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THE DISPARID CRINOID SUPERFAMILIES  
HOMOCRINACEA (ORD.-SIL.) AND CINCINNATICRINACEA (ORD.)

A dissertation submitted to the  
Division of Graduate Studies  
of the University of Cincinnati  
in partial fulfillment of the  
requirements for the degree of

DOCTOR OF PHILOSOPHY

in the Department of Geology  
of the Graduate School of Arts and Science

1974

by

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# UNIVERSITY OF CINCINNATI

April 30 1974

*I hereby recommend that the thesis prepared under my supervision by* John Michael Warn

*entitled* The Disparid Crinoid Superfamilies Homocrinacea (Ord.-Sil.) and Cincinnatiacrinacea (Ord.)

*be accepted as fulfilling this part of the requirements for the degree of* Doctor of Philosophy

*Approved by:*

Dwight C. Coster  
William C. Spyer  
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ABSTRACT

The discovery that Heterocrinus heterodactylus Hall, 1847 (type species of Heterocrinus) is unrecognizable necessitates new names for crinoid taxa from Champlainian and Cincinnati strata. The new genus Cincinnatiocrinus is erected to accommodate the new species C. varibrachialus (type species of Cincinnatiocrinus) and Ulrich's (1882) species H. pentagonus. The superfamily Heterocrinacea (nom. transl. Ubaghs, 1953, ex Heterocrinidae Zittel, 1879) is essentially replaced by the new superfamily Cincinnatiocrinacea, and the new family Cincinnatiocrinidae is essentially substituted for the family Heterocrinidae Zittel, 1879. The family Cincinnatiocrinidae is divided into the two new subfamilies Cincinnatiocrininae (which contains C. varibrachialus, C. pentagonus, Dystactocrinus constrictus, Isotomocrinus tenuis, Ohioocrinus laxus, and O. brauni) and Atopocrininae (which includes only Atopocrinus priscus). The family Homocrinidae Kirk, 1914, (the only family in the Homocrinacea, nom. transl. ex Homocrinidae Kirk, 1914) is also divided into two subfamilies: the subfamily Homocrininae (nom. transl. ex Kirk, 1914, and which includes Homocrinus parvus, Ectenocrinus simplex, E. geniculatus, Ibexocrinus leptus, and Sygcaulocrinus typus) and the new subfamily Daedalocrininae (which contains only Daedalocrinus bellevillensis). Numerous lectotypes and lectoparatypes are established, a number

of species formerly referred to the Heterocrinidae are considered unrecognizable, and synonymizing is undertaken for a number of species believed to fit in the normal variation of earlier described species. Geographic and stratigraphic ranges of taxa are firmly established and diagnoses, descriptions, and illustrations are put forth in a manner to insure easy recognition of taxa.

Cincinnatian stratigraphy of the Ohio-Kentucky-Indiana area is discussed in detail. A study of potential myzostomid (polychaete annelid) galls in a Richmondian crinoid is appended.

## INTRODUCTION

Modern concepts of the disparid inadunate crinoid families Heterocrinidae and Homocrinidae (elevated to superfamilies by Ubaghs, 1953) and their constituents date essentially from Ulrich (1925), the latest monograph on heterocrinids and homocrinids. The forthcoming crinoid section of the Treatise on Invertebrate Paleontology will include few changes: the Treatise will incorporate two new genera, Atopocrinus (a heterocrinid) and Ibexocrinus (a homocrinid), described by Lane (1970) and placed by him in these families; and the Treatise will characterize the genus Heterocrinus as having isotomous rather than heterotomous branching, as it was defined by Ulrich (1925, p. 84) and others (Wachsmuth and Springer, 1886, p. 207; Wachsmuth, 1900, p. 152; Grabau and Shimer, 1910, p. 502; Springer, 1911, p. 27; Springer, 1913, p. 212; Moore and Laudon, 1944, p. 149; and Warn, 1973, p. 12). Ulrich (1925) apparently based his study on small numbers of specimens (for some species, on from one to a few). Modern treatment, with examination of large numbers of specimens and attention to intraspecific variation, appears necessary.

Numerous nomenclatural changes are needed, simply because Heterocrinus heterodactylus (type species of Heterocrinus) is unrecognizable and must be restricted to Hall's (1847) type-specimens (from New York strata). Thus, new names must be considered for taxa from strata in and around

Cincinnati, Ohio formerly attributed to Heterocrinus and H. heterodactylus (the author chooses the new names Cincinnati-crinus and C. varibrachialus for these taxa); and, because Heterocrinus is the type-genus of the familial taxa Heterocrinidae and Heterocrinacea, new names must be considered for these taxa (herein, Cincinnati-crinidae and Cincinnati-crinacea).

The study of Cincinnati-crinacea and Homocrinacea is particularly facilitated at the University of Cincinnati. Type-species of six (Heterocrinus, Atyphocrinus, Dystactocrinus, Ohioocrinus, Ectenocrinus, and Drymocrinus) of the eleven genera placed by Ulrich (1925) in the Heterocrinidae and Homocrinidae have been reported to occur in Cincinnati strata in and around Cincinnati, Ohio. Of the remaining five genera, two were first described from the Hull limestone, Kirkfield, Ontario (Isotomocrinus and Daedalocrinus), one (Sygcaulocrinus) from the Fort Atkinson Member of the Maquoketa Formation of Iowa, one (Columbicrinus) from the Lebanon Limestone of Tennessee, and one (Homocrinus) from the Rochester Shale of New York. Thus, large numbers of Cincinnati-crinids and homocrinids are housed in the University of Cincinnati Geology Museum and in other Cincinnati area museums. As well, large pockets of Cincinnati-crinus varibrachialus (type of Cincinnati-crinus) and Ectenocrinus simplex (type of Ectenocrinus) have recently been discovered

in the area. Finally, the Kopf Collection at Cincinnati is one of the finest North American echinoderm collections and contains hundreds of Kirkfield crinoids.

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#### REPOSITORIES AND THEIR ABBREVIATIONS

Specimens referred to in this work are listed by catalogue numbers with the repository names abbreviated as follows:

AMNH	American Museum of Natural History, New York, New York
BM	British Museum (Natural History), London, England
CFM	Field Museum of Natural History, Chicago, Illinois (numbers preceded by UC denote specimens in the University of Chicago Walker Museum Collection)
GSC	Geological Survey of Canada, Ottawa, Ontario
HM	Hunterian Museum (Geology), The University, Glasgow, Scotland
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
MU	Geology Museum, Department of Geology, Miami University, Oxford, Ohio
NYSM	New York State Museum, Albany, New York
OM	Orton Museum, Department of Geology, Ohio State University, Columbus, Ohio
ROM	Royal Ontario Museum, Toronto, Ontario
SUI	Geology Department, The University of Iowa, Iowa City, Iowa

- UCGM University of Cincinnati Geology Museum, Department  
of Geology, University of Cincinnati, Cincinnati,  
Ohio (numbers preceded by K. denote specimens  
in the Kopf Collection)
- UM Geology Department, University of Minnesota,  
Minneapolis, Minnesota
- USNM United States National Museum, Smithsonian  
Institution, Washington, D. C. (numbers  
preceded by S. denote specimens in the  
Springer Collection)
- YPM Peabody Museum of Natural History, Yale University,  
New Haven, Connecticut

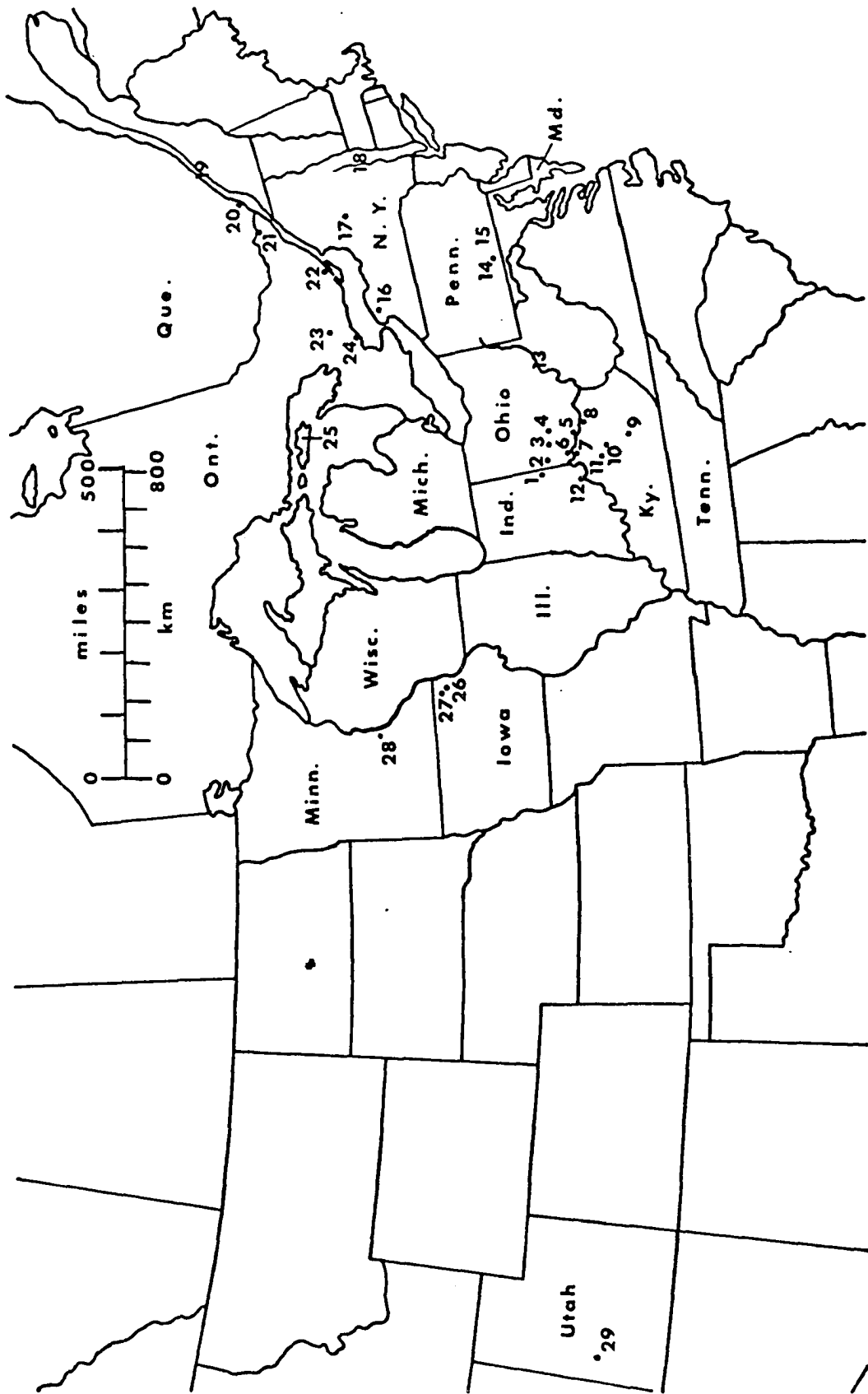
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Text-fig. 1. Cities and states referred to in text.

Numbers represent the following:

1—Richmond, Indiana	15—Swatara Gap
2—Oxford, Ohio	16—Lockport, New York
3—Lebanon, Ohio	17—Trenton Falls, New York
4—Wilmington, Ohio	18—Hudson River
5—Point Pleasant, Ohio	19—St. Lawrence River
6—Cincinnati, Ohio	20—Montreal, Quebec
7—Ludlow, Covington, and Newport, Kentucky	21—Ottawa, Ontario
8—Maysville, Kentucky	22—Belleville, Ontario
9—Preachersville, Kentucky	23—Kirkfield, Ontario
10—Lexington, Kentucky	24—Toronto, Ontario
11—Frankfurt, Kentucky	25—Manitoulin Island
12—Madison, Indiana	26—Clermont, Iowa
13—Ohio River	27—Fort Atkinson, Iowa
14—Ft. Loudon, Pennsylvania	28—St. Paul, Minnesota
	29—Ibex, Utah

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## STRATIGRAPHY

Cincinnaticrinacea and Homocrinacea range from White-rockian to Niagaran strata from western North America (Utah) to eastern North America (New York and Quebec). Various members of the two superfamilies occur in the Kanosh Shale of Utah (Whiterockian); the Decorah Shale, St. Paul, Minnesota (Kirkfieldian); the Hull beds, Kirkfield, Ontario (Kirkfieldian); the Hull (Kirkfieldian?), Sherman Fall (Shermanian?), and Coburg (Edenian?) beds of Ottawa and Montreal; the Whetstone Gulf Formation of northwestern New York (Edenian?); the Sheguiandah Formation of the Manitoulin Island area of Canada (Edenian); the Edenian and Maysvillian (upper) portion of the Martinsburg Formation of Maryland and southern Pennsylvania; the Maquoketa Formation of Iowa (Richmondian?); and the Rochester Shale near Lockport, New York (Niagaran)—Text-fig. 1 is a map that shows the location of cities and towns referred to in the text. No attempt, beyond Text-fig. 2 and references under the respective occurrences of taxa, will be made to discuss these strata. However, seven of the thirteen cincinnaticrinacean and homocrinacean species recognized here occur in Cincinnatian strata in the southwestern Ohio-southeastern Indiana-northern Kentucky area, and Cincinnatian stratigraphy and stratigraphic nomenclature deserves attention.

Historical survey of Cincinnatian stratigraphy

In 1829 Vanuxem (p. 256) correlated Cincinnatian rocks of Ohio and Kentucky (and perhaps Champlainian strata of

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Text-fig. 2. Correlation of Ordovician and Silurian time-stratigraphic standards of North America and Europe and pertinent rock units of geographic areas where crinoids studied herein occur. Areas with diagonal lines = strata representing that time missing, blank areas = strata unexposed or considered not pertinent by the author, T = Tremadoc, and A = Arenig. Although all rock units are time-transgressive, only those that have been demonstrated to be so are so illustrated; others are bounded by straight lines. (From Twenhofel, et al., 1954, with modification from Weiss and Sweet, 1964, Peck, 1966, and Sweet and Bergström, 1971.)

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EUROPEAN STAGES	SYSTEM	N. AMERICA SERIES and STAGES	CINCINNATI AREA	ONTARIO	N. WESTERN NEW YORK	MARYLAND and SOUTHERN PENN.	OTHERS	
LUDLOW	SILURIAN	Upper	<i>Cayuga</i>	Bass Island	Cableskill			
				Salina	Salina			
				Guelph	Lockport-Guelph			
WEN-LOCK	SILURIAN	Middle	<i>Niagaran</i>	Bisher	Manistique	Decew		
				Crab Orchard	St Edward	Rochester	Clinton	
LANDOVERY	SILURIAN	Lower	<i>Medinan</i>	Brassfield	Cataract	Albion		
ASHGILL	ORDOVICIAN	Upper	CINCINNATIAN	<i>Richmondian</i>	Bull Fork	Queenston	Queenston	<i>Junonia</i>
				<i>Maysvillian</i>	Grant Lake	Dundas	Oswego	
				<i>Edenian</i>	Fairview	"Billings"	Pulaski	Whetstone-Gulf
CARADOC	ORDOVICIAN	Middle	CHAMPLAINIAN	<i>Shermanian</i>	Kape	Coburg	Coburg	<i>Morinsburg</i>
				<i>Kirkfieldian</i>	Lexington	Sherman Fall	Sherman Fall	
				<i>Rocklandian</i>	Tyrone	Hull	Hull	Oranda
LLANDEILO	ORDOVICIAN	Middle	CHAMPLAINIAN	<i>Blackriveran</i>	High Bridge	Rockland	Rockland	Chambersburg
				<i>Chazyan</i>	Oregon			
LLANVIRN	ORDOVICIAN	Lower	CHAMPLAINIAN	<i>Whiterockian</i>	Camp Nelson			Kanosh of Utah
				<i>Canadian</i>				

of Kentucky) with strata at Trenton Falls, New York. Hall (1842, p. 61) proposed age equivalence of shales at Newport, Kentucky (directly across the Ohio River from Cincinnati) with the New York Utica and the underlying limestone exposed in the Ohio River only at low-water with the Trenton of New York. In 1843, Hall referred strata at Cincinnati to the Hudson River Group (Hudson River was used by Mather, Emmons, Vanuxem, and other early New York geologists mainly for rocks of Late Ordovician age exposed in the Hudson River Valley, New York). Hall also correlated a body of underlying strata (containing Triarthrus eatoni—T. becki of older literature) with the New York Utica and the lowermost strata exposed at Cincinnati with the New York Trenton (with reservation). Thus, from 1843 to 1865 the name Hudson River Group was widely used for strata at Cincinnati.

In 1859, Mather (p. 6) used the name "Cincinnati limestone" in passing for strata at Cincinnati. First usage of Cincinnati as a stratigraphic term, however, is usually attributed to Meek and Worthen (1865, p. 155, and in reports on the geology of Illinois—Worthen, 1866; Meek and Worthen, 1868), who suggested that the name Cincinnati Group be substituted for Hudson River Group, because the strata at Cincinnati and the New York Hudson River Group are of different age. Orton (1873, p. 369) proposed that it is "probable that the lowermost beds of Cincinnati are the proper equivalent of

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Text-fig. 3. Orton's (1873) rock-stratigraphic classification of the Cincinnati Group. All ratios are shale to limestone.

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		thick- ness	description
Cincinnati group	Lebanon beds	300' (92m)	predominantly limestones (shale: limestone somewhat higher than 1:1 in the lower portion and somewhat lower than 1:1 in the higher portion) lying between the highest stratum of the Cincinnati hills and the lowest Silurian (Brass- field) beds and outcropping no closer than 20 miles (32 km) from Cincinnati
	Hill Quarry beds	125- 150' (38- 46m)	shale and limestone about equal (ratios of less than 5 or 6:1 and approaching 1:1); outcropping just below the tops of the hills at Cincinnati; extensively quarried
	Eden shales	250' (76m)	predominantly shale (shale to limestone ratios of about 4:1 and up to 10:1); named for exposures in Eden Park in Cincinnati
	River Quarry beds	50' (15m)	4-8" (10-20 cm) thick limestones, commonly with rippled surfaces, made up of crinoid parts; sh:ls = 4:1; quarried in Cincinnati
	Point Pleasant beds	50' (15m)	thick (16-18"—41-46 cm), barren limestones and shales outcropping in the north bank of the Ohio River at Point Pleasant, Ohio

the Utica Slate [of New York]." Orton (1873) divided the Cincinnati Group into five lithic units (in ascending order): Point Pleasant beds; River Quarry beds; Middle, or Eden, shales; Hill Quarry beds; and Lebanon beds.

The River Quarry beds, Eden shales, and Hill Quarry beds, all named for strata exposed in the immediate vicinity of Cincinnati, were lumped together by Orton as the Cincinnati beds. The name Point Pleasant was used for strata exposed some distance upriver from Cincinnati (the town Point Pleasant is situated about 25 miles—about 40 km—upriver from downtown Cincinnati), while the name Lebanon was applied to strata outcropping on top of the Ohio River hills nowhere closer than 20 miles (about 32 km) from Cincinnati. Orton defined the units as (refer to Text-fig. 3):

- 1) Cincinnati Group—750 to 800 feet (about 230 to 245 m) of alternating beds of blue "clay" (shale or mudstone) and blue-gray limestone outcropping in and around Cincinnati, Ohio and including the Point Pleasant beds, Cincinnati beds, and Lebanon beds;
- 2) Point Pleasant beds—lowest 50 feet (about 15 m) of the Cincinnati Group with lighter-colored, essentially barren limestones and shales and thicker (16 to 18 inches—about 41 to 46 cm) limestones than overlying beds and outcropping in the north bank of the Ohio River about 25 miles (about 40 km) east of Cincinnati;

- 3) Cincinnati beds—425 to 450 feet (about 130 to 137 m) of the Cincinnati Group beginning at low-water of the Ohio River in Cincinnati and extending to the tops of the hills, having a shale to limestone ratio of at least 5:3, and including the River Quarry beds, Eden shales, and Hill Quarry beds;
- 4) River Quarry beds—50 feet (about 15 m) of firm and compact limestones (commonly with rippled surfaces) of about 4 to 8 inches (about 10 to 20 cm) thickness (but sometimes up to 2 feet—about 60 cm), made up almost entirely of crinoid columns alternating with thicker shales, with a shale to limestone ratio of 4:1 and quarried in the Cincinnati area;
- 5) Eden shales—250 feet (about 76 m) of predominantly shale (with a shale to limestone ratio of at least 4:1 and as high as 10:1) named for exposures in Eden Park);
- 6) Hill Quarry beds—125 to 150 feet (about 38 to 46 m) of more limy rock (with shale to limestone ratios of less than 5 or 6:1 and approaching 1:1) outcropping just below the tops of the hills at Cincinnati and extensively quarried;
- 7) Lebanon beds—about 300 feet (about 92 m) of predominantly limy rock (shale to limestone somewhat higher than 1:1 in the lower portion and somewhat lower than 1:1 in the higher portion) lying between the highest stratum of the Cincinnati hills and the lowermost Silurian beds and

outcropping no closer than 20 miles (about 32 km) from Cincinnati (with good exposures at Madison and Richmond, Indiana and Oxford and Lebanon, Ohio).

Orton (1873) represents the first good lithostratigraphic study of Cincinnati strata at Cincinnati (for much of the classical period of American geology, lithologies at Cincinnati were overshadowed by the strata's abundance of fossils).

U. P. James (1879) reconsidered correlation of Cincinnati and New York strata. He reported that of 500 species in strata at Cincinnati only about 100 occur in the Trenton, Utica, and Hudson River of New York; of that 100, 65 are confined to the Trenton, 18 to Utica and Hudson River, and 17 are shared by all three. James concluded that Trenton would be a better designation than previously used Hudson River but opted for Cincinnati Group because of the obvious faunal dissimilarity of local strata to that of New York.

In 1881, S. A. Miller (p. 268-269; 283-287) presented a new correlation of Cincinnati and New York strata: the River Quarry beds with the upper part of the Trenton Group, the Eden shales with the Utica Group; and the Hill Quarry and Lebanon beds with the Hudson River Group. The names Trenton, Utica, and Hudson River unfortunately came to be used in place of Orton's lithic names.

In 1891, J. F. James recognized a problem that has only recently (Weiss et al., 1965, p. 18-19) been resolved. James compared the beds exposed at Point Pleasant, Ohio (= Orton's

Point Pleasant beds) with those exposed during low-water in the Ohio River at Ludlow, Kentucky (= Orton's River Quarry beds) and found no difference. This is the earliest implication that Orton (1873) had given different names to two bodies of rock (which Orton thought were distinct) that are now known to be portions of one unit, the Point Pleasant Formation.

Winchell and Ulrich (1897, p. ci-cv) used the term "Cincinnati Period" for rocks occupying a position between Trenton (including Point Pleasant beds) and the Silurian Brassfield Formation and rejected associations of the Hill Quarry and Lebanon beds with the New York Hudson River Group. Rather, they correlated the Hill Quarry beds with the Lorraine Group of New York and Ontario. They then replaced Hudson River with Lorraine, and, because Lebanon was preoccupied (Safford, 1851, p. 353-355, had used Lebanon for part of the Stones River Group in Tennessee), replaced Lebanon with Richmond. Thus, the names Trenton, Utica, Lorraine, and Richmond came to be used for units at Cincinnati that were essentially equal to Orton's Point Pleasant beds (and River Quarry beds), Eden shales, Hill Quarry beds, and Lebanon beds. Clarke and Schuchert (1899, p. 876-877) dropped usage of Hudson River even for New York strata in favor of Cincinnatian, with the divisions Utica (= Orton's Eden shales), Lorraine ( $\approx$  Orton's Hill Quarry beds), and Richmond ( $\approx$  Orton's Lebanon beds), for the North American Upper Ordovician, and

the name Hudson River finally ceased to be applied to strata at Cincinnati.

