandis* (Ulrich), 1897 (p. 0121).
- 7-9. Left-lateral, dorsal, and ventral views of a silicified paralectotype ( $\times 2$ ). Lebanon Formation, Lebanon, Tenn. USNM 315668.
- 10-13. Dorsal, left-anterolateral, left-lateral, and ventral views of silicified lectotype embedded in fine-grained limestone ( $\times 2$ ). Same collection as figures 7-9 above. USNM 315667.
14. *Phragmolites compressus* Conrad, 1838 (p. 0120). Left-lateral view of silicified holotype of *P. similis* (Ulrich), which herein is placed in synonymy with *P. compressus* ( $\times 2$ ). Museum label reads "Lowville beds, Black River Group, near High Bridge, Mercer Co., Kentucky." USNM 47568.



*TROPIDODISCUS, TEMNODISCUS, AND PHRAGMOLITES*

PLATE 43

- FIGURES 1-3. *Phragmolites grandis* (Ulrich), 1897 (p. O121). Left-lateral, dorsal, and ventral views of a silicified paralectotype, a juvenile ( $\times 6$ ). Lebanon Formation, Lebanon, Tenn. USNM 387018.
- 4-12. *Phragmolites cellulosus* (Ulrich and Scofield), 1897 (p. O122).
- 4-6. Left-lateral, dorsal, and ventral views of shelled specimen ( $\times 6$ ). Museum label reads "Orthis bed of Trenton Group (Hermitage Formation), central Tennessee." USNM 61029.
- 7-9. Dorsal, ventral, and right-lateral views of shelled specimen ( $\times 6$ ). Museum label reads "Bed 1, Trenton Group (Hermitage Formation), 2 miles south of Belfast, Tennessee." USNM 47562.
- 10-12. Dorsal, ventral, and right-lateral views of shelled specimen ( $\times 6$ ). Museum label reads "Pelecypod beds, Hermitage Formation, 1.5 miles south of Woodbury, Tennessee." USNM 79250.



*PHRAGMOLITES*

## PLATE 44

FIGURES 1-4. *Phragmolites compressus* Conrad, 1838 (p. O120).

1. Left-lateral view of calcitic specimen embedded in limestone ( $\times 5.75$ ). Museum label reads "Lower part of Trenton and perhaps Black River, 2-4 miles north of Burgin, Mercer Co., Kentucky." USNM 387019.

2-4. Left-lateral, dorsal, and ventral views of silicified specimen with ventral half of shell broken away ( $\times 5.75$ ). Same collection as figure 1 above (probably from a different sample). USNM 387020.

5-7. *Phragmolites bellulus* (Ulrich), 1897 (p. O123). Left-lateral, dorsal, and ventral views of calcitic holotype ( $\times 6$ ). Fairmount biofacies, Fairview Formation, Covington, Ky. USNM 45751.

8-10. *Phragmolites dyeri* (Hall), 1872 (p. O124). Right-lateral, dorsal, and ventral views of an Ulrich and Scofield (1897) calcitic hypotype ( $\times 6$ ). Waynesville biofacies, Bull Fork Formation, Butler Co., Ohio. USNM 315673.