Nickles (1902, p. 56-98) equated Orton's Point Pleasant beds and River Quarry beds and subdivided the Utica, Lorraine, and Richmond at Cincinnati into a number of faunal zones (mainly on the basis of maximum abundance of various species of brachiopods and bryozoa). Foerste (1905) discarded New York nomenclature altogether for use in the Cincinnati area and divided strata at Cincinnati into Point Pleasant beds (= Orton's Point Pleasant and River Quarry beds), Eden (= Orton's Eden shales), Maysville (a new name for Orton's Hill Quarry beds and lowermost Lebanon beds), and Richmond (= the remainder of the Lebanon beds). Foerste described the Fulton beds as the lowermost 4 or 5 feet (about 1.2 or 1.5 m) of shales of the Eden containing the trilobite Triarthrus eatoni (Foerste called it T. becki). Bassler (1906, p. 8-10) moved the Maysville-Richmond boundary to equal that of Orton's Hill Quarry-Lebanon boundary, correlated the Fulton beds with the New York Utica, and gave geographical names of local derivation to Nickles' bryozoan zones, which he treated as members.

Foerste (1914, p. 251) concluded that beds of the "Lorraine of New York show much greater affinities with the... Lorraine...of Quebec than with any part of the Cincinnati...of Ohio...." Fenneman (1916), in anticipation of the Ulrich and Bassler USGS Cincinnati Folio, used Cynthiana in

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Text-fig. 4. Cincinnati stratigraphy of the Cincinnati area (from a University of Cincinnati Geology Museum display).

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STAGES	SUBDIVISIONS BASED ON LITHOLOGY AND FOSSILS		SUBDIVISIONS BASED ON LITHOLOGY		STAGES
	after Caster, Dalve' & Pope (1955)		after Peck (1966) and Weiss & Sweet (1964)	after Gray (1972)	
RICHMONDIAN	WHITEWATER	ELKHORN		DRAKES (IN PART)	WHITEWATER
		UPPER WHITEWATER		SALUDA MEMBER	
		SALUDA			
		LOWER WHITEWATER			
		LIBERTY		BULL FORK	after Peck (1966)
	ARNHEIM/WAYNESVILLE	BLANCHESTER			
		CLARKSVILLE			
		FORT ANCIENT			
		OREGONIA			
		SUNSET			
MAYSVILLIAN	M' MILLAN	MOUNT AUBURN		GRANT LAKE	DILLSBORO
		CORRYVILLE			
	FAIRVIEW	BELLEVUE		FAIRVIEW	
		FAIRMOUNT			
		MOUNT HOPE			
EDENIAN	LATONIA	M' MICKEN		KOPE	KOPE
		SOUTHGATE			
		ECONOMY			
				MAQUOKETA GROUP	
				RICHMONDIAN	
				MAYSVILLIAN	
				EDENIAN	

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place of Point Pleasant, divided the Eden into Utica below and Latonia above, and used Nickles' (1902) divisions (with Bassler's, 1906, names) of the Maysvillian and Richmond. The Ulrich and Bassler Cincinnati Folio, intended as the much needed standard for future work in the Cincinnati area, was unfortunately never published (the USGS refused to accept Ulrich and Bassler's location of the Ordovician-Silurian boundary at the base of the Richmond, and Ulrich and Bassler were unrelenting in their position—K. E. Caster, personal communication, October 1973). In fact, the incomplete manuscript became lost for some time and was discovered among Bassler's effects after his death (in 1961). The manuscript is available in the open file of the USGS library, Washington, D. C.

In 1925, Wilmarth (p. 86) pointed out that the USGS was at that time employing the term Cincinnati Series with the same limits as those given by Winchell and Ulrich (1897) and Clarke and Schuchert (1899). Caster, Dalvé, and Pope (1955, Text-fig. 3) restricted the name Eden to use as a stadial term (this had come to be its common usage) and replaced Eden with Latonia as the lithic name (Text-fig. 4). In 1959, Sweet et al. (p. 1030-1032) revived Eden as a formational name; but Weiss and Sweet (1964) objected to use of Eden as both a rock-stratigraphic unit and a time-stratigraphic unit and replaced Eden Formation with Kope Formation (they restricted the name Eden to use as a stadial division).

Weiss et al. (1965) discussed Orton's (1873) Point Pleasant, River Quarry, and Eden beds. They concluded that Orton's River Quarry beds are not a different unit from Orton's Point Pleasant beds and that the entire mass of sub-Eden supra-Lexington limestones and shales in the Ohio River Valley should be called Point Pleasant (p. 19)—whether to use Cynthiana (with Point Pleasant as a member) or the older term Point Pleasant as the name of this formation was raised as a problem needing solution (p. 21). They, however, used Eden as a lithic name, rejected Fulton as a rock unit (they said that what earlier workers referred to as Fulton is really the Triarthrus eatoni zone), and rejected the rock names Bassler (1906) had given to Nickles' (1902) faunal zones for their biostratigraphic rather than lithostratigraphic nature (p. 25-28).

Peck (1966), confronted with a Cincinnati stratigraphic nomenclature rife with lithic names for faunal units, practically began anew in the Maysville, Kentucky area. Peck, using Weiss and Sweet's (1964) Kope Formation and accepting the Fairview Formation as a valid lithic unit, defined two new units, the Grant Lake Limestone (overlying the Fairview) and the overlying Bull Fork Formation. In addition, at Maysville Peck found the Preachersville Member of the Drakes Formation (described by Weir et al., 1965), which apparently does not occur in the immediate vicinity of Cincinnati or on the west side of the Cincinnati Arch.

Anstey and Fowler (1969) opined that Eden should be retained as a rock-stratigraphic name and that Kope should be disregarded. Their reasoning was that Eden could no longer be used as a stadial name because of overlap with the New York Trentonian and thus was available for us as a rock name. Sweet and Bergström (1971), after illustrating this overlap (they showed that the upper part of the Trenton Group is the same age as Edenian and Maysvillian strata in the Cincinnati area) rejected Trentonian and Coburgian in favor of the older stadial names Edenian (Orton, 1873), Maysvillian (Foerste, 1905), and Richmondian (Winchell and Ulrich, 1897). Because Eden is a valid stadial name, Sweet and Bergström reinstated Kope as a rock name to avoid confusion of dual usage of Eden (as both a stadial and formational name).

Thus, the present state of stratigraphic nomenclature in the Cincinnati, Ohio area, as synthesized from the preceding works, can be summarized as follows (it is essentially the nomenclature used by the United States and Kentucky Geological Surveys jointly mapping Middle and Upper Ordovician strata in Kentucky and by the majority of Ohio and Kentucky students of Cincinnati stratigraphy):

Rock-stratigraphic units in the Cincinnati area

The name Cincinnati Group was first used by Meek and Worthen (1865, p. 155) for blue-gray and gray limestones and shales outcropping in and around Cincinnati, Ohio.

Although the fossils of the Cincinnati area had been the subject of considerable study during the early and middle 1800's, the strata's lithologies and relationships were without detailed description until Orton (1873). Orton divided the Cincinnati Group into five lithic units (in ascending order): Point Pleasant beds (exposed at Point Pleasant, Ohio), River Quarry beds (in and along the Ohio River at Cincinnati), Eden shales (outcropping in Eden Park, Cincinnati), Hill Quarry beds (at the tops of the Cincinnati hills), and Lebanon beds (exposed at Lebanon, Ohio). The Point Pleasant beds and River Quarry beds have been shown (James, 1891; Nickles, 1902, p. 56-58; Foerste, 1905, p. 151; Weiss et al., 1965, p. 19) to be parts of the same lithic unit, the Point Pleasant Formation. The lithic unit named Eden shales by Orton has been replaced by Kope Formation (Weiss and Sweet, 1964); Fairview Formation (Bassler, 1906) and Grant Lake Limestone (Peck, 1966) have essentially been substituted for Orton's Hill Quarry beds; and most of Orton's Lebanon beds are now called the Bull Fork Formation (Peck, 1966). Beds comprising the Point Pleasant Formation were removed from the Cincinnati Group by Hall (1842, p. 61), Miller et al. (1879, p. 193-194), and Orton (1888, p. 5). Thus, the Cincinnati Group presently contains the Kope Formation, Fairview Formation, Grant Lake Limestone, and Bull Fork Formation. Stratigraphers tend

not to use the name Cincinnati as a rock-stratigraphic unit. Rather, they reserve the name Cincinnati for use in time-stratigraphic nomenclature and avoid dual usage.

The Point Pleasant Formation, named for strata at Point Pleasant, Ohio by Orton (1873), is the lowest unit exposed in the Cincinnati region. According to Weiss et al. (1965), it consists of thin and medium bedded, light to dark gray, fossiliferous, biogenic limestones parted by gray shales and mudstones. Limestone and shale each make up about 50% of the unit; the mean clastic ratio (limestone:shale and mudstone) calculated for successive 0.9 m units is 1.0. Thickness ranges from a few feet (about a meter) to nearly 70 feet (about 21 m). The unit is believed to be Shermanian (and partly Edenian upriver from Cincinnati) in the Ohio River Valley.

The Kope Formation, named for exposures in Kope Hollow near Levanna, Ohio by Weiss and Sweet (1964), conformably overlies the Point Pleasant Formation and consists of lenses and discontinuous thin bedded, gray and bluish gray, highly fossiliferous, biogenic limestones (up to about a foot thick—about 30 cm thick) and thicker sequences of gray, bluish gray, and greenish gray, less fossiliferous shales and mudstones. The Kope is made up of 75% (or more) shale and mudstone and 25% (or less) limestone; the mean clastic ratio for 0.9 m units is 3.25.

Thickness ranges from 150 to 270 feet (about 46 to 82 m). The Kope is Edenian in the immediate area of Cincinnati, but the upper part becomes Maysvillian to the east and southwest away from Cincinnati. The Point Pleasant-Kope boundary is gradational and can be observed with certainty only where a number of feet (a few meters) of strata on either side of the boundary are exposed. The contact is placed at the base of the lowest series (at least 1.5 feet—about 0.5 m—thick) of Kope mudrocks that lie on the uppermost limestone of the Point Pleasant Formation.

The Fairview Formation, named for exposures in and around Fairview Park, Cincinnati by Bassler (1906), conformably overlies the Kope and, as described by Peck (1966), consists of alternating sequences of thin to medium bedded, gray, biogenic limestones and partings and thin beds of gray mudstones and shales. The Fairview is composed of 50 to 60% limestone and 40 to 50% mudstone and shale; the mean clastic ratio calculated for 0.9 m intervals is 0.5. Thickness ranges from about 80 to 115 feet (about 24 to 35 m). The Fairview is essentially Maysvillian, but in some areas the lowermost part is Edenian. The Kope-Fairview contact is somewhat tenuous except in a few outcrops; it is marked at the base of the first thick (over 8 inches or about 20 cm) limestone that is succeeded by limestone in significantly more abundance than mudrock and that

overlies the highest series (at least 1.5 feet—about 0.5 m) of Kope mudrock. In some areas the Fairview becomes more limy near the top, so that a fairly thick sequence must be observed to pick the contact with certainty.

The Grant Lake Limestone, first described by Peck (1966) from exposures along Kentucky Route 1449 northeast of Grant Lake near Maysville, Kentucky, conformably overlies the Fairview and consists of irregularly thin bedded, rubbly, fossiliferous, gray limestones alternating with irregular partings and thin beds of fossiliferous, gray shales and mudstones. The Grant Lake is made up of 70 to 90% limestone and has a thickness of 100 to 120 feet (about 30 to 37 m). The age of the Grant Lake in and around its type area is Maysvillian but has not been established elsewhere with certainty. The Fairview-Grant Lake contact is placed at the base of the lowest sequence of irregularly bedded argillaceous Grant Lake limestones; the boundary is often transitional, but even when not transitional, it is inconspicuous.

The Bull Fork Formation, named by Peck (1966) for Bull Fork Creek near Plumville (which is near Maysville), Kentucky, and described from exposures along Kentucky Route 1443 near Springdale (also near Maysville), Kentucky, conformably overlies the Grant Lake Limestone. It is composed of alternating thin to medium bedded, gray, bluish gray,

and greenish gray, quite fossiliferous, sometimes argillaceous limestones and gray and greenish gray, fossiliferous shales and mudstones. Clastic ratios (shale and mudstone:limestone) increase from about 1:4 near the base to 4:1 near the top. The Richmondian Bull Fork is about 200 feet (about 61 m) thick in its type area and thins southward. The Grant Lake-Bull Fork contact is usually transitional and is placed at the base of the lowest sequence of rubbly, argillaceous Grant Lake limestones.

The Preachersville Member of the Drakes Formation was named by Weir et al. (1965) for outcrops along Kentucky Route 39 about 2 miles (about 3.3 km) southeast of Preachersville, Kentucky. In the Ohio Valley the Preachersville occurs only along the east side of the Cincinnati Arch (actually the Preachersville occurs around the east side of the Arch from near Dayton, Ohio in the north to south of Lexington, Kentucky), where it conformably overlies the Bull Fork and consists of green and reddish purple, calcareous to dolomitic, essentially barren mudstones and thin, gray to brown, essentially barren, dolomitic limestones and dolomites. Mudstone comprises about 90% of the unit. Thickness in the Maysville area ranges from 25 to 30 feet (about 8 to 9 m) and increases southward. In the Ohio Valley, the Preachersville is apparently

Richmondian. The Preachersville and Bull Fork lithologies are transitional and the Bull Fork-Preachersville contact is placed at the top of the highest fossiliferous Bull Fork limestone. The boundary between the Preachersville and the overlying Silurian Brassfield Formation may be conformable and transitional locally. It is placed at the base of the lowest sequence of thicker bedded, brown Brassfield dolomites and dolomitic limestones. In most areas, however, the Brassfield rests unconformably on the Preachersville, the Whitewater (as used by Gray, 1972), or the Bull Fork.

#### Time-stratigraphic units in the Cincinnati area

Since Winchell and Ulrich (1897) and Clarke and Schuchert (1899), the Cincinnati Series has been used as the North American Late Ordovician time-stratigraphic unit; and, since Foerste (1905) and Cumings (1908), the names Edenian, Maysvillian, and Richmondian have been used as Cincinnati stadial divisions. Although two Cincinnati stages have names derived from localities outside Ohio (Maysvillian was named for Maysville, Kentucky, while Richmondian was named for Richmond, Indiana), according to Sweet and Bergström (1971, p. 614-616) all have their reference sections in southwestern Ohio as established in Orton's (1873) report. The Edenian reference section is without doubt in southwestern Ohio. Orton's unit Eden

shales (Edenian Stage) was named for exposures in Eden Park, Cincinnati, Ohio. However, location of Maysvillian and Richmondian reference sections in southwestern Ohio is less demonstrable.

When Foerste (1905, p. 150) used the name Maysville, he did so for strata at Cincinnati; but Foerste's Maysville section may have been at Maysville, Kentucky: "...the name Maysville is here suggested for the strata at Cincinnati hitherto identified as Lorraine. Along the railroad south of Maysville, Kentucky, from the first cut a little over a mile from town to the overhead bridge a mile north of Summit a magnificent series of exposures gives a complete section of all the subdivisions of the Maysville division...." The Richmond reference section is a similar case. Winchell and Ulrich (1897, p. ciii) first used the name: "Resting on the Lorraine [around Cincinnati, Ohio] there is a series of alternating thin bedded shales and limestones and in some localities finally a sandstone, in all quite 350 feet thick in southwestern Ohio and southeastern Indiana. Almost the entire series is excellently exposed at Richmond, Indiana, so that the name Richmond group which we propose to apply to the series is eminently appropriate.\* [with the following footnote from the bottom of page ciii] Prof. Orton's [1873] name "Lebanon" would have been adopted had his name not been used before for a division of the Trenton by Prof. Safford [1851]. The Rich-

mond exposures besides are larger and more characteristic of the group than those near Lebanon, Ohio." As well, although Winchell and Ulrich's Richmond group is nearly equivalent to Orton's Lebanon beds, Foerste's Maysville is markedly different from Orton's Hill Quarry beds. The difference, simplified, is that Orton included strata that was later called Arnheim (a name used by Foerste, 1905, in place of Nickles', preoccupied Warren—Text-fig. 4) in the Richmond, while Foerste agreed with Nickles in including the Arnheim in the Maysville. Whatever the valid reference sections for the Maysvillian and Richmondian Stages, reference sections have come to be exposures in southwestern Ohio—the bluffs along Clifton Avenue and in Bellevue and Fairview Parks, Cincinnati (in the case of Maysvillian) and exposures in railroad and highway cuts around and some distance south of Lebanon, Ohio (in the case of Richmondian).

The Cincinnati stadal reference sections need study. Ranges of species should be firmly established in the reference sections with extrapolation away from Cincinnati; thus far, only conodonts have received adequate modern biostratigraphic attention. The following organisms have been used as indices for Cincinnati stages. Although the author has chosen organisms that are considered most trustworthy by modern workers, the list is at best a poor one (perhaps except for conodonts).

### Conodonts

According to Kohut and Sweet (1968, p. 1460), an association typical of Edenian and older strata is Cyrtoniodus flexuosus, Drepanodus suberectus, Ozarkodina tenuis, Phragmodus undatus, and Plectodina furcata furcata. The combination of Ambalodus, Keislognathus, Sagittodontus, probably Prioniodus, and Scolopodus, and perhaps Eoligonodina (genera more characteristic of the Anglo-Scandinavian-Appalachian province) marks early Edenian time; the combination of Phragmodus undatus, Dichognathus, and Belodina is late Edenian and early Maysvillian, while that combination without Belodina is late Maysvillian or early Richmondian (Sweet *et al.*, 1959, p. 1038). This significance of Belodina was affirmed by Pulse and Sweet (1960, p. 245), who reported that all strata with Belodina are Maysvillian or older. In addition, Pulse and Sweet (1960, p. 243-246) submitted that Trichonodella angulata and T. subundulata are not known from rocks older than Edenian and that Prioniodina delecta and T. tenuis are Edenian and Maysvillian. According to Branson *et al.* (1951, p. 4), Zygognathus, Rhipidognathus, and abundance and variety of Paltodus species marks Richmondian.

### Graptolites

Graptolites fall short of the abundance and variety of most other groups in strata around Cincinnati.

Climacograptus typicalis, long thought to be a good Edenian indicator, is now known from both younger and older strata (Pulse and Sweet, 1960, p. 239; Berry, 1960), although Orthograptus truncatus richmondensis is apparently limited to Richmondian rock (Berry, 1966).

#### Corals

No corals are known from Edenian or Maysvillian strata around Cincinnati (actually, a few corals have been found in the Kope Formation at Newport, Kentucky and are presently under study—Richard S. Laub, personal communication, October 1973), however corals are abundant in Richmondian strata. Browne (1964; 1965) reported that Favistella alveolata, Foerstephyllum vacuum, Tetradium approximatum, Calopoecia huronensis, Aulacera, Grewingkia rustica, G. divaricans, and Saffordophyllum floweri are common in Richmondian strata. In addition, Paleofavosites is Richmondian and younger.

#### Brachiopods

Resserella emacerata (? = Onniella) has been reported (Caster, Dalvé, and Pope, 1955, Text-fig. 3) to be Edenian; Platystrophia hopensis is Maysvillian (Weiss et al., 1965, p. 36-37); Rhynchotrema dentatum, Leptaena richmondensis (? = Kiaeromena), Resserella meeki (? = Onniella), Strophomena planumbona (? = S. rugosa), and Lepidocyclus capax are apparently Richmondian (Caster, Dalvé, and Pope, 1955, Text-fig. 3).

## Bryozoa

Constellaria florida and Escharopora falciformis are reported to be Maysvillian (Caster, Dalvé, and Pope, 1955, Text-fig. 3; Weiss et al., 1965, p. 36-37).

## Trilobites

Cryptolithus tessellatus appears to be early Maysvillian or older (Sweet et al., 1959; Pulse and Sweet, 1960), while Triarthrus eatoni has been used as an index of earliest Edenian as well as the nominate species of the faunal zone named Fulton by Foerste (1905, p. 150)—Weiss et al. (1965, p. 26-28), although Caster, Dalvé, and Pope (1955, Text-fig. 3 and Pl. 2, fig. 17) reported that T. eatoni also occurs at a higher (younger) horizon.

## Crinoids

The common occurrence of crinoids in pockets makes them only occasionally useful in correlation. However, the abundance of pockets in strata around Cincinnati increases their value in local correlation, where Ectenocrinus geniculatus is earliest Edenian, Cincinnatiocrinus varibrachialis is Edenian and Maysvillian, Ohioocrinus (although rare) is known only from Maysvillian strata, and C. pentagonus is Maysvillian and Richmondian. On a broader scale, Cincinnatiocrinus is relatively widespread (southwestern Ohio, northern Kentucky, southeastern Indiana, northwestern New York, southern Pennsylvania, and Maryland)

and limited to Cincinnati strata, while Isotomocrinus and Daedalocrinus, although less widespread (Ontario, Quebec, New York, and Minnesota for the former and Ontario for the latter), are confined to late Champlainian strata (Kirkfieldian to Shermanian).

## SYSTEMATIC DESCRIPTIONS

## Class Crinoidea Miller, 1821

## Subclass Inadunata Wachsmuth &amp; Springer, 1885

Diagnosis—Crinoids with plates of the dorsal cup joined firmly together by close suture, with a subtegmenal mouth, and with arms free above the radials (hereafter abbreviated RR) or, in some members, above the first primibrachials (IBrr<sub>1</sub>) or second primibrachials (IBrr<sub>2</sub>).

Discussion—Inadunates range from Ordovician (although Sprinkle, 1973, p. 177-183, Pls. 42-43, described an apparent crinoid, subclass and order undetermined, from the Burgess Shale—Middle Cambrian—of British Columbia) to Triassic. They are abundant in Paleozoic strata, but only one family (Erisocrinidae) occurs in strata later than Permian. Moore and Laudon (1943) divided inadunates into two orders, the monocyclic Disparata (equivalent to Bather's, 1899, Monocyclica Inadunata) with 14 families, and the dicyclic Cladoidea (equivalent to Bather's, 1899, Dicyclica Inadunata) with 39 families. Moore (1952) changed the ordinal names Disparata and Cladoidea to Disparida (? from Latin dispar, meaning different, plus the ordinal ending -ida) and Cladida (? from Latin clado, or Greek klados, meaning branch, twig, or stem, plus -ida) and elevated part of the Disparida, the Hybocrinidae, to ordinal level. Knapp (1969) segregated cladids with downflaring IBB (infrabasals) into his new inadunate order, Declinida. Comprehensive and

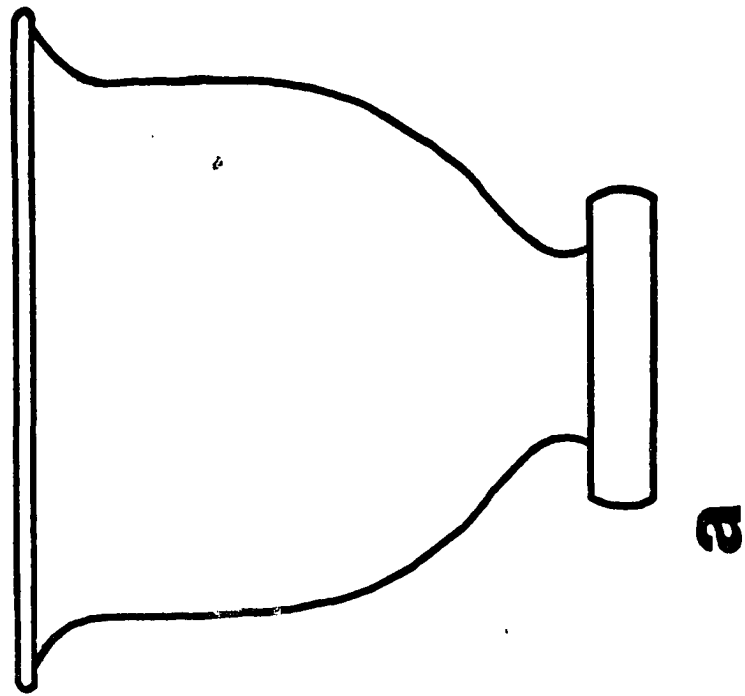
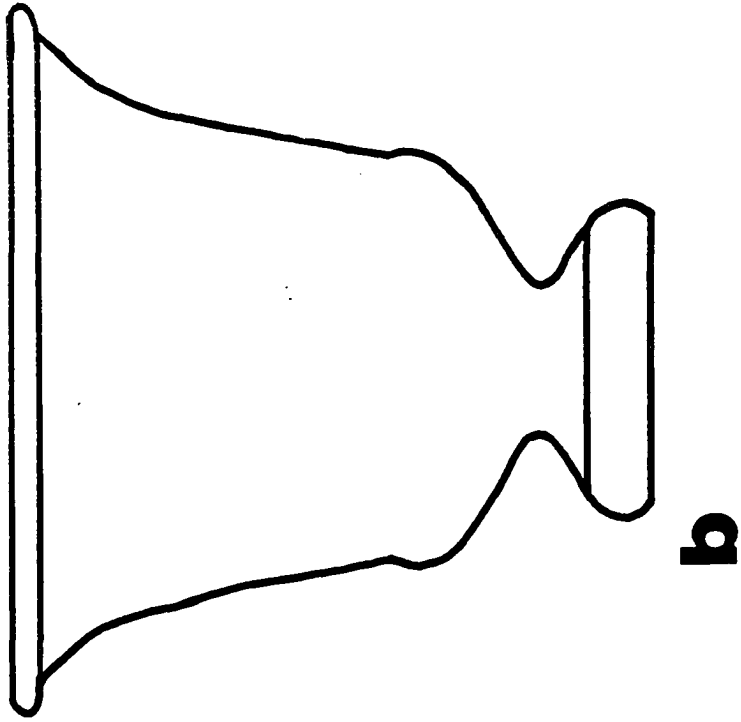
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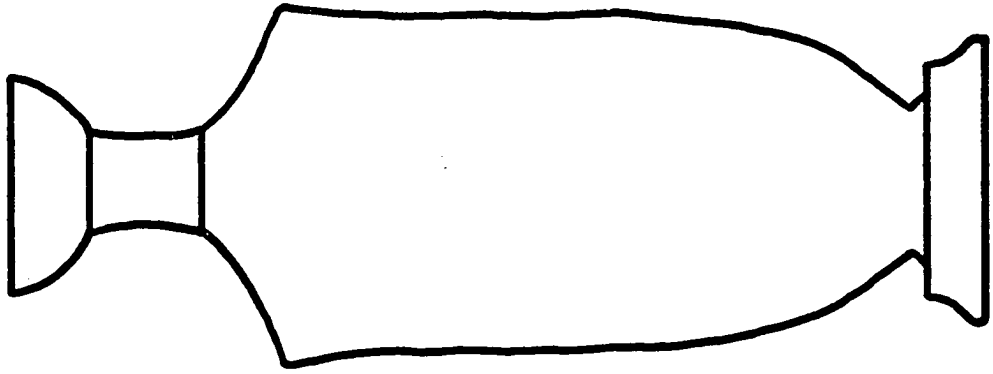
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Text-fig. 5. Shapes of Greek vases. a—bell krater, b—kalyx krater, c-d—lekythos, e-f—skyphos, and g-h—kylix. All handles have been removed to emphasize shape of the "cup" of the vase as it compares with dorsal cup shape in crinoids. A dorsal cup shaped like a or b is krateriform, like c or d lekythosiform, like e or f skyphosiform, or like g or h kylixiform. Vase shapes are from Caskey (1922).

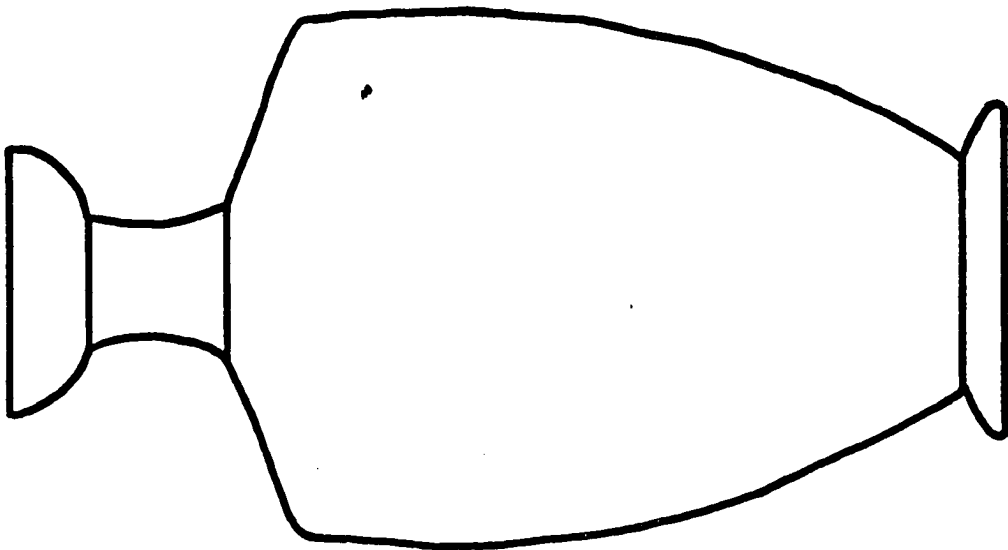
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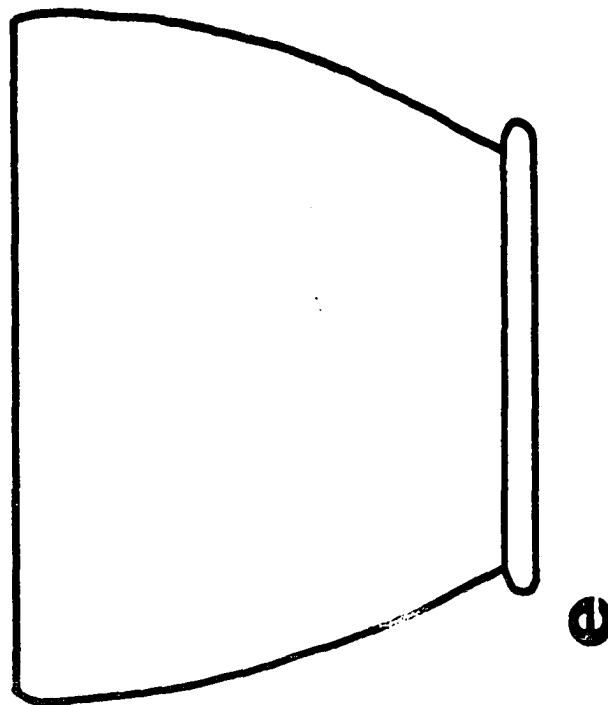
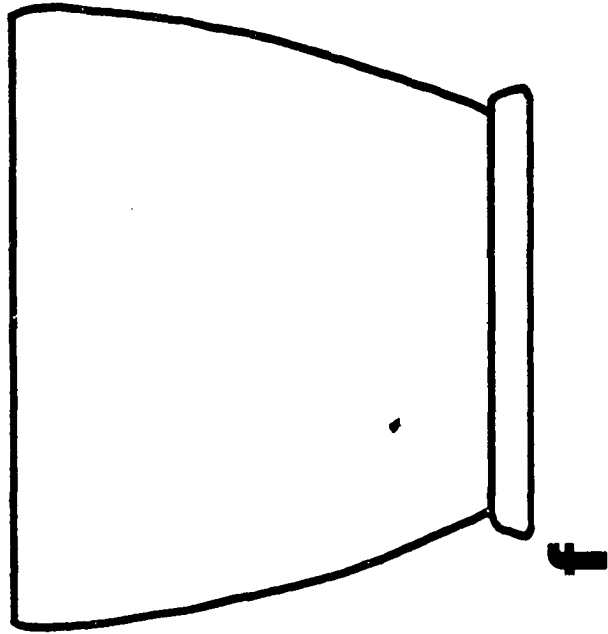


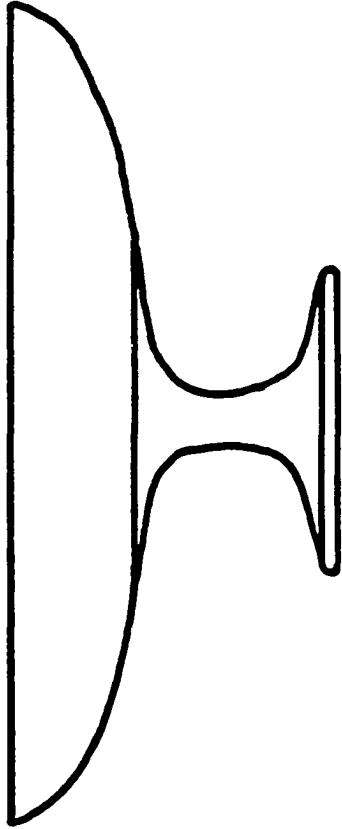


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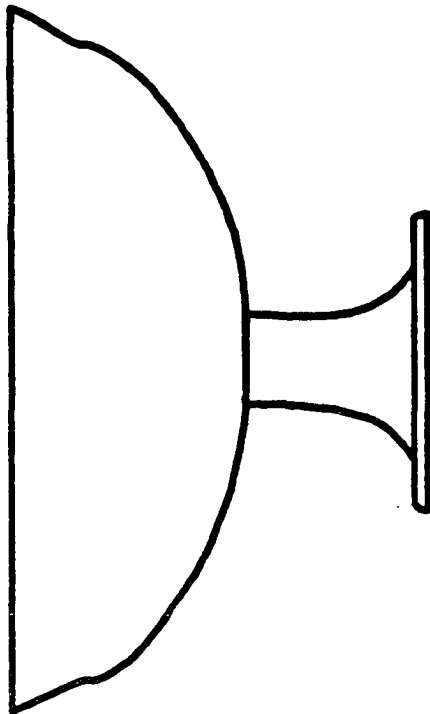


**c**





**h**



**g**

relatively contemporary discussions of inadunates are given by Moore and Laudon (1943, p. 21-64) and Moore (1962).

Order Disparida Moore & Laudon, 1943

(nom. corrig. Moore, 1952, p. 613

ex Disparata Moore & Laudon, 1943, p. 24)

Diagnosis—Monocyclic inadunates with conical cup and an armlike anal series branching off the C ray.

Discussion—Disparids are characterized by structural dissimilarity among the five rays of individuals and among corresponding rays of different families. Moore and Laudon (1943, p. 24-29) envisioned two general groupings: a homo-synbathocrinid stock and a hybocrinid stock. The hybocrinid stock, consisting of one family, the Hybocrinidae, with a "bowl-shaped" (krateriform, i.e., shaped like a Greek krater—Text-fig. 5) dorsal cup and with unbranched round arms distinctly narrower than the underlying RR, was made by Moore (1952) into the new order Hybocrinida. The homo-synbathocrinid stock, or Disparida as Moore (1952) viewed it, included the remaining 13 monocyclic families and was characterized by a steeply conical lekythosiform to skyphosiform—Text-fig. 5) dorsal cup, an armlike anal sac branching off the C ray, and wide branched arms that articulate along the entire distal edge of the RR. Disparids range from Ordovician to Permian.

Members of four disparid families (the Cincinnaticrinidae, Homocrinidae, Anomalocrinidae, and Iocrinidae) occur in Cincinnati strata in the Cincinnati, Ohio area.

	1	2	3	4	5	6	7	8	9	10
<u>Cincinnaticrinus</u>										Ci
<u>Dystactocrinus</u>					He	He	He	He	He	Ci
<u>Isotomocrinus</u>					He	He	He	He	He	Ci
<u>Ohioocrinus</u>	He	He	He	He	He	He	He	He	He	Ci
<u>Atopocrinus</u>									He	Ci
<u>Homocrinus</u>	Cy	De	Cy	Ho	Ho	Ho	Ho	Ho	Ho	Ho
<u>Ectenocrinus</u>	He	He	He	He	Ho	He	Ho	Ho	Ho	Ho
<u>Ibexocrinus</u>									Ho	Ho
<u>Syscauloocrinus</u>					Ho	Ho	Ho	Ho	Ho	Ho
<u>Daedalocrinus</u>					Ho	Ho	Ho	Ho	Ho	Ho

Table 1. Historical summary of the classification of members of the Cincinnaticrinacea and Homocrinacea. Column headings are: 1)Wachsmuth and Springer (1886), 2)Eather (1900), 3)Springer (1913), 4)Jaekel (1918), 5)Ulrich (1925), 6)Bassler (1938), 7)Moore and Laudon (1943), 8)Moore (1962), 9)the crinoid treatise, and 10)herein. Abbreviations for families are: He—Heterocrinidae, Ho—Homocrinidae, Cy—Cyathocrinidae, De—Dendrocrinidae, and Ci—Cincinnaticrinidae.

The closely related Cincinnaticrinidae and Homocrinidae are discussed here. The Iocrinidae, while in need of modern treatment, are more distantly related to other Cincinnatian disparid families, and their study is postponed for work with forms with which they are more closely allied (Synbathocrinidae, Myelodactylidae, and Eustenocrinidae). Nothing new can be added to knowledge of the Anomalocrinidae at this time, and anomalocrinids are discussed only in passing. The Cincinnaticrinidae show similarities to the Homocrinidae and the Anomalocrinidae additional to disparid similarities, although the Homocrinidae and Anomalocrinidae have little affinity to one another. Table 1 is an historical summary of classification of these crinoids.

Superfamily Cincinnaticrinacea (new herein)

Diagnosis—Disparid inadunate crinoids with a conical dorsal cup having undivided RR in three rays (in the A, B, and D rays) and compound RR in two rays (in the C and E rays).

Description—The cincinnaticrinacean dorsal cup has five symmetrically pentagonal, sub-hexagonal, or hexagonal BB (basals) of nearly equal size and shape. Both the compound and the fused RR are inverted pentagons (with slight modification in the C and D rays of members of the Cincinnaticrininae); compound RR are divided about

equally into a pentagonal iR below and a quadrilateral sR above. The five rays bifurcate isotomously to form ten arms, after which branching is isotomous or alternating heterotomous. In the arms, no cover plates are known, and they may have been absent. The arms are commonly folded tightly together to make observation of the food grooves difficult except in fortuitously broken or disarticulated specimens, but scrutiny of exposed food grooves and end-on examination of broken arms in numerous specimens has not disclosed the existence of cover plates. In adults, at least, the column is quinquepartite, with each columnal composed of five, radially disposed, fused plates or pentameres.

Discussion—The superfamily Cincinnaticrinacea is erected essentially to replace Heterocrinacea (Zittel's, 1879, family elevated to superfamilial status by Ubaghs, 1953), whose type-genus (Heterocrinus) is unrecognizable. Four previously described genera—Dystactocrinus, Isotomocrinus, Ohiocrinus, and Atopocrinus—are available for selection as type-genus. Dystactocrinus and Ohiocrinus are rejected because they are rare and their morphology not well known; Atopocrinus and Isotomocrinus are rejected because they are less typical of the superfamily than Cincinnaticrinus (Atopocrinus has a brachianal and multi-pinnulate Brr, while Isotomocrinus is the only isotomously

branching member of an otherwise heterotomously branching group). Cincinnatiocrinus, while new (in name but not in concept), is selected because it is both most typical of the superfamily and most common of the five included genera.

Zittel (1879, p. 343 and 358-359) included in his family Heterocrinidae Heterocrinus Hall, Graphiocrinus Köninck, Erisocrinus Meek and Worthen, Philocrinus Köninck, and Stemmatocrinus Trautschold (Table 1). These are forms with fairly simple, monocyclic or dicyclic, dorsal cups with five BB (or five BB and five IBB) and five RR supporting long, branched or simple, arms. Wachsmuth and Springer (1886, p. 127-128) removed dicyclic forms, leaving only Heterocrinus, which they split into Stenocrinus Wachsmuth and Springer (= Heterocrinus Hall), Heterocrinus Hall, Wachsmuth and Springer (= Ectenocrinus Miller), and Ohioocrinus Wachsmuth and Springer, and added Iocrinus Hall. Bather (1893, p. 35) added Anomalocrinus Meek and Worthen (Wachsmuth and Springer, 1886, p. 135 had used Anomalocrinus as nominate genus of their new family Anomalocrinidae) and Herptocrinus Salter (= Myelodactylus Hall).

Ulrich (1925) established the modern concept of the Heterocrinidae (monocyclic inadunates with conical cup having two compound and three fused RR). Ulrich transferred Ectenocrinus to the Homocrinidae (to which he added his new genera Daedalocrinus, Drymocrinus, and Sygcaulo-

crinus), reinstated the Anomalocrinidae with Anomalocrinus and his new genus Geraocrinus (the latter was included with reservation), and removed Iocrinus. To the preestablished heterocrinids Heterocrinus and Ohiocrinus, Ulrich added his new genera Atyphocrinus, Columbicrinus, Dystactocrinus, and Isotomocrinus.

Bassler (1938, p. 16-17) added a number of genera to the family, but of these additions only the European genera Caleidocrinus Waagen and Jahn and Ristnacrinus Öpik were accepted as heterocrinids by Moore and Laudon (1943, p. 31). Moore and Laudon (1944, p. 149) included Lichenocrinus, an omnium gatherum of Ordovician crinoid bases containing, among other things, the juvenile holdfast of Heterocrinus. Ramsbottom (1961, p. 39) removed Caleidocrinus to the Iocrinidae, a move with which Moore (1962, p. 39) agreed. Moore (1962, p. 35) transferred Ristnacrinus to the Eustenocrinidae. Lane (1970, p. 14) expanded the concept of the family somewhat with addition of his new genus Atopocrinus (Atopocrinus became the only member of the Heterocrinidae with the anal series branching off the C ray  $I\text{Br}_1$ —termed brachianal by Moore, 1962).

Although Ulrich's (1925) concept of the Heterocrinidae is accepted, nomenclatural and taxonomic changes are needed. The need for taxonomic change was voiced, for example, by Ramsbottom (1961, p. 10) who, when confronted with

identification of what he thought were British heterocrinids, declined: "Following the brief revision of the Ordovician Heterocrinidae given by Ulrich (1925) it is now difficult to determine generically many species which would formerly have been assigned to Heterocrinus...." It is evident that cincinnaticrinaceans have been "oversplit"—that many genera and species need clearer delineation. Along this line, Heterocrinus is shown to be unrecognizable, and a new genus, Cincinnaticrinus, is erected to house the Cincinnati area specimens formerly referred to Heterocrinus. Atyphocrinus is considered a junior synonym of Dystactocrinus. Columbicrinus, while exhibiting cincinnaticrinacean cup features, is unrecognizable because the holotype (and only known specimen, from the Lebanon limestone of central Tennessee) of the type (and only) species, C. crassus, is an incomplete specimen and lacks diagnostic features (the specimen has no arms or column—Pl. 2, figs. 4-5). Thus, the new superfamily Cincinnaticrinacea contains Cincinnati-  
crinus (new herein); Atopocrinus Lane, 1970; Dystacto-  
crinus Ulrich, 1925; Isotomocrinus Ulrich, 1925; and Ohio-  
crinus Wachsmuth and Springer, 1886.

That the arms of cincinnaticrinaceans are usually folded tightly together may have been due to a detrimental influx of sediment and consequent contraction of muscles during catastrophic death or to relaxation of muscles with

ligamental folding of the arms after death—perhaps the former, for existing crinoids have muscles to close the arms and ligaments to open them (Hyman, 1955, p. 60). However, Paleozoic crinoids may have had only ligaments in the arms (Van Sant and Lane, 1964, p. 40), probably for closing the arms with extension initiated by the water-vascular system.

The Cincinnaticrinacea show similarities (beyond those of the order Disparida) to the Homocrinacea and Anomalocrinacea. Cincinnaticrinacea and Anomalocrinacea have two compound RR (in the C and E rays) and three fused RR (in the A, B, and d rays) and, except for Atopocrinus, similar placement of  $X_1$ . However, they have divergent cup shapes (Cincinnaticrinacea have conical cups, while Anomalocrinacea have krateriform cups), dissimilar arms (Cincinnaticrinacea have subcircular arms as wide as the underlying RR, while Anomalocrinids have nearly round arms significantly narrower than the underlying RR), and different branching (Cincinnaticrinacea have isotomous and alternating heterotomous arms, while Anomalocrinacea have endotomous and alternating endotomous-exotomous arms—Text-fig. 5). Cincinnaticrinacea and Homocrinacea have similar cup shapes, arm size and shape, and placement of  $X_1$  (except for Atopocrinus), but Homocrinacea have three compound RR (in the B, C, and E rays) and only two fused

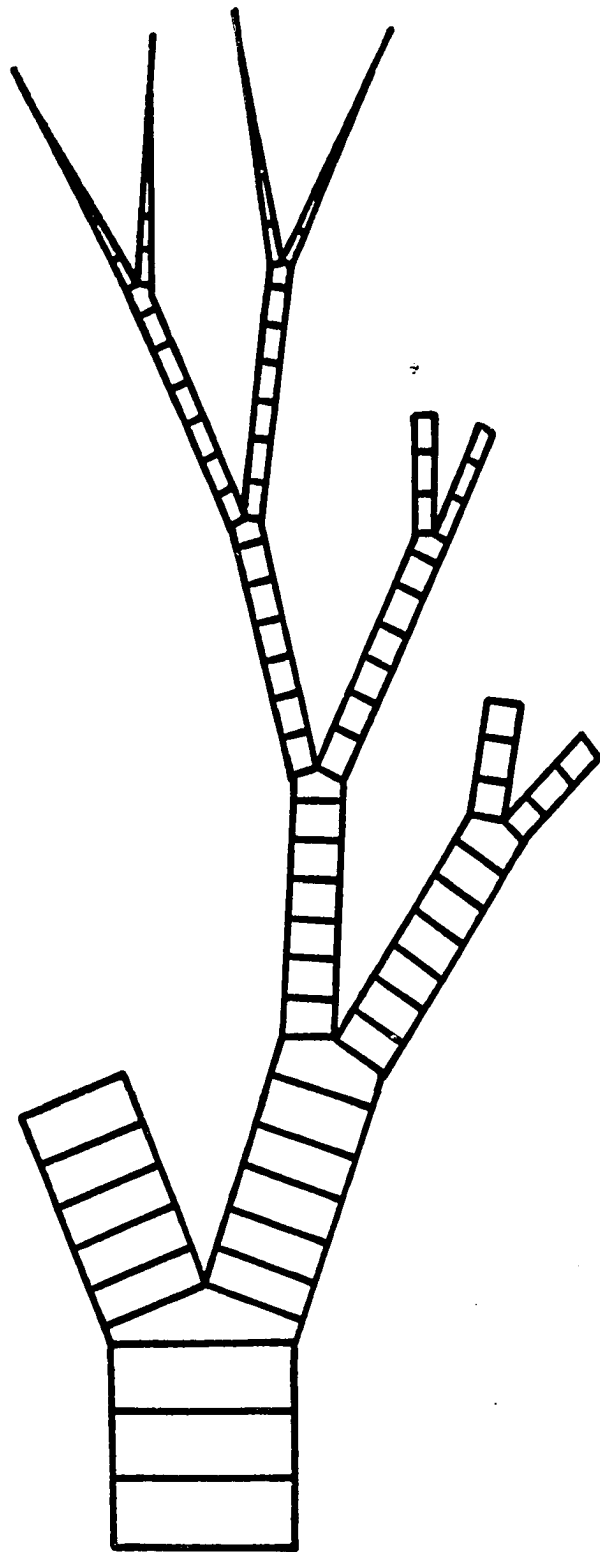
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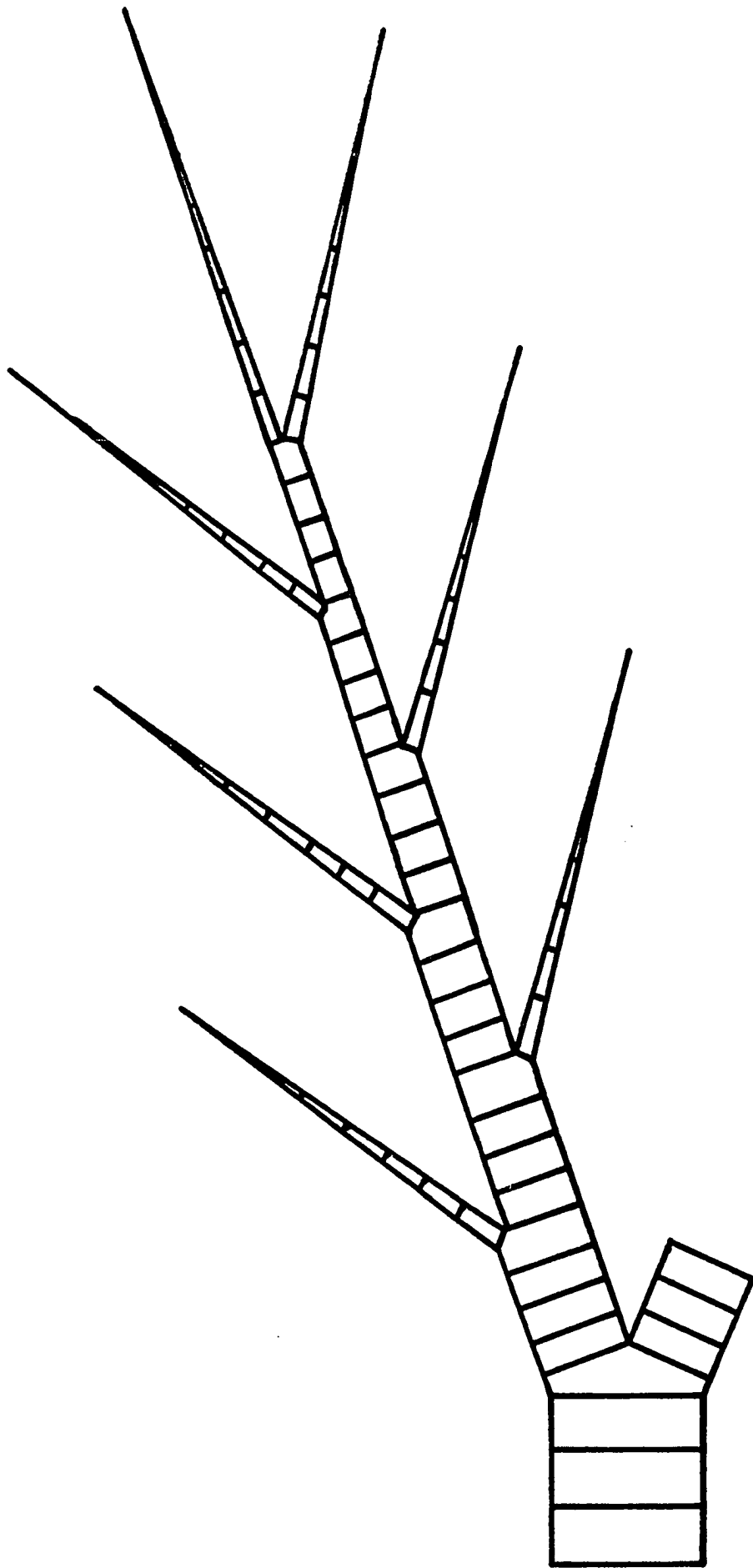
Text-fig. 6. Types of arm branching. Each drawing (all stylized) represents one ray with an isotomous branch to form two arms—only one of which is fully illustrated. a—isotomous, b—alternating heterotomous, c—exotomous, d—endotomous, e—alternating exotomous-endotomous, and f—alternating endotomous-exotomous. b, c, d, e, and f are forms of heterotomous branching.