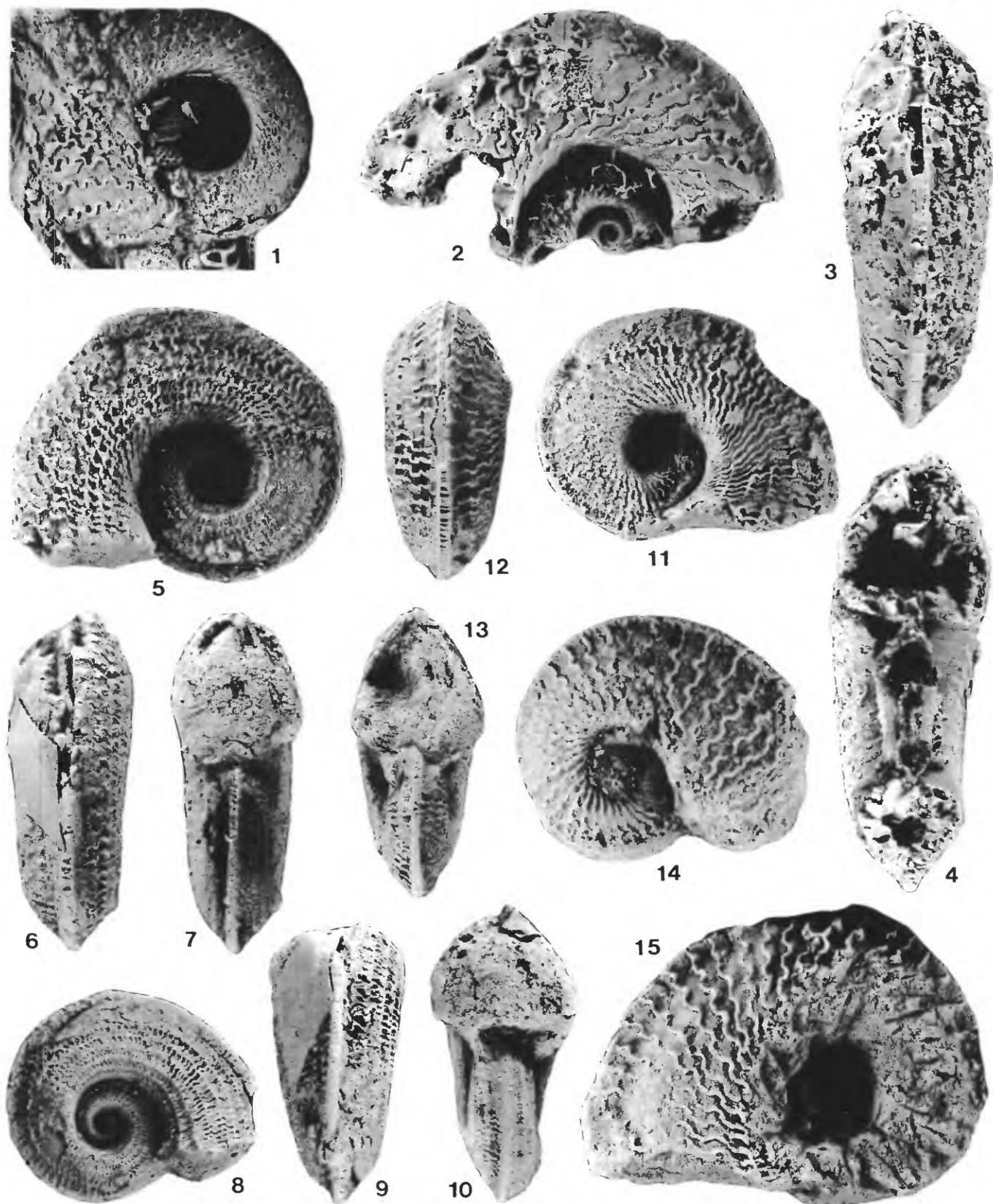
11-15. *Phragmolites elegans* (Miller), 1874 (p. O123).

11-13. Right-lateral, dorsal, and ventral views of an Ulrich and Scofield (1897) calcitic hypotype ( $\times 6$ ). Corryville biofacies, Grant Lake or Bull Fork Formation, Cincinnati, Ohio. USNM 315669.