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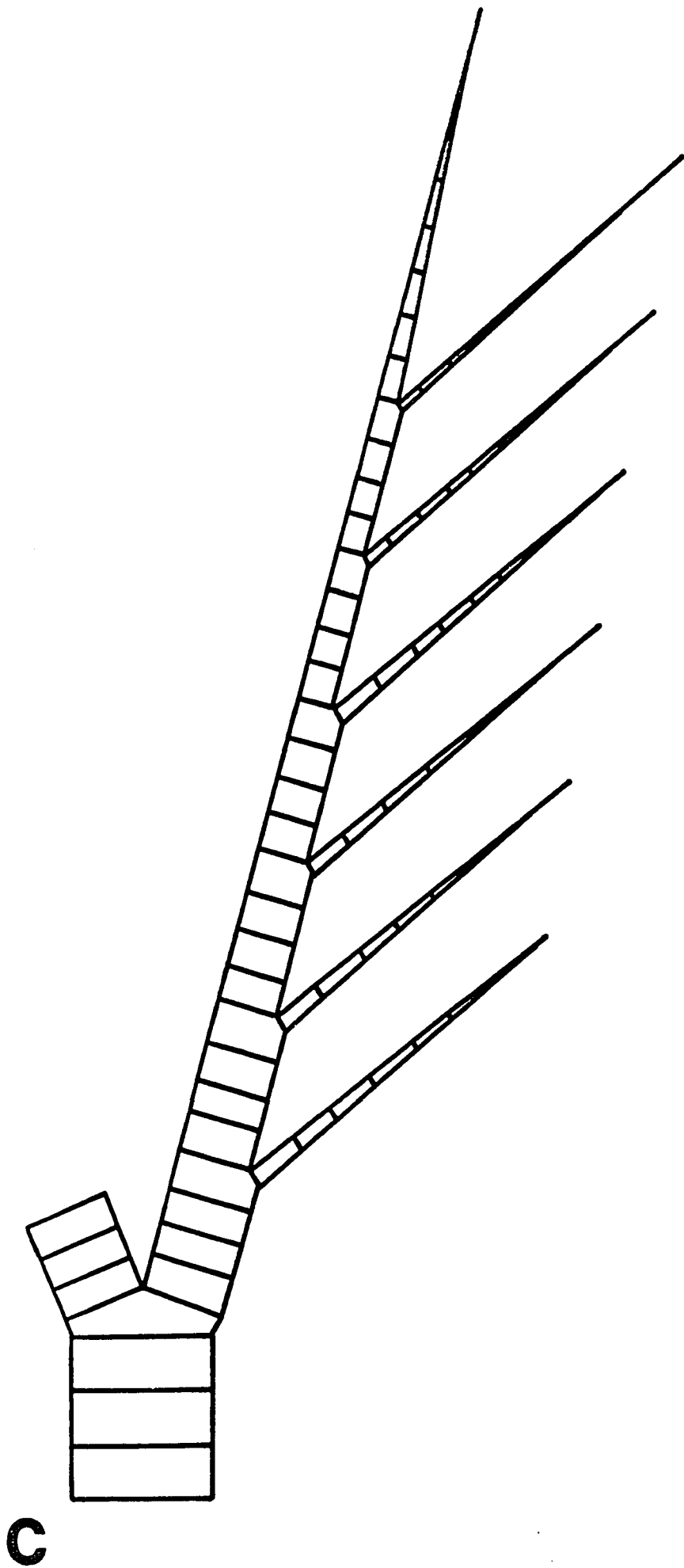
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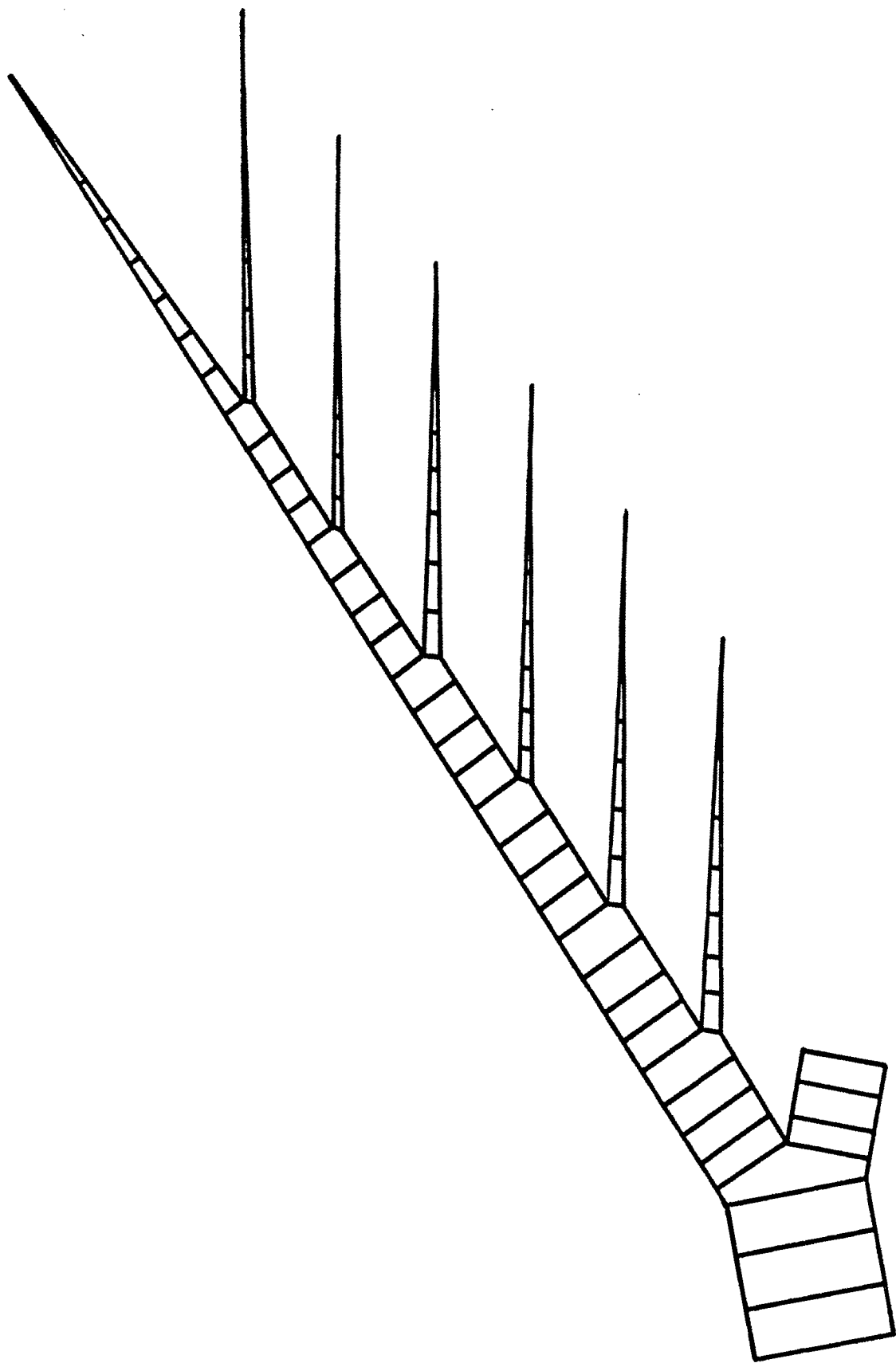
**a**



**b**

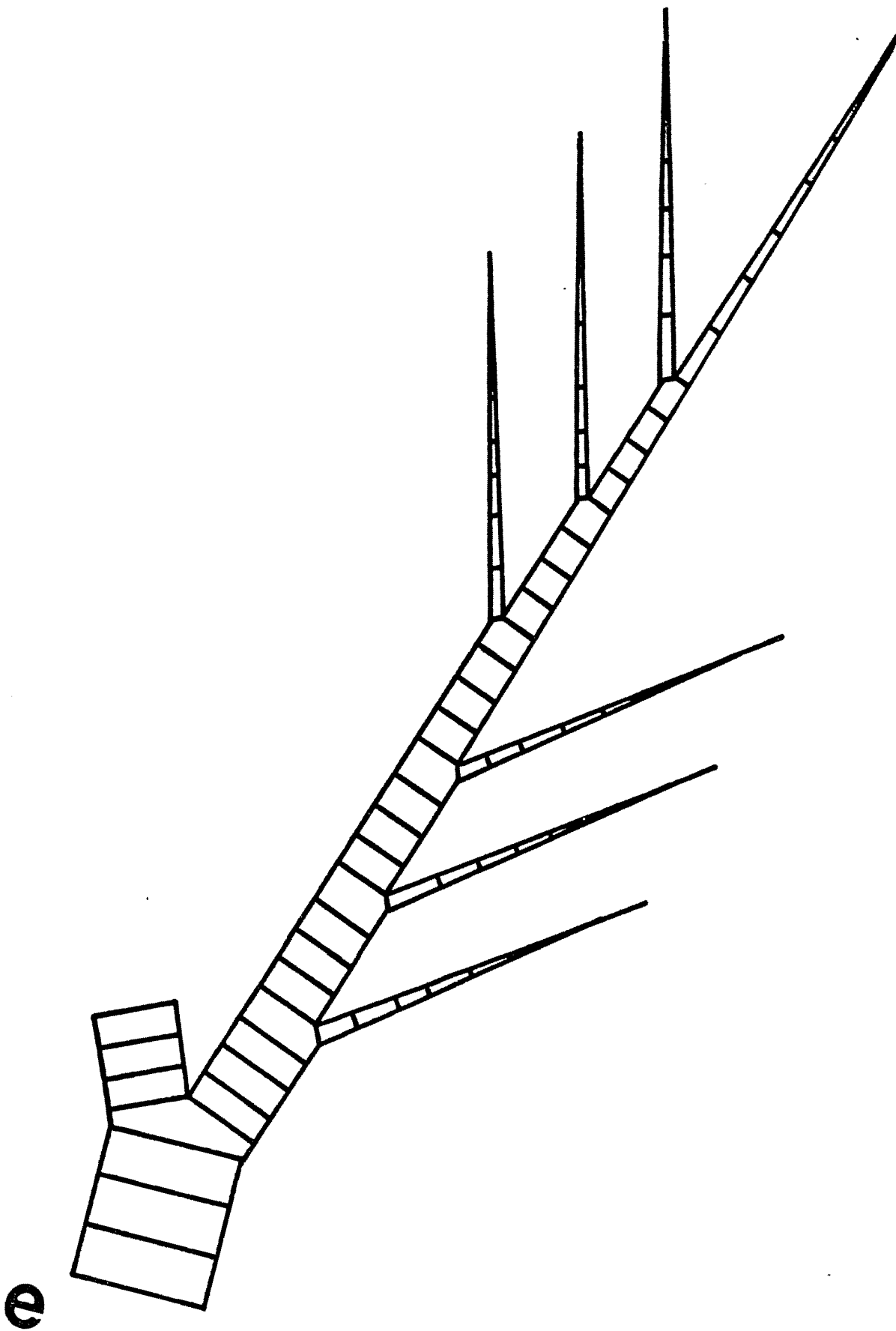


**C**

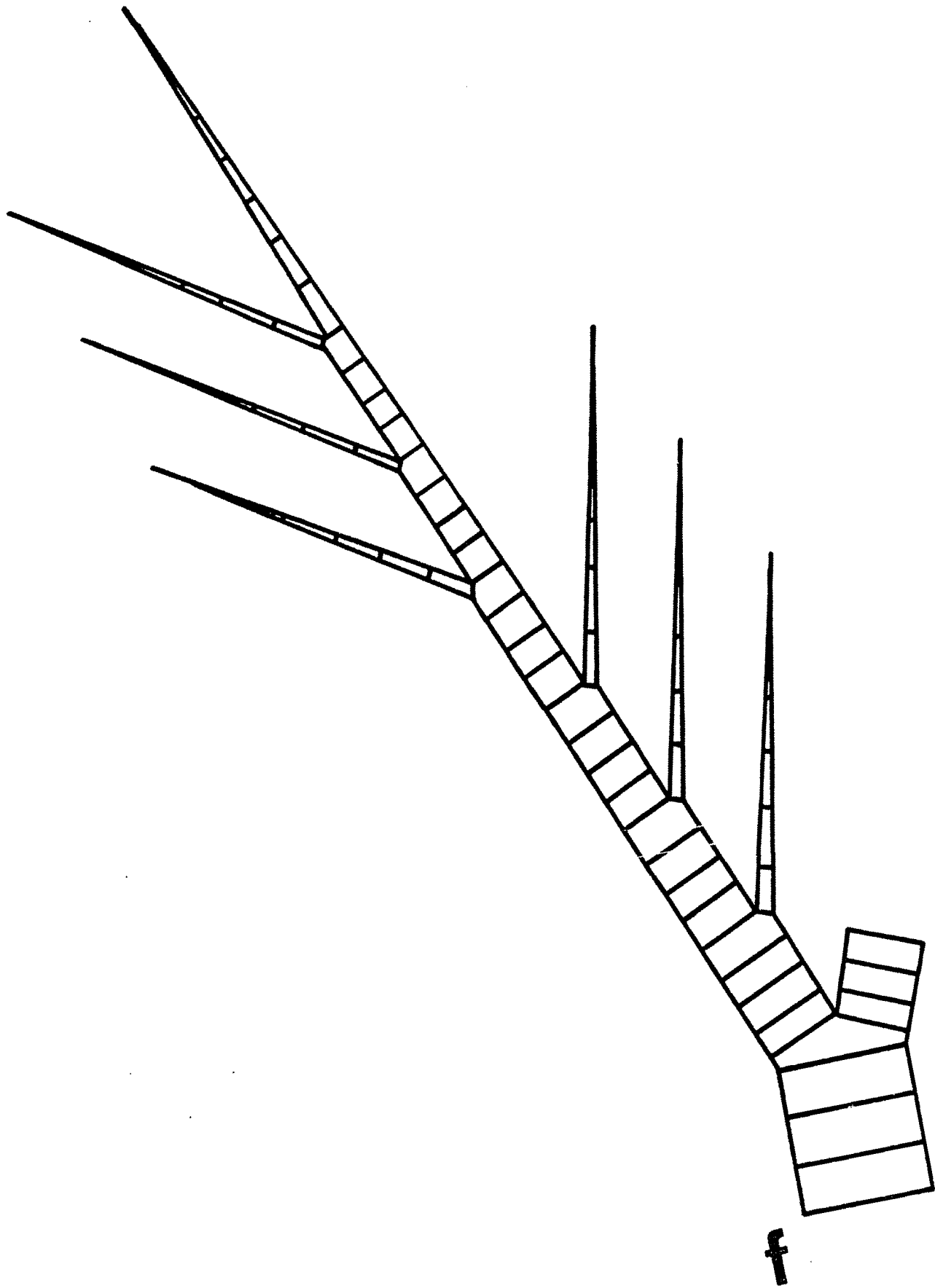


**d**

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RR (in the A and D rays). The homocrinids Ectenocrinus and Sygcauloocrinus have similar branching (alternating heterotomous), but Ectenocrinus has a tripartite rather than quinquepartite column. Daedalocrinus has a similar column but dissimilar branching (endotomous as opposed to isotomous and alternating heterotomous). Moore and Laudon (1943, p. 25) envisioned a closer affinity for heterocrinids (Cincinnatiacrinacea) and homocrinids (Homocrinacea) than for heterocrinids and anomalocrinids (Anomalocrinacea) and suggested that the Heterocrinidae developed from the Homocrinidae or their immediate fore-runners. Whether one judges the Cincinnatiacrinacean-anomalocrinacean or Cincinnatiacrinacean-homocrinacean relationship to be closer depends largely on whether one judges cup and arm shape, branching, number of fused versus compound RR, or column features to be of more or less evolutionary significance. The cladid Ottawacrinacea are also similar to the Cincinnatiacrinacea, but because ottawacrinaceans are dicyclic, the two superfamilies are presently viewed as homeomorphs.

Cincinnatiacrinaceans occur in Whiterockian to Richmondian rocks of western, mideastern, and eastern North America. They have been found throughout Cincinnati strata in the tristate Ohio-Kentucky-Indiana area (around Cincinnati); in Edenian rocks of northwestern New York,

southern Pennsylvania, and Maryland; in Kirkfieldian rocks of Minnesota, Wisconsin, and Illinois; in Kirkfieldian to Shermanian strata of mideastern Canada; and in Whiterockian strata of Utah. In addition, Ulrich (1925) reported heterocrinids (cincinnaticrinaceans) from Black Riverian rocks of Tennessee (Lebanon limestone), Wisconsin (probably from the Decorah shale—apparently Kirkfieldian in large part), and Pennsylvania (Text fig. 1).

Family Cincinnaticrinidae (new herein)

Because this is the only family of the Cincinnaticrinacea, familial characters are the same as for the superfamily. Two subfamilies are envisioned here. The subfamily Cincinnaticrininae comprises those forms which Ulrich (1925) included in his family Heterocrinidae: the Cincinnati forms of Heterocrinus (i.e., Cincinnaticrinus), Dystactocrinus, Isotomocrinus, and Ohioocrinus. The subfamily Atopocrininae is erected to accommodate Atopocrinus, which is a bit farther removed, morphologically and presumably phylogenetically, from other cincinnaticrinids.

Subfamily Cincinnaticrininae (new herein)

Diagnosis—Cincinnaticrinidae with a lekythosiform (steeply conical) dorsal cup; equal-sized compound RR (in the C and E rays) somewhat taller than the equal-sized fused RR (in the A, B, and D rays); and an armlike

anal series resting on the truncated left corner of the C ray sR.

Description—CincinnatiCrininae have RR, both fused and compound, that are taller than broad. The distal left corner of the C ray sR and the distal right corner of the D ray R are truncated to accommodate  $X_1$  (the first anal plate), which is an inverted, parallel-sided pentagon equal in size to or larger than adjacent Brr and resting on the sloping shoulders of the underlying RR (in the C and D rays). In some specimens  $X_1$  enters more deeply into the cup, the proximal point of the pentagon reaching the line of junction of the sR and iR of the C ray. The two or three (at least) successive XX are quadrilateral, so that the anal series is armlike. Thecal plates are usually smooth, but different areas in various specimens are finely nodose, so that all ossicles may have had nodose surfaces.

Each of the five RR supports a series of quadrilateral IBrr.  $IBr_1$  is the largest; it articulates with the underlying R along its entire proximal surface. The  $IBrr_1$  are fixed, i.e., united with the RR by immobile (synarthral?) suture with the  $IBrr_1$  functioning as part of the calyx. The last IBr in each ray is a pentagonal axillary, bearing upon its upper sloping sides two equal-sized arms (to form a total of ten arms) made up of IIBrr, all but the

last quadrilateral. The last is a pentagonal axillary. The number of Brr in each division series appears to be variable in members of the Cincinnaticrininae, both among different rays in single individuals and among the same ~~rays~~ rays in different individuals. (Branching on and beyond the IIBr axillaries varies among the genera of the Cincinnaticrininae).

The column is long (probably up to about a meter), but no complete specimens have been found. Therefore, column length, nature of the column away from the calyx, and nature of attachment (if any in adults) are matters for conjecture. (Relatively good evidence exists for the column and its ontogeny for Cincinnaticrinus varibrachialis (new herein), and the column features of other heterocrinids are probably similar). The column is pentapartite and pentagonal, although pentagonality can be shrouded by secondary overgrowth to produce a round appearance, with the points of the pentagon disposed radially. The articular surfaces of each columnal are petaloid, with five petal-shaped articular facets—one facet per pentamere. The axial canal is small, but conspicuous, star-shaped or pentagonal, with interradian points or angles.

Discussion—Members of the subfamily Cincinnaticrininae occur in Kirkfieldian to Richmondian (? Black Riverian or Rocklandina to Richmondian) rocks of mideastern and eastern

North America. They have been found throughout Cincinnati strata in the tristate Ohio-Kentucky-Indiana area (around Cincinnati); in Edenian rocks of northwestern New York, southern Pennsylvania, and Maryland; in Kirkfieldian rock of Minnesota, Wisconsin, and Illinois; and in Kirkfieldian to Shermanian rocks of mideastern Canada. In addition, Ulrich (1925) reported heterocrinids (Cincinnati crininae) from Black Riverian rocks of Tennessee (Lebanon limestone), Wisconsin (probably from the Kirkfieldian Decorah shale), and Pennsylvania. Ramsbottom (1961, p. 10; Pl. 3, fig. 8; Pl. 6, fig. 5) reported heterocrinids from Ashgillian strata of Scotland and Ireland. Crinoids from these strata (BM and HM crinoids presently under study) appear not to be Cincinnati crinids.

Note: In the following generic and specific synonymies, references that duplicate earlier illustrations or descriptions are listed with the earlier work from which the information was borrowed. For example, Cumings (1908) and Bassler (1919) borrowed Meek's (1873) illustrations of Heterocrinus heterodactylus for use in their works, so those references' (Cumings, 1908; Bassler, 1919) illustrations are listed with Meek (1873) in the Cincinnati crinus vari-brachialis synonymy.

Genus Cincinnaticrinus (new herein)

- 1866 Heterocrinus Hall, Hall, p. 4; Hall, 1872, p. 210 (partim).
- 1873 Heterocrinus Hall, Meek, p. 1 (partim).
- 1880 Heterocrinus Hall, Wachsmuth & Springer, p. 68 (partim).
- 1886 Stenocrinus Wachsmuth & Springer, p. 207 (partim).
- 1911 Heterocrinus Hall, Springer, p. 27.
- 1925 Heterocrinus Hall, Ulrich, p. 83.
- 1925 Heterocrinus Hall, Fritz, p. 10 (partim).
- 1944 Heterocrinus Hall, Moore & Laudon, p. 149.
- 1962 Heterocrinus Hall, Moore, p. 13, Text-fig. 5—3.
- 1973 Heterocrinus Hall, Warn, p. 12 (partim).

Type species—Cincinnaticrinus varibrachialus (new herein)—designation herein—from Edenian and Maysvillian strata of the Cincinnati area, northwestern New York, northern Maryland, and southern Pennsylvania.

Diagnosis—Cincinnaticrininae with a short, straight anal tube made up of three to five facing plates; ten arms exhibiting alternating heterotomous branching; equidimensional (height = width) pentagonal BB; and height of IBrr<sub>1</sub> less than three-fourths the height of the fused RR.

Description—Cincinnaticrinus has the features of the subfamily Cincinnaticrininae with some generic additions. The IBrr<sub>1</sub> are shaped like upright, truncated cones, while the IBrr<sub>2</sub> are inverted, truncated cones. Thus, the junction of the IBrr<sub>1</sub>

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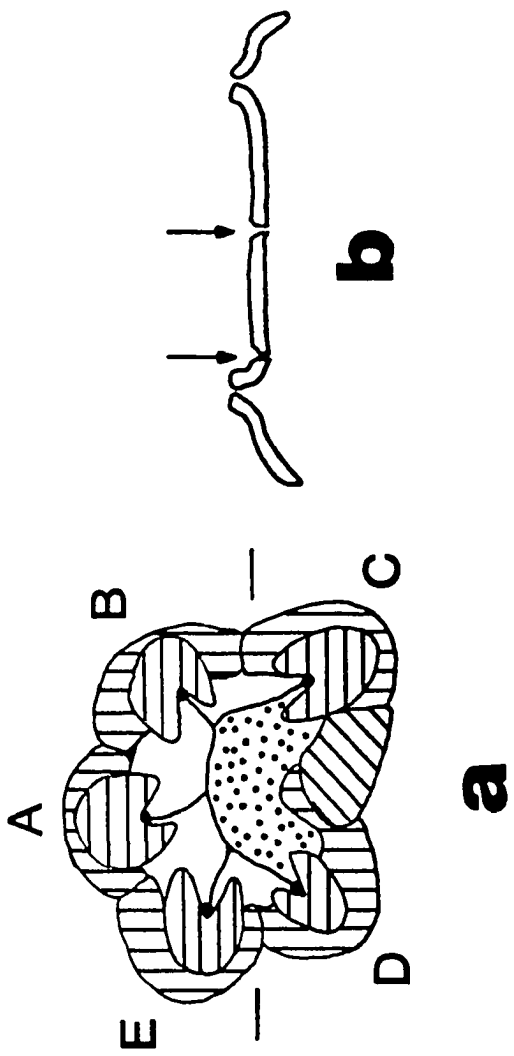
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Text-fig. 7. The tegmen of Cincinnaticrinus varibrachialus.

a is an oral view, a camera lucida drawing of UCGM 40575L (X15); rays are lettered A, B, C, D, and E; scoring is vertical on the RR, horizontal on the IBrr<sub>1</sub>, and diagonal on X<sub>1</sub>; OO are unmarked (except, on the CD interray 0, dots which represent pores); b is a cross-section of the OO (X30) in the plane marked by the two lateral lines in figure a; OO are upturned where they join, presumably over the five ambulacra, and have their outer edges turned down between the IBrr<sub>1</sub>; the two arrows point to funnel-shaped (in cross-section) pores in the CD interray 0.

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and IBrr<sub>2</sub> forms a constriction in the crown that marks the position of the tegmen, above which the arms become free. This constriction appears to have been a plane of weakness that resulted in loss and occasional regeneration of arms. The tegmen of Cincinnaticrinus (probably of C. pentagonus) was described by Ulrich (1925, p. 84) as:

"...gently convex, its middle on a plane with, or slightly beneath the top of, the fixed primibrachs. It is composed of a rather large polygonal central plate around which are many much smaller, loosely fitting plates. The smaller plates arch over the arm furrows, at least three rows being required to cover them. On the posterior side the small plates of the tegmen pass, evidently without break or change, into the anterior wall of the ventral sac."

Although Ulrich was correct in saying that the tegmen is located just proximal to the distal edges of the IBrr<sub>1</sub> (the fixed Brr), tegmen morphology appears to be quite different from what Ulrich described; it is more similar to the description of Wachsmuth and Springer (1886, p. 207) as "...five comparatively large interrarial pieces enclosing a small oral plate...." The tegmen (Text-fig. 7; Pl. 3, figs. 4-5) is actually made up of five relatively large, finely nodose (Ulrich evidently interpreted each node as a plate), interrarial plates, or orals (OO), that have their outer edges curved down into the spaces between adjacent IBrr<sub>1</sub> and

their inner, adjoining edges upturned to form gabled passageways over the subtegmina portions of the ambulacra. Three gabled passageways (one anterior and two lateral) radiate from a central point (presumably over the mouth) to the food grooves of the A, B, and E ray IBrr<sub>1</sub>; the two lateral (B and E ray) passageways bifurcate near their distal ends and send off two posterior passageways to the C and D ray IBrr<sub>1</sub>. The CD interray 0 is apparently porous and served the function of a sieve plate; it gives off numerous small plates from its outer edge that continue up the back of the XX.

The anal structure is armlike, apparently tubular throughout its length, although Ulrich (1925, p. 91) reported that it had been observed in only one of hundreds of specimens; this author has seen a maximum of only five anal plates in any of over a thousand specimens. It seems, then, that the anal tube is made up of an armlike series of three to five facing plates (XX) backed by numerous small polygonal plates given off from the tegmen. Whether or not the numerous small plates that back the XX continue beyond, or distal to, the XX (as in Ohiocrinus) is uncertain, although they evidently do not.

The arm branching of Cincinnatiocrinus, after initial division of the five rays (isotomous as in all Cincinnatiocrinacea) to form ten arms, is alternating heterotomous in

the following manner: the first of the heterotomous divisions (on the IIBr axillaries) produces a large arm as the branch toward the ray (i.e., as the inner branch) and a smaller arm, or armllet, away from the ray; the second heterotomous division (on the IIIBr axillaries) has the arm on the outside and the armllet on the inside; the third has the arm on the inside and the armllet on the outside; etc. The armllets commonly remain simple, but bifurcating armllets have been observed in a few specimens.

The XX and Brr, after initial formation as tall, narrow rectangles, grow faster laterally (marginally) than vertically (perradially). Thus, young (small—calyx height of about 2.5 mm or less) Cincinnati have tall XX and Brr, while older (larger—calyx height of about 2.8 mm or more) Cincinnati have broad IBrr but tall IVBrr and nearly square XX, with gradation in the Brr from broad to tall away from the dorsal cup. In young Cincinnati, the arms are so narrow that they appear to be isotomously branched (Pl. 3, fig.11). Arms, when initially formed, may really be isotomously branched, but with ageing heterotomy becomes increasingly distinct.

Sharply V-shaped grooves (food grooves) with narrow flattened bottoms (Pl. 3, fig. 7) extend down the inner surfaces of the Brr—two converging to one at each axillary (Pl. 3, fig. 7). These grooves deepen gradually proximally,

until they (the five in the IBr series) reach the RR, where they shallow rapidly, after passing beneath the tegmen, and disappear about one-fourth the way down the RR (although the tegmen is known only from Cincinnati, it is probably similar in other Cincinnatiids).

Occurrence—Edenian to Richmondian. Cincinnati is known from the Kope, Fairview, Grant Lake, and Bull Fork Formations of the Cincinnati, Ohio area, from the Whetstone Gulf Formation of northwestern New York; and from the upper part of the Martinsburg Formation of southern Pennsylvania and Maryland.

Discussion—In 1847 James Hall erected the new genus Heterocrinus to include the three new species: H. heterodactylus (p. 279), H. simplex (p. 280), and H. ? gracilis (p. 280). Hall did not designate a type species, nor did he refer to any of the three species as typical (he did, however, emphasize that H. gracilis deserved only provisional placement under the genus). Hall had a concept of the genus Heterocrinus that allowed considerable variation; this likely was his reason in choosing heteros (Greek for different or changed) for the name of the genus. In including the heterocrinid H. heterodactylus with the homocrinid H. simplex (now type species of Ectenocrinus), Hall created a problem that was to be a source of confusion really until Ulrich's (1925) revision of the Heterocrinidae.

Some paleontologists embraced Hall's concept and included forms with three compound and two fused RR (e.g., Heterocrinus simplex) and forms with two compound and three fused RR (e.g., H. heterodactylus), while others limited the genus to forms like H. simplex. Part of the problem was confusion over the type species.

In 1866 (p. 4-6) Hall described three more species of Heterocrinus and compared one of them to H. simplex. Wachsmuth and Springer (1880, p. 69) enumerated known species of Heterocrinus and listed H. heterodactylus as the type species. Later (1886, p. 205-208) these authors recognized that the differences between H. heterodactylus and H. simplex are greater than specific differences, and they redefined Heterocrinus. Of the eleven species which they in 1880 placed in Heterocrinus, they in 1885 transferred H. heterodactylus, along with four other species, to the new genus Stenocrinus with H. heterodactylus as type; they left H. simplex and one other species in Heterocrinus (with H. simplex as type); two species were transferred to Calceocrinus and the remaining two species were assigned to the new genus Ohioocrinus. The Wachsmuth and Springer ideas of 1885 on Stenocrinus and Heterocrinus were not accepted by S. A. Miller (1889), who erected the genus Ectenocrinus with H. simplex as type (p. 242) and listed H. heterodactylus as type of Heterocrinus (p. 252).

Springer (1911) recognized that Wachsmuth and he had mistakenly substituted Heterocrinus simplex as the type of Heterocrinus in place of H. heterodactylus, the valid type: "But through some misunderstanding of types the name Heterocrinus was assigned by us [Wachsmuth and Springer, 1885] to the wrong set of species, H. heterodactylus being Hall's type of that genus; therefore, Stenocrinus must go into synonymy. Heterocrinus must be retained for the H. heterodactylus group...." (Springer, 1911, p. 27).

It seems that Hall, although he did not designate a type, may have felt that H. simplex was typical of Heterocrinus (in succeeding descriptions of new Heterocrinus species, he referred to H. simplex but not to H. heterodactylus); but if, in naming H. heterodactylus, Hall had in mind the concept of what we now call virtual tautonymy, he probably considered H. heterodactylus as typical. Whatever may have been Hall's original views, they are not documented and are therefore not legally pertinent. When Wachsmuth and Springer (1880), possibly applying the convention of page priority or the tautonymic concept (or perhaps having communicated with Hall), listed H. heterodactylus as the type species of Heterocrinus, they established H. heterodactylus as the type species by subsequent designation. (Warn, 1973, p. 10-11). Problems, however, do not end here.

Although the genus Heterocrinus Hall, 1847 and two of its species, H. heterodactylus Hall, 1847 (the valid type of Heterocrinus) and H. juvenis Hall, 1866, have come to be relatively common names, Hall's original descriptions, figures, and type material do not make these taxa recognizable. Modern understanding of these taxa date really from Meek (1873) and Ulrich (1925), who figured new material and described it in detail. H. juvenis is unrecognizable for reasons discussed under Cincinnatiocrinus pentagonus (conceptually similar to Meek's, 1873, H. juvenis). H. heterodactylus, the valid type of Heterocrinus, is unrecognizable because neither Hall's (1847) figures (and description) nor any type material (Pl. 1, figs. 1-6) shows branching beyond the isotomous branches on the IBr axillaries. Meek (1873) recognized this problem when he (p. 13) considered specimens from around Cincinnati referred to H. heterodactylus by Hall (1847): "This is the western form that has always been referred to H. heterodactylus, of Hall; but as the original typical specimen of that species did not show whether or not its arms bifurcate above the division on the last primary radial, ...its identity with that species can scarcely be established beyond doubt." The names Heterocrinus and H. heterodactylus must at present be restricted to Hall's (1847) type material. The new name Cincinnatiocrinus is

used here for the concept of Heterocrinus put forth by Meek (1873), Ulrich (1925) and subsequent workers—i.e., a monocyclic inadunate with three fused and two compound RR, a short, straight, armlike anal tube, and alternating heterotomous branching beyond the isotomous branch on the IBr axillaries. Cincinnatiocrinus varibrachialis, the new name for Meek's (1873) and subsequent workers' concept of H. heterodactylus, is discussed later.

Cincinnatiocrinus appears to differ from Ohioocrinus mainly with respect to the anal sac. Both Ohioocrinus and Cincinnatiocrinus have an anal tube that is an armlike branch of about four plates off the C ray sR. The difference is that in Cincinnatiocrinus the XX are backed by small polygonal plates given off from the tegmen to form a short narrow tube; whereas the four (or five) XX of Ohioocrinus have a backing of small polygonal plates which extends away from the XX (rather than closing around the back to form a tube) and beyond (distal to) the XX as a high, inflated, polyplated coil with wide whorls. For a time the author thought the differences to be preservational (that Ohioocrinus were well-preserved Cincinnatiocrinus); but so many well-preserved Cincinnatiocrinus, all lacking coiled anal sacs, have been examined that it now appears the two are distinct.

Cincinnati probably evolved from an earlier Cincinnati. The step from Isotomocrinus to Cincinnati is simply one of making isotomous arms heterotomous (isotomous to heterotomous is a common evolutionary trend in crinoids—Moore and Laudon, 1943, p. 10) and shortening the anal tube a bit. Cincinnati and Ohio are certainly similar; it is easier to derive Ohio from Cincinnati with coiling and elongation of the polyplated anal sac and elongation of the arms than to do the reverse, although Ohio could be an independent offshoot from Isotomocrinus (the arms of O. brauni are nearly isotomous). Dystactocrinus is also quite like Cincinnati, from which it probably evolved. Evolution of Cincinnati to Dystactocrinus requires only regularization of branching (constancy in number of Brr in each division series in single specimens and among different individuals is apparently an evolutionary endpoint in Cincinnati), broadening of BB, and enlargement of  $IBrr_1$ .

Cincinnati is known from thousands of specimens (all but a few tens from in and around Cincinnati, Ohio) and is easily the best known of Cincinnati. Two species, C. varibrachialus (new herein) and C. pentagonus (Ulrich), 1882, are recognized. Heterocrinus isodactylus Miller, 1875 may belong to Cincinnati but must,

at present, be restricted to its holotype (in reality, Heterocrinus isodactylus may be conspecific with Cincinnatiocrinus pentagonus, but Miller's drawing and description are poor and hardly allow this to be suggested with much authority).

There appears to be a trend in Cincinnatiocrinus toward thicker columns through time. C. varibrachialis has a column with a relatively consistent width (proximal column diameter is about half distal cup diameter) through Edenian and into Maysvillian time. Maysvillian C. pentagonus (with columns having proximal column diameter somewhat smaller than distal cup diameter), however, give way to even broader columned forms in Richmondian time (Richmondian C. pentagonus have columns with proximal diameter about equal to distal cup diameter).

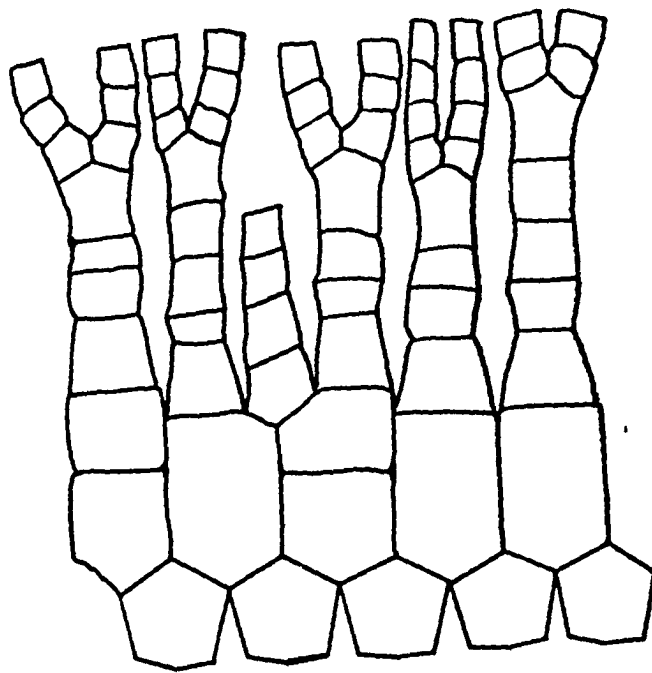
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Text-fig. 8. Exploded diagram of Cincinnati  
crinus  
varibrachialis.

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Text-fig. 9. Five general basal plate shapes in  
cincinnaticrinaceans and homocrinaceans.

a—distally expanding, symmetrically pentagonal

(Cincinnaticrinus varibrachialis, Isotomocrinus  
tenuis, Atopocrinus priscus, and Homocrinus parvus);

b—parallel-sided, symmetrically pentagonal (C.

pentagonus, Ohioocrinus laxus—also e in some members,  
O. brauni, Daedalocrinus bellevillensis, Ectenocrinus  
simplex, E. geniculatus, and Sygcaulocrinus typus—  
in the case of the last three, only the AB interray  
B);

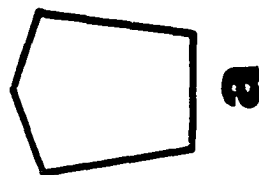
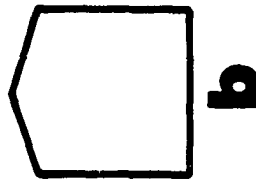
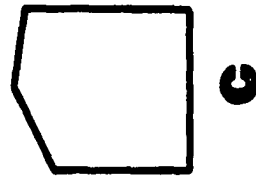
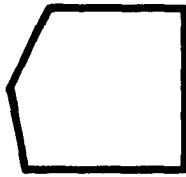
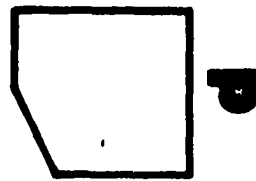
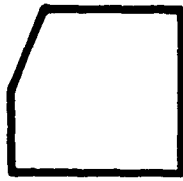
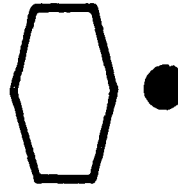
c—asymmetrically pentagonal with one steeply sloping  
and one gently sloping upper side (S. typus—all  
but the AB interray B);

d—asymmetrically pentagonal with one steeply sloping  
and one horizontal upper side (E. simplex and E.  
geniculatus—in both, all but the AB interray B);

e—symmetrically hexagonal (Dystactocrinus constrictus  
and O. laxus—usually b, however, in the latter).

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Cincinnaticrinus varibrachialus (new herein)

Text-fig. 8; Pls. 3-5.

- 1873 Heterocrinus heterodactylus Hall, Meek, p. 12,  
Pl. 1, figs. 1a-b; Cumings, 1908, Pl. 3, figs.  
5, 5a; Bassler, 1919, Pl. 53, figs. 5-6.
- 1925 Heterocrinus heterodactylus Hall, Ulrich, p.  
83, Text-fig. 3a; Moore & Laudon, 1944, Pl.  
52, fig. 11.
- 1925 Heterocrinus difficilis Ulrich in Ruedemann, p. 76.
- 1973 Heterocrinus tenuis Billings, Warn, p. 10, Pl.  
1, figs. 2-19 (non fig. 1).

Primary type material—The holotype is here designated UCGM 3871 (the specimen illustrated by Meek, 1873, Pl. 1, figs. 1a-b as Heterocrinus heterodactylus?). Paratypes are here designated UCGM 40497, 40500, 40502, 40531, 40555, 40556, and 405751. All primary types are from Edenian strata in the Cincinnati, Ohio area.

Diagnosis—Cincinnaticrinus with steeply conical (lekythosiform) cup and narrow column, so that in uncrushed specimens distal cup diameter is at least 1.4 times as great as proximal cup (or proximal column) diameter.

Description—C. varibrachialus, in addition to generic and higher characters, has BB (Text-fig. 9) and RR that expand distally and make the dorsal cup conical. This is more obvious in juveniles, which have globular calyces.

With growth, the angle formed by the edges of the cup (in lateral view) decreases as the sides of the BB and RR approach a parallel condition (compare Pl. 5, figs. 1-2 and 12-13). No new cup plates are added during ontogeny (that is, during that part of the ontogeny that is known), and shapes and relative size ratios of cup ossicles change little (other than widening of the bottoms of the BB and RR). Thus, the smallest (youngest) and largest (oldest) crinoids have dorsal cups that are nearly identical except for size.

Cincinnatiocrinus varibrachialus, with two to seven IBr (commonly three, four, or five), three to seven IIBr (four or five is most common), and four to six IIIBr (commonly four or five), has arms that are more variable than in any other Cincinnatiocrinid aside from Isotomocrinus tenuis, which appears to have similar brachial variability. Ramules given off at heterotomous branches usually remain simple and have more plates, but bifurcating ramules have been observed in a few specimens. Warn (1973) described small (smaller than adjacent Br) doubly convex (marquise) plates occurring in some specimens at various places in the arms (in the IBr series most commonly between  $IBr_1$  and  $IBr_2$ —Pl. 3, fig. 3).

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Text-fig. 10. Localities of Cincinnaticrinus vari-

brachialus collected in connection with this study.

All were (they have been completely collected) in the Kope Formation. Crinoid remains in all but locality 2 were deposited as large ripples.

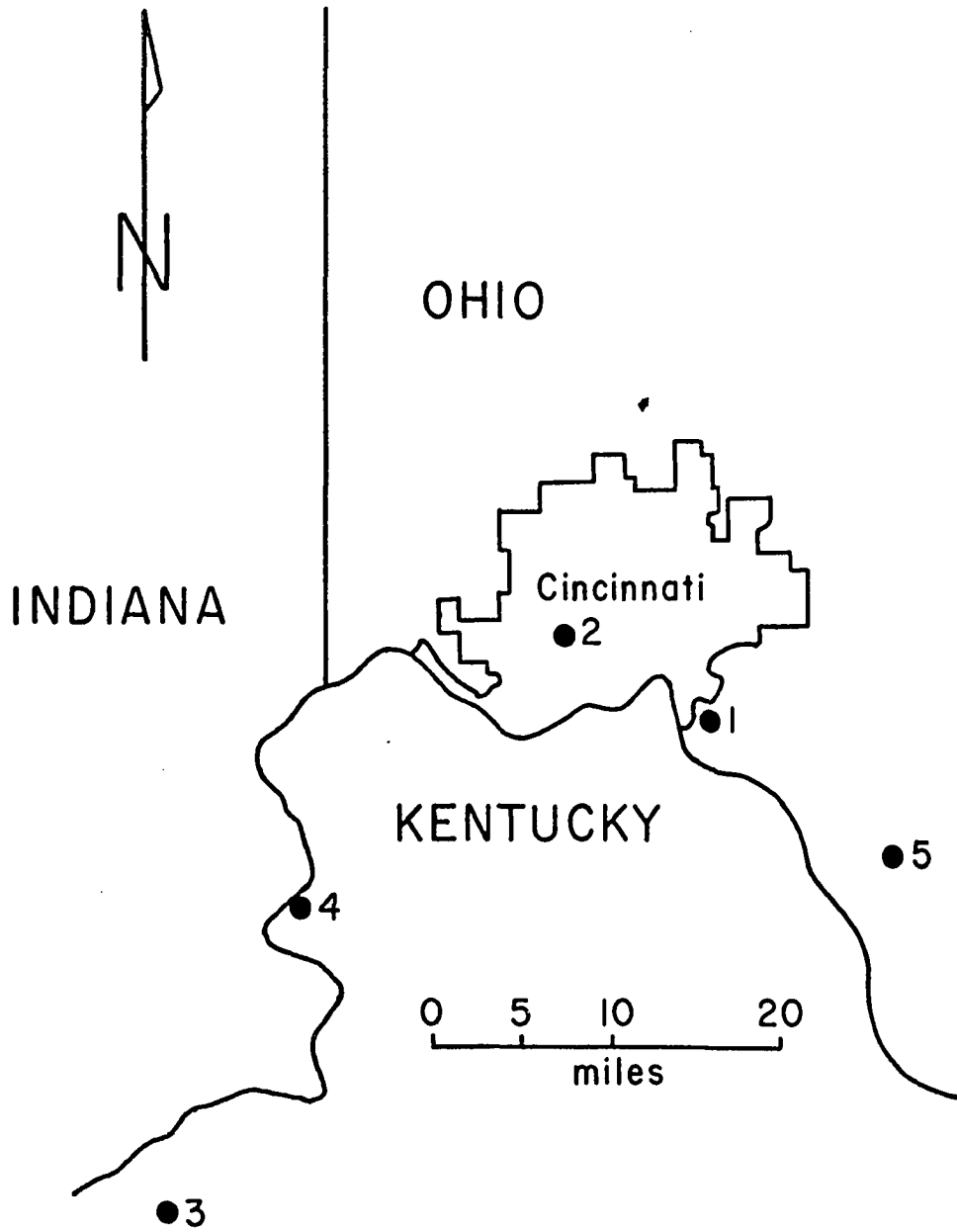
1—N39 06', W84 24' at the base of an old road cut on the east side of Elstun Avenue, 75 yards (nearly 70 meters) south of Beechmont Abenuue. Neither the Kope-Fairview nor the Kope-Point Pleasant contact is visible. Fossil content and elevation of the outcrop suggest occurrence in the Southgate member (Text-fig. 4). Crinoids were found in a north-south trending deposit about 12 feet by 3 feet (nearly 4 meters by 1 meter) in areal extent and about  $\frac{1}{2}$  inch to 4 inches (about  $1\frac{1}{4}$  to 10 centimeters) thick. The deposit was in mudstone and consisted mostly of column fragments, at least 88 tiny Cincinnaticrinus varibrachialus crowns and calyces, 7 tiny Ectenocrinus simplex crowns, 72 juvenile holdfasts, trilobites, brachiopods, gastropods, trepostome bryozoa, and small Mesopaleaster. The trilobites and starfish were apparently scavenging the dead crinoids before burial. Many (all but the 95 cited above) of the crinoids are presently in the hands of amateur collectors.