14. Right-lateral view of calcitic specimen (about  $\times 8$ ). Same collection as figures 11-13 above. USNM 315670.

15. Left-lateral view of large calcitic specimen ( $\times 6.5$ ). Same collection as figures 11-13 above. USNM 315671.

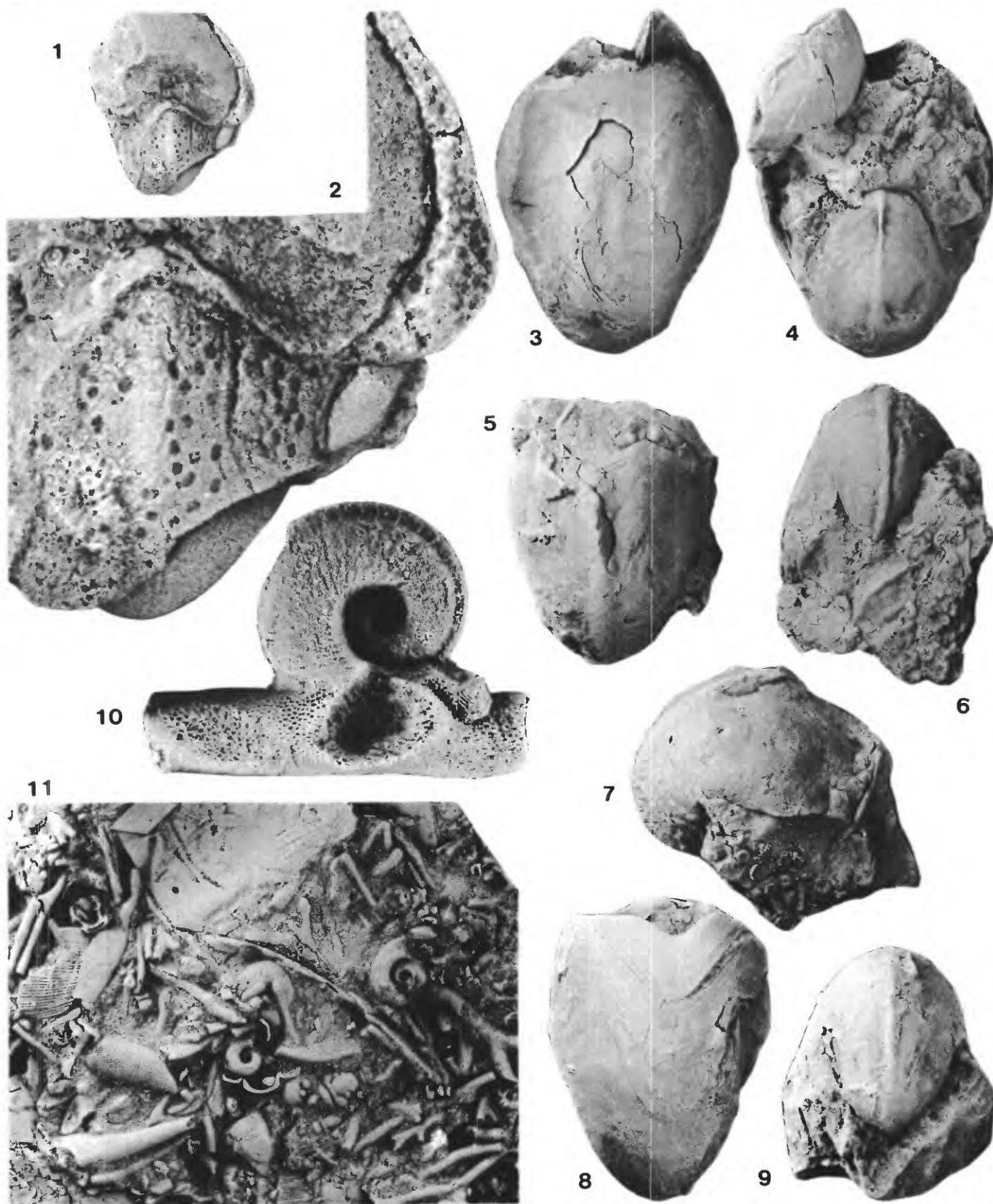




*PHRAGMOLITES*

PLATE 45

- FIGURES 1-9. *Sinuities granistriatus* (Ulrich), 1897 (p. 0113).
- 1, 2. Ventral views of calcitic specimen showing pitting on ventral coil and apertural rim ( $\times 2$ ) and ( $\times 7$ ). Kope Formation, Chilo, Ohio (locality OH-1). UCGM 44298.
  - 3, 4. Dorsal and ventral views of calcitic specimen ( $\times 2$ ). Same collection as figures 1, 2 above. UCGM 44296.
  - 5-7. Dorsal, anteroventral, and left-lateral views of calcitic specimen ( $\times 2$ ). Kope Formation. Carroll Co., Ky. (locality KY-1). UCGM 44306.
  - 8, 9. Dorsal and anterior views of calcitic specimen ( $\times 2$ ). Same collection as figures 1, 2 above. UCGM 44297.
  - 10. *Phragmolites elegans* (Miller), 1874 (p. 0123). Left-lateral view of small calcitic specimen showing common association of species with ramose bryozoans (about  $\times 8$ ). Corryville biofacies, Grant Lake or Bull Fork Formation, Cincinnati, Ohio. USNM 315672.
  - 11. *Phragmolites dyeri* (Hall), 1872 (p. 0124). Small slab showing species in center associated with diverse assemblage of ramose bryozoans, brachiopods, and trilobites ( $\times 1.5$ ). Waynesville biofacies, Bull Fork Formation, Butler Co., Ohio. USNM 315674.



SINUITES AND PHRAGMOLITES



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