- 2—N39 10', W84 34' in the west bank of West Fork Creek 50 yards (about 46 meters) northwest of the intersection of Diehl Road and West Fork Road, 198 feet (about 60 meters) below the Kope-Fairview contact, which is visible along Shepherd Road just west of West Fork Road. Crinoids were found in mudstone and occupied about one square yard (nearly one square meter). Long (up to two feet—about 0.6 meters), unbroken columns lay without consistent orientation. 18 Cincinnaticrinus varibrachialus, 17 Ectenocrinus simplex, and 38 juvenile holdfasts were found.
- 3—N38 39', W85 07' near the top of a large outcrop at the southeast corner of the Carrollton, Kentucky I-71 interchange, 30 to 50 feet (about 9 to 15 meters) below the Kope-Fairview contact. The contact is covered here, but it is visible in outcrops along I-71 on the other side of the Kentucky River. The west-northwest—east-southeast trending deposit was about 3 feet by 6 inches in area and 2 inches thick (about 92 X 15 X 5 centimeters) and consisted of 17 C. varibrachialus, 2 E. simplex, and numerous columns.
- 4—N38 56'30", W84 50' in the creek bed of an unnamed tributary (of the Ohio River) which flows through Rabbit Hash, Kentucky, 70 feet (about 21 meters) below the Kope-Fariview contact which occurs in the

westernmost fork of the tributary about 250 yards (about 80 meters) upstream from the pocket. The pocket consisted of "knotted columns" striking approximately east-west, 82 Cincinnati varibrachialus crowns and calyces, 54 Ectenocrinus simplex, and 21 juvenile holdfasts in mudstone, becoming more limy northward, and finally grading into a biogenic limestone made up in large part of discrete columnals.

5—N38 57'50", W84 14'35" in the bed of Twelve Mile Creek 75 feet (about 23 meters) east of Twelve Mile Road where it crosses the creek about four miles (about  $.6\frac{1}{2}$  kilometers) northeast of New Richmond, Ohio, 23 feet (7 meters) above the Kope-Point Pleasant contact which is visible downstream. The pocket consisted of 403 C. varibrachialus crowns and calyces, 49 E. simplex, 12 Merocrinus curtus, and "knotted columns" about 4 feet by 6 feet (about  $1\frac{1}{4}$  by 2 meters) and  $\frac{1}{2}$  to four inches ( $1\frac{1}{4}$  to 10 centimeters) thick trending northeast-southwest and with the columns striking that same direction (see Warn, 1973, p. 10).

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No complete Cincinnaticrinus varibrachialus specimens (holdfast, column, and crown or calyx) are known. However, that juveniles (and possibly adults) have an obscurely polyplated, inverted saucer-like (lichenocrinid) basal attachment is fairly certain (and has been known for some time—see discussion). In collecting localities 1, 2, and 4 (Text-fig. 10) C. varibrachialus calyces and crowns and lichenocrinid bases and columns have been found in abundant association. As well, an ontogenetic sequence from lichenocrinid to cincinnaticrinid column is evident among separate columns and in single columns collected from these, and other, pockets.

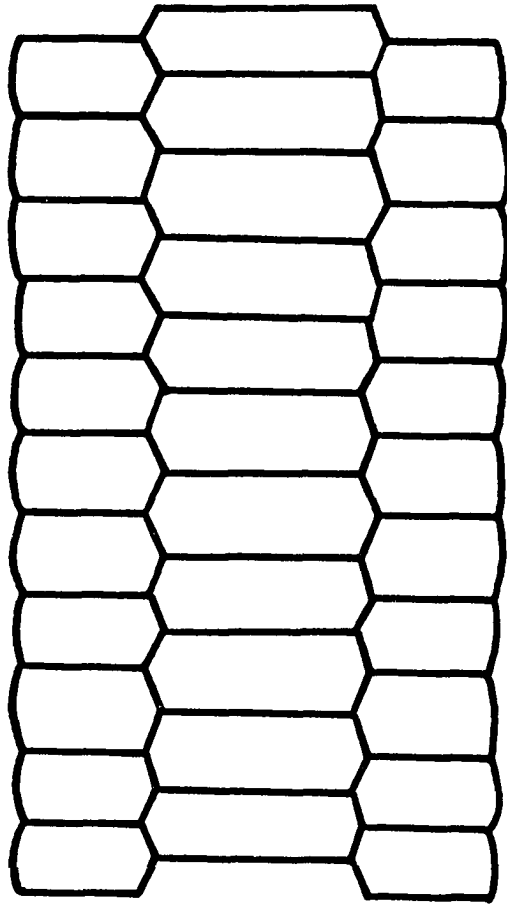
Juvenile C. varibrachialus holdfasts (Pl. 5, figs. 15-16) are roughly circular discs, usually attached to such foreign objects as adult C. varibrachialus columns, other adult crinoid columns, brachiopods, bryozoans, trilobites, pelecypods, or phosphate nodules. They range in diameter from less than one mm to about five mm, with most having a diameter of about two or two and one-half mm. They have a convex, obscurely polyplated, upper wall (roof) and a large flat plate as the lower wall (floor). When the inhabited substrate is not flat, concomitant changes in shape occur, e.g., when encrusting crinoid columns they curl around the column (Pl. 5, fig. 16). The lichenocrinid column protrudes from a central depression or crater in

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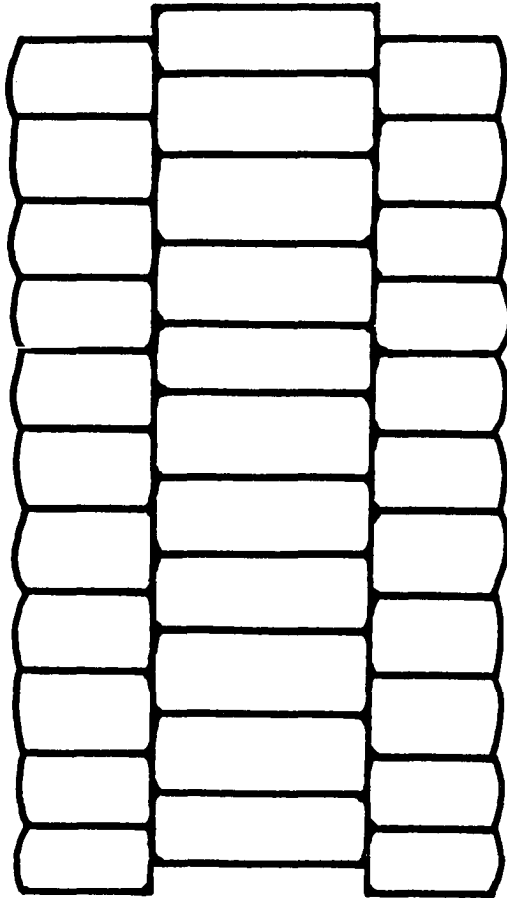
Text-fig. 11. Ontogeny of the Cincinnati vari-  
brachialus column.

a, b, c, and d are portions of the juvenile column viewed progressively more proximally; a is the most distal portion (i.e., nearest the holdfast) and is composed of five vertical series of hexagonal plates with the plates of each series alternating with laterally adjacent plates to form zigzag sutures between series; these grade proximally into a section (b) with alternating plates that abut, so that a straight suture is formed between series; farther proximally, abutting plates come to lie in parallel planes to form circlets of five plates (c); still farther proximally the circlets of five plates fuse to form pentapartite columnals (d). e and f are portions of the adult column; the oldest portion of the adult (f) is round with equal-sized columnals, which are apparently first secreted as pentagonal columnals and become round with secondary secretion of stereom; this grades proximally into a portion (e) with larger, more rounded columnals (in some specimens an additional proximal portion is made up of equal-sized pentagonal columnals).

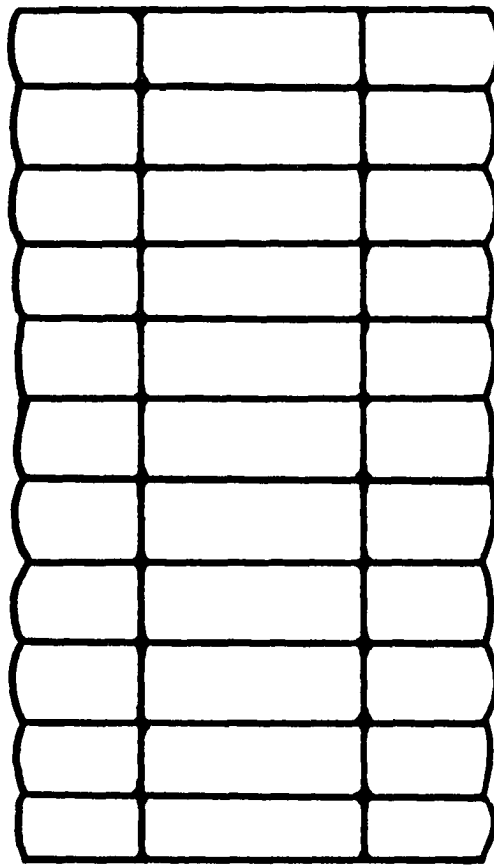
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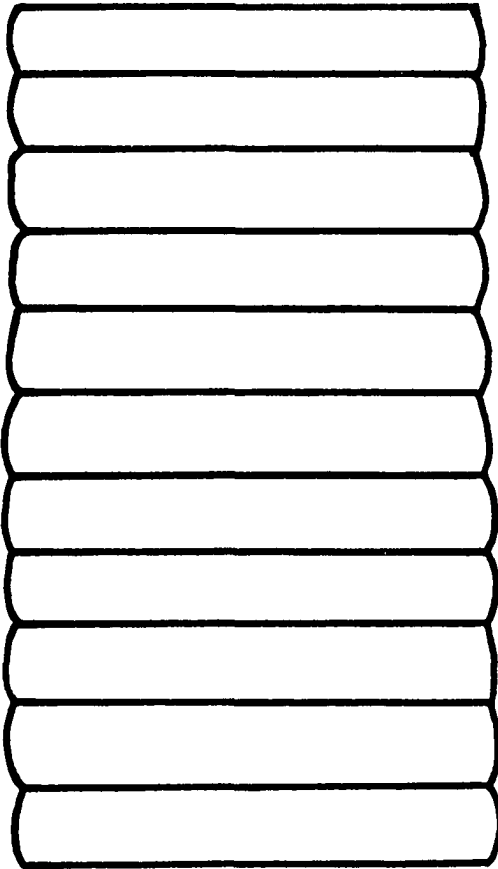
**a**



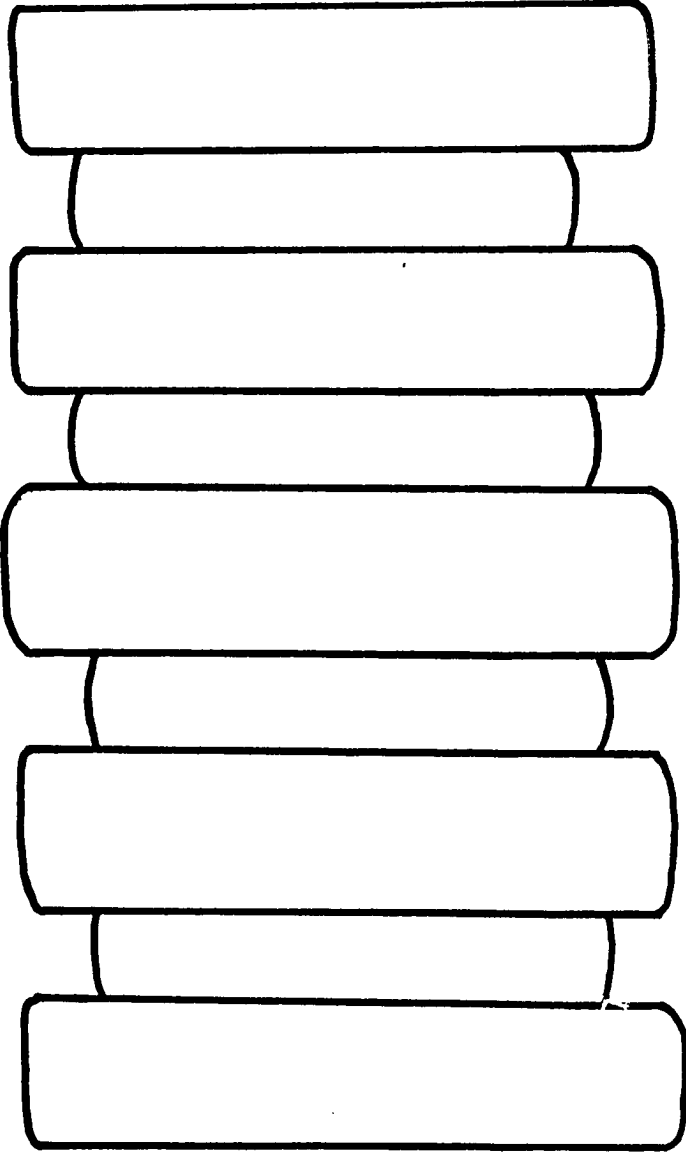
**b**



**C**



**d**



**e**


**f**

the roof. Internally, five primary lamellae extend from the periphery of the holdfast and meet at the center. These lamellae rest upright on the floor. Second, third, and fourth order lamellae are inserted serially between the primary lamellae and may or may not reach the center. The lamellae (Pl. 5, fig. 15) appear to support the roof. (For detailed information on lichenocrinid bases in general, affinities unknown, look to Faber, 1929).

Juvenile Cincinnatiocrinus varibrachialus columns (lichenocrinid columns—Pl. 3, figs. 3 and 10) show an interesting morphologic (and apparently ontogenetic) sequence. They are composed distally (*i.e.*, adjacent to the base) of five vertical series of hexagonal plates with the plates of each series alternating with laterally adjacent plates (*i.e.*, plates of adjacent series) to form zigzag sutures between series (Text-fig. 11). These grade proximally into a section with alternating plates that abut, so that a straight suture is formed between series (Text-fig. 11). Farther proximally, abutting plates come to lie in parallel planes to form circlets of five plates (Text-fig. 11). Each circlet has one plate from each of the five series. Transition to the Cincinnatiocrinid column occurs with gradation into columnals by fusion of the five plates (pentameres). Thus, the most proximal (youngest) part of the juvenile column (= distal and oldest of adult ?)

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Text-fig. 12. Ranges of cincinnaticrinacean and homocrinacean species. European stages are on the left of the column; North American series and stages are on the right.

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Ludlow	SILURIAN	Cayugan		
Wenlock		Niagaran	<u>I. H. parvus</u>	
Llandovery		Medinan		
Ashgill	ORDOVICIAN	Cincinnatian	Richmondian	<u>I. S. typus</u>
			Maysvillian	<u>C. pentagonus</u> <u>D. constrictus</u> <u>I. O. laxus, O. brauni</u>
			Edenian	<u>E. simplex</u> <u>C. varibrachialus</u>
Caradoc		Shermanian		<u>I. E. geniculatus</u>
			Kirkfieldian	<u>I. tenuis</u>
			Rocklandian	<u>D. bellevillensis</u>
Llandeilo		Champlainian	Black Riveran	
Llanvirn			Chazyan	
			Whiterockian	<u>-I. lepton, A. priscus</u>
Arenig		Canadian		
Tremadoc				

is round with equal-sized columnals (Text-fig. 11), each made up of five pentameres.

The adult Cincinnatiocrinus varibrachialus column is either pentagonal proximally grading distally into terete, or round throughout. The proximal pentagonal part can be made up of two sets of columnals: larger, more rounded columnals and smaller, markedly pentagonal columnals inserted between the larger columnals. Each columnal is composed of five fused plates with each plate forming a point in the pentagonal columnals. With secondary secretion of stereom (seemingly a normal feature of column ageing), the column becomes round, but the former pentagonal column can be seen inside the round sheath in cross-section.

Occurrence—Edenian and Maysvillian from the Kope and Fairview Formations around Cincinnati, Ohio; the Whetstone Gulf Formation of northwestern New York; and the Martinsburg Formation in Maryland and southern Pennsylvania. Ruedemann (1925, p. 70) briefly described from zone I of the Whetstone Gulf Heterocrinus difficilis (that was to be further described later, but never was, by E. O. Ulrich), which is considered to be a junior synonym of C. varibrachialus. This author has found C. varibrachialus only in the Kope Formation, in which crinoids are fairly common, weathering more easily out

of the predominantly shaley unit than from the more limy Fairview above. The dominantly calcareous Fairview ("Hill Quarry beds") is less propitious for well-preserved cincinnaticrinids. However, during the 1800's and early 1900's dozens of quarries were operating in the Cincinnati area and more good Fairview exposures were available then than now. Fortunately, area museums have specimens from the "Hill Quarry beds" (Fairview Formation) collected around the turn of the century.

Discussion—Cincinnaticrinus varibrachialus is erected to house the taxon that Meek (1873) and Ulrich (1925) made known as Heterocrinus heterodactylus. H. heterodactylus must be considered as unrecognizable, because Hall's (1847) type material (AMNH 1116/1—Pl. 1, figs. 4-6, AMNH 1116/2—Pl. 1, fig. 3, and AMNH 1116/3—Pl. 1, figs. 1-2), illustrations (Hall, 1847, Pl. 76, figs. 1a-o), and description (Hall, 1847, p. 279) impart no knowledge of the character of branching.

The trivial name varibrachialus is chosen to describe the variability in number of Brr per division series so characteristic of this species. Originally the word "brachial" was used as an adjective to denote arm ossicles (e.g., brachial plates or ossicles; primibrachial plates or ossicles). In modern times, the word "brachial" has come to be widely used in an abbreviated sense as a noun to

denote arm ossicles (e.g., brachials, primibrachials); and abbreviation is often carried even further (e.g., brachs, primibrachs). The trivial name varibrachialus, chosen for its descriptiveness, is somewhat awkward, in that it represents latinization of an anglicized Latin word. However, it is chosen over the original Latin brachialis, for brachialis means "of the arm", the use of which (as varibrachialis) would give the name too much breadth of meaning (varibrachialis would mean simply arm variation). The trivial name varibrachialus, though of awkward derivation, is more meaningful (varibrachialus is used to denote variation in number of Brr per division series in the arms of this species).

The variability in number of IBrr (and higher Br series), both in single individuals and among different individuals, appears to be a feature unique to cincinnati-crinids. The author (1973) interpreted the smaller marquise-shaped Brr as intercalates and judged intercalation of Brr to sufficiently explain the brachial variability in Cincinnati-crinus varibrachialus. In that paper, 61 different IBr arrangements were reported from a single pocket of 72 crowns (specimens with all five IBr series still intact), 116 partial crowns (one to four IBr series), and 219 calyces (no complete IBr series). (Similar variation and variation in additional populations

has since been found). Kesling and Strimple (1971) reported, in Eutaxocrinus wideneri (a flexible crinoid), IBr and IIBr variation (considered mutation by Kesling and Strimple) from a basic plan of two IBrr per ray and three or four IIBrr per arm; in cincinnaticrinids, however, variation within limits (e.g., two to seven IBrr for Cincinnaticrinus varibrachialus) seems to be the rule, rather than an exception.

Lichenocrinus was described by Hall (1866, p. 9) for what the author has referred to as lichenocrinid bases. Hall thought these to be the "bodies" of parasitic crinoids because of their consistent attachment to other organisms. Meek (1871, 1872b, 1872c) and Sardeson (1899, p. 275) theorized that Lichenocrinus might actually represent basal attachments of crinoids. Schuchert (1904, p. 268) stated more definitely that Lichenocrinus are bases of crinoids. Springer (1917, p. 11) reported the affinity of Heterocrinus and lichenocrinid bases but cited no evidence: "This curious disc-like body [lichenocrinid base] ...is now known to be the encrusting root of a very small crinoid of the Heterocrinus type". Perhaps Springer was referring to material sent to him for description by an amateur collector, George M. Austin, in 1903 (see below). Foerste

(1925, p. 102-103) alluded to complete juvenile heterocrinids with lichenocrinid bases and column in the USNM collection. Unfortunately, Foerste could not discern the plate arrangement of the calyx, and the author has been unable to locate the specimens (perhaps Foerste, too, was referring to the Austin material—see below). Bassler (1928) indicated that George M. Austin (from Wilmington, Ohio) had discovered evidence for the lichenocrinid-heterocrinid affinity in 1898 and had (in 1903) communicated his discovery to Frank Springer for description, which Springer never did. Faber (1929, p/ 455-456) reported that in 1898 he, G. Ashman, and A. Albers found three tiny crinoids complete with lichenocrinid bases. According to Faber, these specimens were never illustrated or described and disappeared, along with part of Albers' collection, just before Albers' death. Fenton (1929) discussed Austin's 1898 material (USNM 89862a-f—the material that Springer was to have described) in detail. Reexamination of this material confirms Fenton's observation that some heterocrinids (cincinnati- crinids) and some lichenocrinids represent different parts of the same organism. USNM 89862a-f consists of 20 lichenocrinid bases attached to Rafinesquina, an Isotelus fragment, and trepostome bryozoan fragments associated with lichenocrinid columns and three juvenile Cincinnati- crinus sp. cf. C. pentagonus crowns from Richmondian strata near Clarksville,

Ohio. One of these crowns appears to have been attached to one of the lichenocrinid columns; only a 0.8 mm long furrow, presumably the result of loss of a portion of the column from the slab, separates the crown from the column.

While earlier workers' evidence, as well as recent observation, indicates a lichenocrinid base-juvenile Cincinnaticrinus varibrachialus (and probably C. pentagonus) affinity, resolution of the matter of priority of Lichenocrinus as a generic name is delayed until more information, hopefully from discovery of complete specimens is available. Considerable morphologic variation in lichenocrinid bases suggest that juveniles of a variety of Cincinnati crinoids have lichenocrinid holdfasts.

Miller (1874) described the axial changes in the Heterocrinus heterodactylus (C. varibrachialus) column through much of its length but said nothing of the lichenocrinid nature of the distal (juvenile) column and base. Bather (1891, p. , Text-fig. ; 1900, p. 89, Text-fig. 3) showed a similar distal-proximal columnar gradation for the cladid Botryocrinus decadactylus from the Wenlock limestone.

It appears that, in adults, new columnals are added both at the base of the calyx and intercalated serially for a short distance distally between older columnals. Columnals are, in both cases, first added as five discrete

radial plates which fuse to form pentagonal columnals. Older columnals become round with secondary secretion of stereom. Addition of new columnals may, at some stage in ontogeny, cease and all columnals become round. Thus, most adult columns have a proximal section made up of pentagonal columnals, grading distally into a series of pentagonal columnals alternating with larger rounded columnals, and finally into a distal region of round columnals only. Some columns (of younger crinoids?) are pentagonal for proportionally greater distances, while others (of older crinoids?) are round throughout their observed length. This is in apparent agreement with "Jackson's law" (Jackson, 1896; 1899), which is essentially: In organisms possessing organs which grow by the serial addition of parts, the ontogeny of the organ tends to rehearse its phylogeny.

Warn (1974, see Appendix—paper to be published in July 1974 issue of *Journal of Paleontology*) described swellings, which he interpreted as myzostome galls, in columns of Heterocrinus juvenis (Cincinnatiocrinus pentagonus). The author has seen similar galls in columns of C. varibrachialus and Ectenocrinus simplex.

The rarity of complete juvenile C. varibrachialus is probably a result of breakage of the fragile column during or after death, either before burial or during exposure and subsequent collecting (however, the association of lichenocrinid bases with juvenile C. varibrachialus crowns is pervading). No complete adult specimens (*i.e.*, none

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Text-fig. 13. Ontogenetic change in the life habit of  
Cincinnaticrinus varibrachialus.

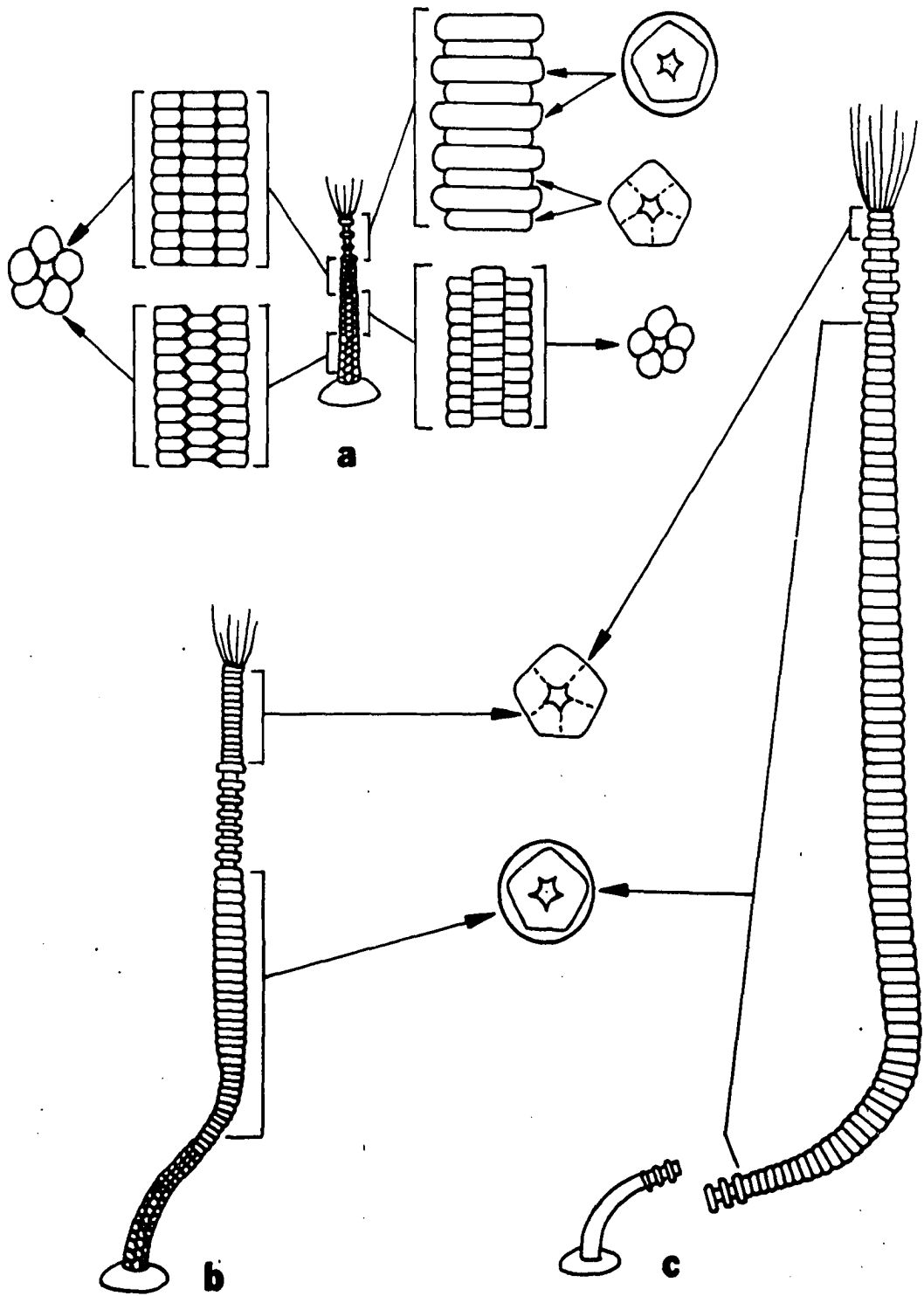
a—attached juvenile with polyplated (lichenocrinid)  
column and holdfast,

b—attached adult with expanded, "adult" column proximal  
to the thin, juvenile (lichenocrinid) column,

c—adult breaks free (whether because of increased  
current activity or autotomized is unknown) at the  
attenuated juvenile column and thereafter lives  
unattached.

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with holdfasts) and no associations of large crowns and holdfasts are known. This may be due to post-mortem transport and differential deposition of crowns and proximal parts of the columns apart from the holdfasts and distal parts of the columns. On the other hand, evidence suggests that adults were eleutherozoic. The delicate, attenuated "lichenocrinid" distal column would seem to have been inadequate to support the adults upright during life and would have easily broken in currents, if not autotomized (Text-fig. 13). As well, occasionally sections of Cincinnaticrinus columns are found with a single rounded, apparently abraded, end.

Warn (1973, p. 13, Table 1) has shown that various species of Heterocrinus described during the classical period of paleontology were characterized as having different IBr arrangements; yet, the brachial arrangements of any of these species would fit into the normal intraspecific variation of C. varibrachialus. It may be that H. exilis Hall, 1866, H. exiguus Meek, 1872a, H. propinquus Meek, 1873, and C. varibrachialus (new herein) are conspecific. However, type material for H. exiguus and H. propinquus has not been located; H. exilis is apparently based on a juvenile of questionable affinity; and figures and descriptions do not allow calling this taxon (C. varibrachialus) one of the earlier described species.

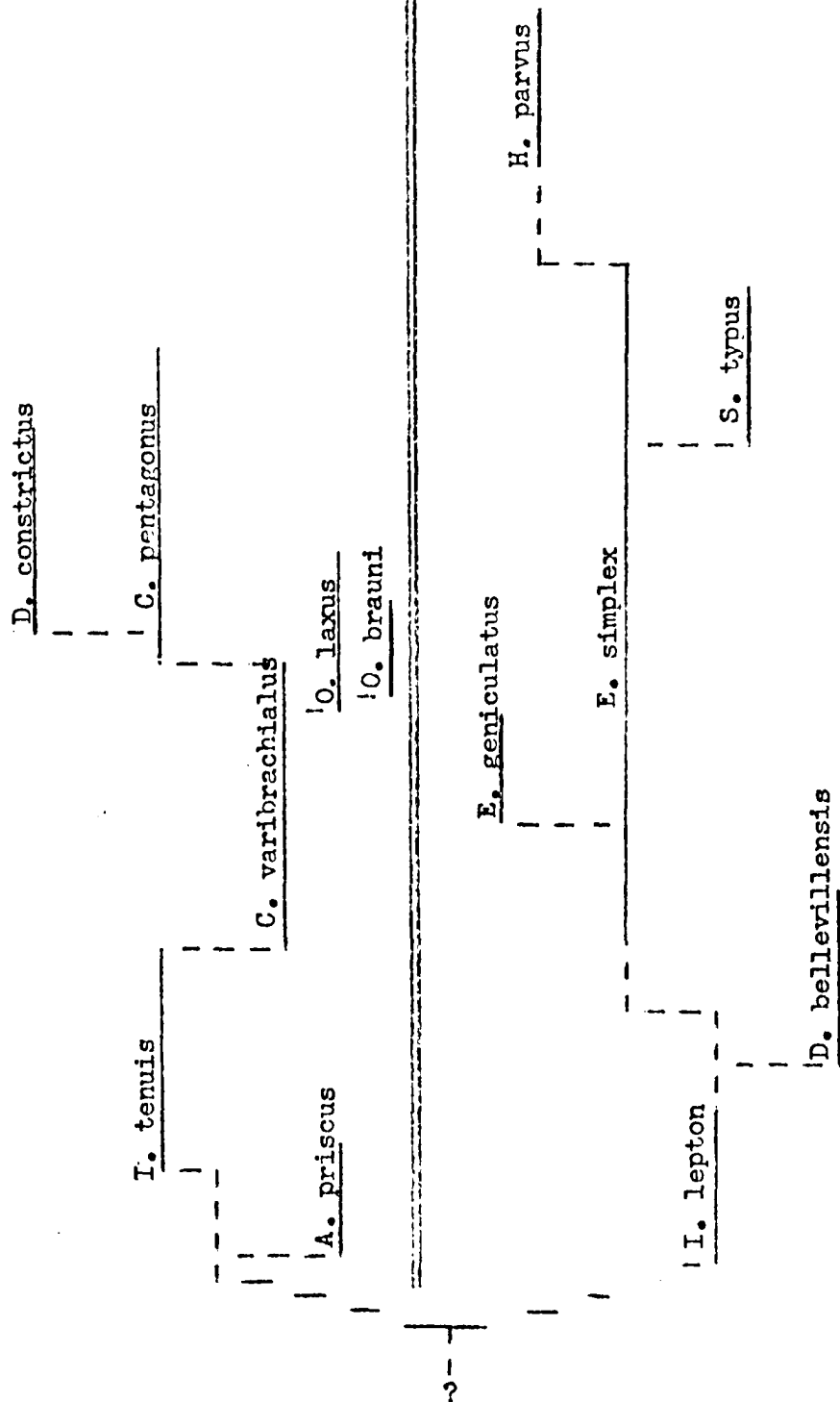
It is not surprising that such workers as Hall, Meek, and Ulrich assumed intraspecific constancy in number

of IBrr per ray. IBr variability is presently known from no fossil crinoids other than cincinnaticrinids (and one purportedly anomalous population of Eutaxocrinus wideneri). Indeed, all Recent comatulids (non-stalked crinoids) have either two or four IBrr per ray, although in Hyman's (1955, p. 92) opinion, the generic allocation of existing pentacrinites (stalked crinoids) is in a state of confusion, largely because of the use of number of Brr in each division series as a taxobasis.

Cincinnaticrinus varibrachialus probably evolved from Isotomocrinus tenuis by reduction of the anal tube and by transformation of isotomous to alternating heterotomous branching. In other respects the two genera and species are similar. C. varibrachialus seems to have given rise to C. pentagonus. Such evolution would have encompassed widening of the column and proximal calyx and initiation of the trend toward regularization of branching, which in cincinnaticrinids culminates in Dystactocrinus constrictus.

## CINCINNATICRINACEA

## HOMOCRINACEA



Text-fig. 14. Phylogeny of the Cincinnaticrinacea and Homocrinacea.

Cincinnaticrinus pentagonus (Ulrich), 1882

Pl. 6.

- 1873 Heterocrinus juvenis Hall, Meek, p. 10, Pl. 1, figs. 3a-c; Cumings, 1908, Pl. 3, figs. 3, 3a-b; Ulrich, 1925, Text-fig. 4c.
- 1882 Heterocrinus pentagonus Ulrich, p. 176, Pl. 5, figs. 10, 10a.
- 1974 Heterocrinus juvenis Hall, Warn, Pl. 1, figs. 1, 9. (see appendix B—paper to be published in June 1974 issue of Journal of Paleontology).

Primary type material—YPM 24801 and 24802 are syntypes of H. pentagonus Ulrich, 1882. YPM 24801 is herein designated lectotype and YPM 24802 lectoparatype of H. pentagonus. Both are Maysvillian from Cincinnati, Ohio.

Diagnosis—Cincinnaticrinus with cylindrical dorsal cup and wide column, so that in uncrushed specimens distal cup diameter is less than 1.4 times as great as proximal cup (or proximal column) diameter.

Description—C. pentagonus has parallel-sided pentagonal BB (Text-fig. 8) and large, distally tapering IBrr<sub>1</sub> (although the IBrr<sub>1</sub> are less than three-fourths as tall as the fused RR). The dorsal cup is hardly wider than the proximal column, and the arms, when folded (as is nearly always the case), continue nearly straight from the calyx, so that crowns attached to sections of column are not

conspicuous features as in other cincinnaticrinids (and as in most crinoids), where the crowns are conspicuous expansions at the ends of the columns. As in Cincinnaticrinus varibrachialus, no new cup plates are added during the known part of ontogeny, and the smallest and largest C. pentagonus dorsal cups are nearly identical but for size.

Brachial variability in C. pentagonus, while less well known (a peculiarity of C. pentagonus is that specimens are seldom found with arms above the IBrr<sub>1</sub>—the fixed IBrr), seems to be somewhat smaller than in C. varibrachialus. C. pentagonus seems to vary little (three to five IBrr) around a basic plan of four IBrr per ray. Variability beyond the IBr series is now well known. The column of C. pentagonus is like that of C. varibrachialus, but broader and with a greater propensity for roundness.

Occurrence—Maysvillian and Richmondian. C. pentagonus is known from the Fairview, Grant Lake, and Bull Fork Formations of the Cincinnati, Ohio area. Heterocrinus juvenis Hall, Meek (= C. pentagonus) was reported by Meek (1873, p. 12) from the "...upper part of the Cincinnati group near Lebanon, Ohio" (of demonstrably Richmondian age). Ulrich (1882, p. 176) described H. pentagonus "...from the Cincinnati group at Cincinnati about 375 feet [about 115 m] above low-water mark in the Ohio river" (the Fairview outcrops at that elevation in Cincinnati).

Discussion—Cincinnaticrinus pentagonus is the new name used for what Meek (1873) called Heterocrinus juvenis Hall, 1866. Just what Hall's concept of H. juvenis was is unfortunately unclear—in large part because of questionable type material. Hall described H. juvenis in 1866 but did not illustrate it until 1871. Whitfield and Hovey (1898, p. 24-25) listed AMNH 1173/1 as the holotype of H. juvenis and the specimen figured by Hall (1871, Pl. 1, figs. 9-10; 1872, Pl. 5, figs. 9-10). However, the specimen which presently carries this American Museum number and label is neither that figured by Hall nor that described by Whitfield and Hovey as the type. The holotype was reported by Whitfield and Hovey (1898, p. 24-25) to have been a free calyx, and Hall's (1871; 1872) figures are two views of a free calyx, but AMNH 1173/1 is a specimen imbedded in a slab (Pl. 2, fig. 5). Further, Hall's (1871; 1872) figures and (1866; 1872) description are of a juvenile with diameters of distal calyx and proximal column nearly equal (this feature is part of the concept of C. pentagonus), while AMNH 1173/1 is probably (the specimen is far from complete) a juvenile C. varibrachialus with distal cup diameter nearly twice that of the column (or proximal cup). Hall's original specimen has evidently been lost or misplaced.

It seems that division of Cincinnaticrinus into two species is somewhat artificial, because there is convergence

of distal cup diameter to proximal cup (and proximal column) diameter ratios in the two. In this respect the following facts are known: 1) young (small—cup height of about 2.5 mm or less) Cincinnaticrinus pentagonus have ratios equal to about 1.2, while young (similarly sized) C. varibrachialus have ratios of about 2.0; 2) with age, the column and proximal cup of both broaden relative to the distal cup, but the column of C. varibrachialus widens proportionally more than that of C. pentagonus so that with increasing size (age) C. varibrachialus ratios become smaller faster; 3) Cincinnaticrinus populations with ratios of about 0.9 to 1.3 appear to be segregated from populations with ratios of about 1.5 to 2.2 (the former group appears to be Maysvillian and Richmondian, while the latter is Edenian and Maysvillian). Choice of 1.4 as the major differentiating feature of the two species is a bit arbitrary; it is the number (expressed to the nearest tenth) that falls closest to the midpoint between the highest observed ratio (to the nearest tenth) in populations clustering around 1 and the lowest observed ratio (to the nearest tenth) in populations clustering around 2. That diagnosis of species of Cincinnaticrinus requires measurement of uncrushed (nearly round in oral or aboral view) dorsal cups is a problem, for such preservation is uncommon, though the

problem is not without solution. In general, the distal cup is flattened more than the proximal cup and column, with increase (apparent) in ratios. One can, by averaging the shortest and longest diameters in each of the two planes of measurement, convert an apparent ratio (from a distorted specimen) to an approximation of the "real" ratio that is probably close enough to be useful.

Cincinnatiocrinus pentagonus likely evolved from C. varibrachialis with broadening of the column (presumably a response to increased current activity) and proximal cup and reduction in number of IBrr. C. pentagonus probably gave rise to Dystactocrinus constrictus with increased regularization in number of IBrr, broadening of BB, and enlargement of IBrr<sub>1</sub>.

Genus Dystactocrinus Ulrich, 1925

- 1925 Dystactocrinus Ulrich, p. 87.
- 1925 Atyphocrinus Ulrich, p. 85.
- 1943 Dystactocrinus Ulrich, Moore & Laudon, p. 14,  
Text-fig. 1.
- 1944 Dystactocrinus Ulrich, Moore & Laudon, p. 149.
- 1962 Dystactocrinus Ulrich, Moore, p. 13, Text-fig.  
5—1a-b (1b is a copy of Hall, 1871, Pl. 1,  
fig. 13 as Heterocrinus constrictus).
- 1962 Atyphocrinus Ulrich, Moore, p. 13, Text-fig.  
5—6a-c (6b-c are from Ulrich, 1925, Text-  
fig. 4a-b as Atyphocrinus corryvillensis).

Type species—Heterocrinus constrictus Hall, 1871 from Maysvillian strata at Cincinnati by original designation of Ulrich (1925, p. 87).

Diagnosis—Cincinnati crininae with an anal tube evidently like that of Cincinnati crininae; with ten arms having alternating heterotomous branching; with  $IBrr_1$  large, nearly the same size as the fused RR (width of  $IBrr_1$  is nearly equal to that of the fused RR and height is three-fourths or more the height of the fused RR); and with distinctly hexagonal BB, noticeably broader than tall (Text-fig. 9e).

Description—In addition to familial and higher characters, Dystactocrinus has markedly hexagonal BB, three-fourths or less as tall as wide. In general, plates of the dorsal cup tend to be shorter and broader

than in other cincinnaticrinids. The IBrr<sub>1</sub> are large, rectangular (in plan view—actually, the IBrr<sub>1</sub> are tumescent and, thus, are shaped like a barrel cut longitudinally in half), and about the same size as the fused RR. A constriction occurs in the crown in the plane of the distal ends of the IBrr<sub>1</sub>.

The arms are broad (broader than in other cincinnaticrinids), while the armllets are narrow (about the same as in other cincinnaticrinids), so that the arm to armllet width ratio is high and is a striking feature. Dystactocrinus has only two or three IBrr per ray and three or four IIBrr per arm, with armllets beyond the IIBr axillaries branching off every third or fourth Br. The proportionally small size of the armllets and the extent of regularization of branching (not attained by other cincinnaticrinids) gives the arms the near appearance of pinnulation (in reality, there is gradation in crinoids from heterotomous branching to pinnulation, with armllets in the former becoming pinnules in the latter; use of the term pinnulation, while descriptive in some cases, emphasizes differences between some related forms which are actually slight and clouds phylogenetic relationships, e.g., armllets of Cincinnaticrinus, with heterotomous branching, are certainly homologues of pinnules in closely related Ectenocrinus, said to be pinnulated, and the use

of different terms for such similar branching is unfortunate). The broadness of the arms of Dystactocrinus prohibits them from being folded into a tight bundle (as in other cincinnaticrinids) and causes the crown to expand distally. This distal crown expansion emphasizes the constriction at the bottom of the free arms (at the articulation of the IBrr<sub>1</sub> and IBrr<sub>2</sub>)—thus, Hall's specific name. The column of Dystactocrinus is like that of Cincinnaticrinus varibrachialus but with a greater tendency toward roundness.

Occurrence—Maysvillian (?Kirkfieldian, Shermanian, or Edenian, and Maysvillian). Dystactocrinus (monospecific) is known from only a few specimens from the Fairview and Grant Lake Formations of Cincinnati and environs. Hall (1872, p. 211) described D. constrictus (as Heterocrinus constrictus) from a single specimen from limestone of the "Hudson-river group" at Cincinnati; Meek (1873, p. 4) reported that Hall's specimen had been found about 100 feet below the tops of the hills at Cincinnati and that another species, H. compactus (a junior synonym of D. constrictus) occurs at the same level (Fairview Formation). Ulrich (1925, p. 85) described Atyphocrinus corryvillensis (a junior synonym of D. constrictus from the Corryville member of the McMillan formation at Cincinnati (= Grant Lake Limestone).

Ulrich (1925, p. 88) alluded to two undescribed species (each represented by a single specimen) of Dystactocrinus from older strata—one from the "Trenton limestone" at Ottawa, Ontario (= Hull-Kirkfieldian, Sherman Fall-Shermanian, or Coburg beds-Edenian?), and another from the "Cynthiana limestone" at West Covington, Kentucky (= Point Pleasant Formation). The Point Pleasant at Cincinnati is Shermanian and the "Trenton limestone" of New York and Canada has been shown to be Edenian and Maysvillian (Sweet and Bergström, 1972).

Discussion—Dystactocrinus evolved from Cincinnatiocrinus by enlargement of  $IBrr_1$ , broadening and/or shortening of BB, reduction in number of IBrr, and regularization of branching. Dystactocrinus gave rise to no known successors.

Dystactocrinus constrictus (Hall), 1871

Pl. 7.

- 1871        Heterocrinus constrictus Hall, Pl. 1, figs.  
13-14; Hall, 1872, p. 210, P. 5, figs. 13-14;  
Meek, 1873, Pl. 1, figs. 10a-b; Ulrich, 1925,  
p. 87, Text-fig. 6a; Moore, 1962, Pl. 1,  
figs. 1a-b.
- 1873        Heterocrinus constrictus Hall, Meek, p. 3.
- 1873        Heterocrinus constrictus var. compactus Meek,  
p. 4, Pl. 1, fig. 11.
- 1925        Atyphocrinus corryvillensis Ulrich, p. 85,  
Text-figs. 4a-b.
- 1925        Dystactocrinus constrictus (Hall), Ulrich,  
p. 87, Text-figs. 6b-e, p. 88.
- 1944        Dystactocrinus constrictus (Hall), Moore  
& Laudon, Pl. 52, fig. 11.

Primary type material—HMCZ 2165 (Hall, 1871, Pl. 1, figs. 13-14 and herein, Pl. 7, figs. 5-7) from Maysvillian strata at Cincinnati is the holotype of H. constrictus Hall, 1871.

Because D. constrictus is at present the only known species of Dystactocrinus, the specific diagnosis, description, and occurrence are the same as for the genus.

Discussion—D. constrictus, while having numerous features in common with Cincinnatiocrinus varibrachialis,

differs from it in having wider cup plates, the tendency to reduce IBrr from four or five to two or three, branches on every third or fourth IIIBr and higher, and the marked contrast in width of the arms and armlets. In the last three of these four respects, Dystactocrinus constrictus is more like the Cincinnati homocrinid Ectenocrinus simplex. It is, however, certainly a cincinnaticrinid and shows closer relation to Cincinnaticrinus pentagonus (which has a tendency to broaden cup plates and to reduce IBrr from four or five to three or four). In addition, both C. pentagonus and D. constrictus have broad columns. It appears that C. pentagonus gave rise to D. constrictus.

Ohioocrinus exilis Foerste, 1914 (p. 125, Pl. 1, fig. 7) has armlets that are markedly smaller than the arms and may be conspecific with D. constrictus, but the holotype (USNM 78718—Pl. 2, fig. 2), and only known specimen, consists only of arms, and assignment to D. constrictus is uncertain.

Genus Isotomocrinus Ulrich, 1925

- 1925      Isotomocrinus Ulrich, p. 86.  
 1944      Isotomocrinus Ulrich, Moore & Laudon, p. 149.  
 1962      Isotomocrinus Ulrich, Moore, p. 13, Text-fig. 5—2.

Type species—Isotomocrinus typus Ulrich, 1925 by original designation (1925, p. 87), although it is a junior synonym of Heterocrinus tenuis Billings, 1857.

Diagnosis—Cincinnati-crininae with isotomous branching.

Description—Isotomocrinus has the general features of the subfamily and, aside from its isotomous branching and anal sac, is like Cincinnati-crinus. The anal sac is tubular, as in Cincinnati-crinus, but is somewhat broader and much longer and composed of more facing plates (at least seven or eight). The sides of the dorsal cup (in lateral view) form the largest angle of all Cincinnati-crininae; this is a product of distally expanding BB (as in C. varibrachialis) and RR. In this connection, Isotomocrinus has C and D ray RR that are wider than in other Cincinnati-crinids and wider than other RR (in the A, B, and E rays) in single specimens. Thus, the C and D ray arms are far apart, which apparently makes room for the broad anal tube.

The IBrr<sub>1</sub> taper more and the IBrr<sub>2</sub> expand less, if at all, than in other Cincinnati-crinids, which makes for proportionally narrower arms; the arms are long with few

branches. There are two to six IBrr per ray and four to nine IIBrr (and higher series) per arm. Brachial variability seems to be similar to that in Cincinnati-crinus varibrachialis, both for individuals and for the genus (and species) in general.

The column is pentapartite with interr radial pentameres and with a pentagonal lumen having radially disposed points. The column is pentagonal near the cup and becomes gradually more rounded distally. There appear to be two sets of columnals of different size alternating in position proximally, but only one size distally. Distal columnals evidently become similar in size and shape with secondary overgrowth.

Occurrence—Kirkfieldian (? Black Riverian to Kirkfieldian, Shermanian, or Edenian; Rocklandian to Kirkfieldian, Shermanian, or Edenian; Kirkfieldian to Shermanian or Edenian). Isotomocrinus is known from the Hull beds of Kirkfield, Ontario; Hull, Sherman Fall, and/or Coburg beds of Ottawa and Montreal; the "Trenton limestone" at Trenton Falls, New York; and the Decorah shale, St. Paul, Minnesota (UM 9274). Billings (1857, p. 274; 1859, p. 50) described Heterocrinus tenuis from the "Trenton limestone" of Ottawa and Montreal (= Hull, Sherman Fall, and/or Coburg beds). Springer (1911, p. 25) alluded to the same species in the Hull crinoid beds at Kirkfield, Ontario. Wilson (1946, p. 32) listed

it from Hull (GSC localities 34 and 37), Sherman Fall (GSC locality 44), and Coburg (GSC localities 4, 9, 13, 38, 39, 52, and 53) beds of Ontario and Quebec. Ulrich (1925, p. 87) alluded to two undescribed species: one from "limestone of Black River age" of central Pennsylvania (? = pre-Rocklandian Hatter or Hunter limestones), another from "Upper Black River" of Wisconsin (? = unnamed pre-Rocklandian limestones or the Kirkfieldian Decorah shale). Isotomocrinus is common in the Hull crinoid beds at Kirkfield Quarry, Kirkfield, Ontario.

Discussion—Isotomocrinus appears to have been the progenitor of all Cincinnaticrininae, and possible of anomalocrinids, as well. Evolution of Isotomocrinus to Cincinnaticrinus occurred with alteration of isotomous to alternating heterotomous branching and shortening of the anal tube. Isotomocrinus may have arisen from Atopocrinus or Ectenocrinus; or, Isotomocrinus and Atopocrinus or Isotomocrinus and Ectenocrinus may share an as yet unknown common ancestor.

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Text-fig. 15. Isotomocrinus tenuis.

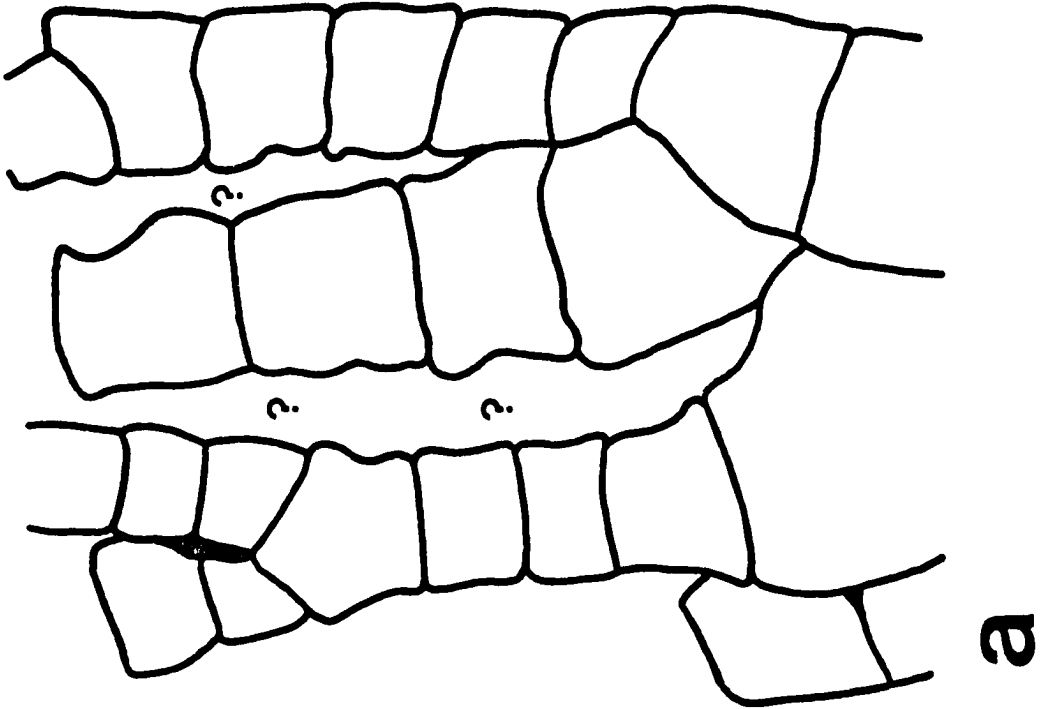
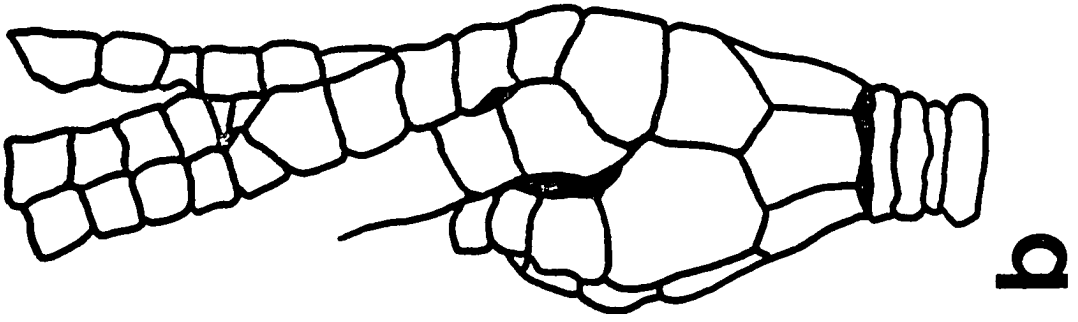
USNM S.2077a-b are the primary types of I. typus Ulrich, 1925, which is a junior synonym of Heterocrinus tenuis Billings, 1857.

a—camera lucida drawing of a CD interray view of USNM S.2077a, X22.8; areas with question marks contain what appear to be disarticulated anal backing plates;

b—camera lucida drawing of a CD interray view of USNM S.2077b, X11.4.

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- Isotomocrinus tenuis (Billings), 1857  
Pl. 8; Text-fig. 15.
- 1857 Heterocrinus tenuis Billings, p. 273.
- 1859 Heterocrinus tenuis Billings, Billings, p. 50,  
Pl. 4, figs. 6a-b, Pl. 10, figs. 1a-c.
- 1911 Heterocrinus tenuis Billings, Springer, p. 25.
- 1918 Heterocrinus tenuis Billings, Jaekel, p. 85,  
Text-fig. 79.
- 1925 Isotomocrinus typus Ulrich, p. 87, Text-figs. 5a-b.
- 1925 Heterocrinus juvenis Hall, Fritz, p. 10, Text-  
fig. 7.
- 1944 Isotomocrinus typus Ulrich, Moore & Laudon, Pl.  
52, fig. 11.
- 1946 Heterocrinus tenuis Billings, Wilson, p. 32.
- ?1971 Ectenocrinus n. sp. Steele & Sinclair, Pl. 16,  
figs. 10-11.
- 1973 Heterocrinus tenuis Billings, Warn, p. 10, Pl.  
1, fig. 1 (non figs. 2-19).

Primary type material—GSC 1438 (the only remaining of Billings's syntypes) was designated lectotype of H. tenuis by Wilson (1946, p. 32—Warn, 1973, p. 11-12). GSC 1438 was adequately illustrated by Warn (1973, Pl. 1, fig. 1) but is illustrated again here (Pl. 8, fig. 5). USNM S.2077a (Pl. 8, figs. 1&4) is the holotype of I. typus,

a junior synonym of Isotomocrinus tenuis. USNM S.2077b (Pl. 8, figs. 2&4) and USNM S.2077c (Pl. 8, figs. 3&4) are paratypes of I. typus. GSC 1438 is from the Kirkfieldian Hull beds at Ottawa, Ontario, while USNM S.2077a, b, and c are from the Kirkfieldian crinoid beds at Kirkfield, Ontario.

Because I. tenuis is at present the only known species of Isotomocrinus, the specific diagnosis, description, and occurrence are the same as for the genus.

Discussion—I. tenuis is known from the Trenton limestone of Kirkfield and Ottawa, Ontario and Montreal, Quebec. Numerous good specimens, mainly from Kirkfield, are housed in the collections of: Royal Ontario Museum, Geological Survey of Canada, United States National Museum, and University of Cincinnati Geological Museum (in the Kopf Collection).

The specimen figured by Steele and Sinclair (1971, Pl. 16, figs. 10-11) as a new species of Ectenocrinus appears to be a Cincinnati crinid. It resembles both I. tenuis and Cincinnatiocrinus varibrachialus but shows no arm branching—critical for differentiation between these two species. Because its occurrence is more reconcilable with I. tenuis than with C. varibrachialus, the author has tentatively referred it to I. tenuis. The specimen has a

more steeply conical cup than in other Isotomocrinus tenuis specimens and a smaller  $X_1$  than any other cincinnaticrinid.

A good case can be made for evolution of Cincinnati-crinus varibrachialus from Isotomocrinus tenuis with reduction of the anal tube and transformation of isotomous to alternating heterotomous branching. In fact, I. tenuis probably gave rise, directly or indirectly, to all other Cincinnaticrininae. Choosing a progenitor for I. tenuis is a greater problem. No known crinoid (other than a member of the Cincinnaticrininae) exhibits an obvious close morphological relationship with I. tenuis (including Atopocrinus, the only older cincinnaticrinid) to merit consideration as a progenitor of I. tenuis.

Genus Ohioocrinus Wachsmuth & Springer, 1886

- 1886        Ohioocrinus Wachsmuth & Springer, p. 208.
- 1889        Ohioocrinus Wachsmuth & Springer, Miller, p. 263.
- 1900        Ohioocrinus Wachsmuth & Springer, Wachsmuth,  
              p. 152.
- 1911        Ohioocrinus Wachsmuth & Springer, Springer, p. 27.
- 1913        Ohioocrinus Wachsmuth & Springer, Springer,  
              . p. 212.
- 1925        Ohioocrinus Wachsmuth & Springer, Ulrich, p. 90.
- 1962        Ohioocrinus Wachsmuth & Springer, Moore, p. 13,  
              Text-fig. 5—4a-d (4a, b, & d are from Ulrich,  
              1925, p. 90, Text-fig. 7a-c).

Type species—Heterocrinus laxus Hall, 1866 by original designation of Wachsmuth and Springer (1886, p. 208).

Diagnosis—Cincinnatiocrininae with spirally coiled anal sac and ten arms exhibiting alternating heterotomous branching.

Description—Like Cincinnatiocrinus, Ohioocrinus has an anal sac that is an armlike branch of four (or possibly five) facing plates (XX) off the C ray sR, with numerous small backing plates proliferated from the tegmen. In Cincinnatiocrinus the backing plates close around the back of the XX to form a short, straight tube; but in Ohioocrinus the backing plates extend away from, and beyond, the XX as a high, inflated, polygonally polyplated, high-spined

coil with wide whorls (Text-fig. 17). In contrast to Wachsmuth and Springer's (1886, p. 208) description of the anal sac as composed of "...numerous hexagonal pieces, arranged alternately, and in longitudinal rows," the backing plates are polygonal (quadrangular, pentagonal, hexagonal, or septagonal) and are apparently not arranged in definite rows or circlets. In other respects (column morphology, B and IBr shape, etc.) Ohioocrinus is like Cincinnatiocrinus.

Occurrence—Maysvillian. Ohioocrinus is known from the Fairview Formation from Cincinnati, Ohio and Madison, Indiana.

Discussion—For a time, the author thought Cincinnatiocrinus and Ohioocrinus to be congeneric, for it seemed that Ohioocrinus (specimens with spiral anal sacs) were simply Cincinnatiocrinus with preservation of the polyplated sac. This view was bolstered by Wachsmuth and Springer's (1886, p. 208) footnote to the description of their new genus Ohioocrinus:

"Ohioocrinus resembles Stenocrinus [a junior synonym of Heterocrinus but used for Meek's, 1873 concept of Heterocrinus that is herein called Cincinnatiocrinus] very closely, and can only be upheld by the form of the ventral tube. We [Wachsmuth and Springer] never saw the appendage of Stenocrinus [Cincinnatiocrinus], but Mr. S. A. Miller claims it to be distinct, and this induced us to make the separation."

However, so many beautifully preserved Cincinnatiocrinus with the anal sac ending as a short tube are now known that the two seem to be distinct, as Miller postulated.

Ulrich (1925, p. 90) described Ohioocrinus as having a dorsal cup structurally similar to those of Cincinnatiocrinus and Dystactocrinus but with great variation due to "breakage and irregular regeneration of parts." Ulrich did not know the repository of Hall's holotype (HMCZ 2167) of Heterocrinus laxus, type species of Ohioocrinus, but had at least six specimens (USNM 42304a-e and an unlocated specimen represented by Ulrich, 1925, Text-figs. 9 and 9a) which he had in 1882 used as the basis for his new species H. oehanus and which he thought were perhaps conspecific with H. laxus. For H. laxus, Ulrich substituted (at least conceptually) H. oehanus as the type species of Ohioocrinus. Three of the four best (of the six) syntypes of H. oehanus are abnormal specimens (Text-figs. 16a-b-c), which caused Ulrich to characterize Ohioocrinus as having great cup variability. This author, after comparing the types of H. laxus and H. oehanus, believes the two to be conspecific. H. oehanus is, then, a junior synonym of H. laxus.

Ohioocrinus evolved from Cincinnatiocrinus with elongation, inflation, and coiling of the tubelike anal sac and gave rise to no known successors.

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Text-fig. 16. Ulrich's (1882) abnormal specimens of Heterocrinus oehanus (junior synonym of Ohiocrinus laxus).

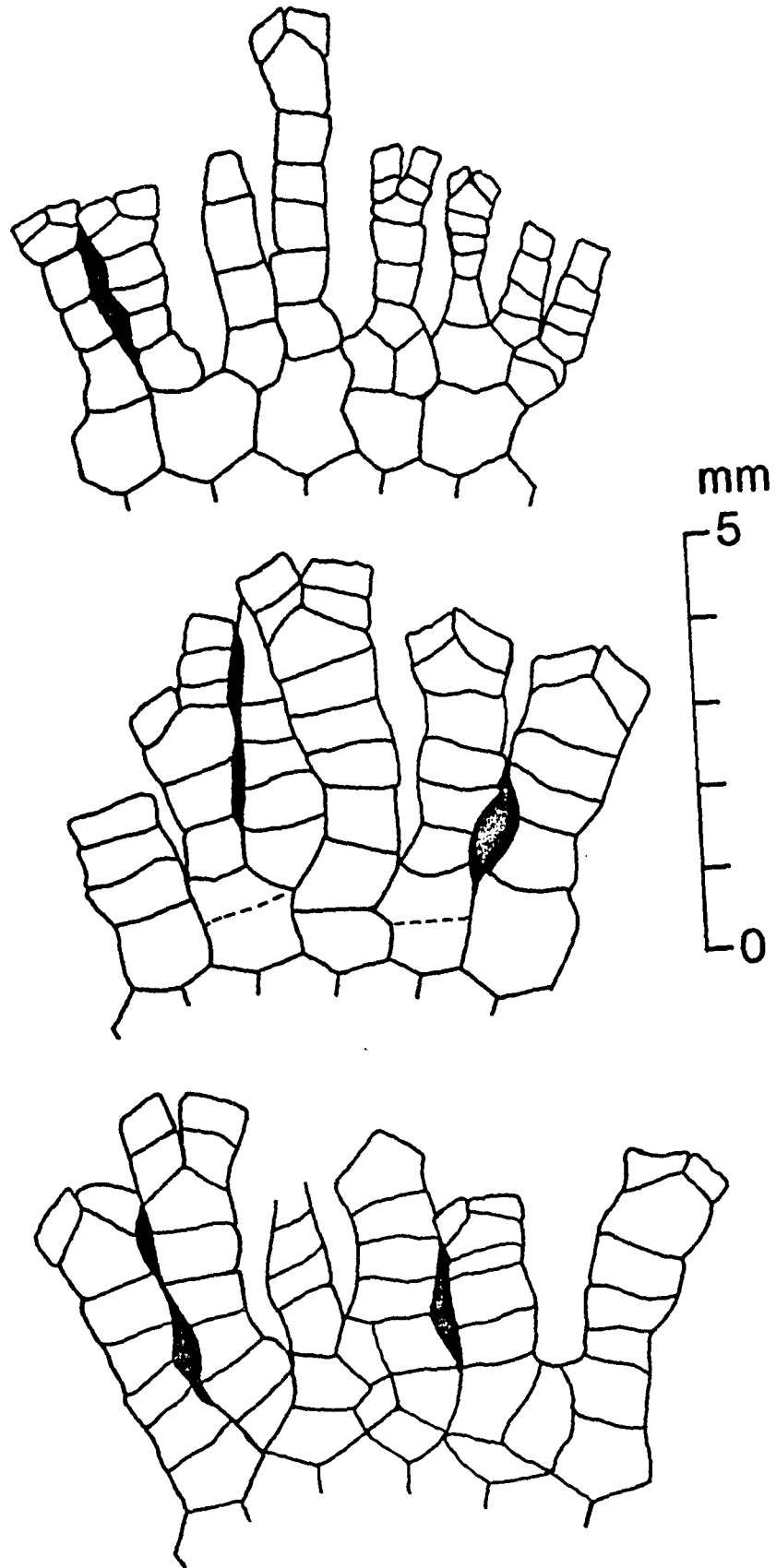
a—exploded diagram of USNM 42304a,

b—exploded diagram of USNM 42304b,

c—exploded diagram of USNM 42304c.

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Ohioocrinus laxus (Hall), 1871

Pl. 9; Text-figs. 16a-c.

- 1871 Heterocrinus laxus Hall, Pl. 1, fig. 15; Hall, 1872, Pl. 5, fig. 15.
- 1872 Heterocrinus laxus Hall, Hall, p. 211.
- 1873 Heterocrinus laxus Hall, Meek, p. 5, Pl. 1, fig. 12.
- 1882 Heterocrinus (Iocrinus) oehanus Ulrich, p. 175, Pl. 5, figs. 9, 9a-c.
- 1925 Ohioocrinus laxus (Hall), Ulrich, p. 90, Text-fig. 7a.
- 1925 Ohioocrinus oehanus (Ulrich), Ulrich, p. 90.
- 1962 Ohioocrinus laxus (Hall), Moore, Pl. 1, fig. 5.

Primary type material—HMCZ 2165 (Pl. 7, figs. 5-7) is the holotype of H. laxus Hall, 1871.

Diagnosis—Ohioocrinus with markedly heterotomous branching, i.e., with arms strikingly broader than the armllets.

Description—O. laxus has a distally expanding crown that widens uniformly and long arms with numerous branches (six to ten per arm). Each division series has three to seven Brr (four or five is most common). Number of Brr per division series appears to be variable, both in and among individuals, but not to the extent as in Cincinnatiocrinus varibrachialus. Whereas a single specimen of C. varibrachialus might have as many as four different

numbers of IBrr in the five rays (e.g., UCGM 40500 with the following IBr arrangement: A-2, B-4, C-4, D-3, E-5), a single specimen of Ohioocrinus laxus would have fewer different numbers of IBrr in five rays (e.g., HMCZ 2167 with: A-5, B-4, C-4, D-4, E-4). This diminished variability is apparently true also for higher division series. Thus, while total intraspecific variation in number of Brr per division series in O. laxus is as great as in Cincinnatiocrinus varibrachialus, variation in single individuals is greater in C. varibrachialus. Armlets given off at the axillaries bifurcate two or three times and appear to reach the tips of the arms.

Occurrence—Maysvillian. O. laxus is known from at least seven specimens from the Fairview Formation at Cincinnati. Hall (1872, p. 211) described Heterocrinus laxus from the "Hudson-river group" at Cincinnati. Ulrich (1882, p. 176) described H. oehanus, a junior synonym of O. laxus, from "on the hills back of Cincinnati, Ohio at an elevation of about 325 feet above low-water mark in the Ohio river" (= Fairview Formation).

Discussion—USNM 42304a (Pl. 9, fig. 9; Text-fig. 16a) is herein designated lectotype and the specimen figured by Ulrich (1882, Pl. 5, figs. 9, 9a) and USNM 42304b-e (Text-figs. 16b-c) lectoparatypes of H. oehanus Ulrich, 1882, a junior synonym of H. laxus Hall, 1871, the

type species of Ohioocrinus. The specimen represented by figures 9 and 9a has not been located, although a note, apparently in Ulrich's handwriting, accompanying the USNM type specimens purports: "Remainder of Oeh's spms. [specimens] are at Yale." However, search at Peabody Museum of Natural History, Yale University (1973) failed to reveal other specimens.

O. laxus arose from Cincinnatiocrinus varibrachialis by elongation, inflation, and coiling of the anal sac and elongation of the arms, either directly, or with O. brauni as intermediary.

O. laxus and Dystactocrinus constrictus may really be conspecific. Wachsmuth and Springer (1886, p. 208) placed Heterocrinus constrictus Hall, 1872 (type of Dystactocrinus Ulrich, 1925) in their new genus Ohioocrinus (with H. laxus Hall, 1871 as type). O. laxus has broad arms and narrow armlets, as does D. constrictus, and the BB approach marked hexagonality (as in D. constrictus). One specimen (UCGM 23048; Pl. 9, fig. 1) of O. laxus particularly resembles D. constrictus. At present, however, the two are considered distinct, for examination (including X-ray) of specimens referred here to D. constrictus has brought to light no spiral anal sac.

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Text-fig. 17. Ohioocrinus brauni.

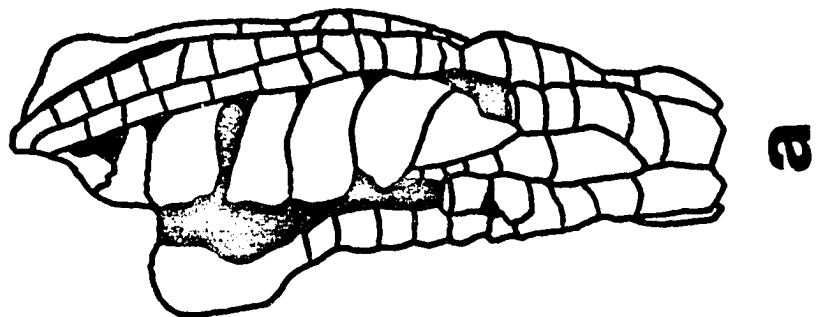
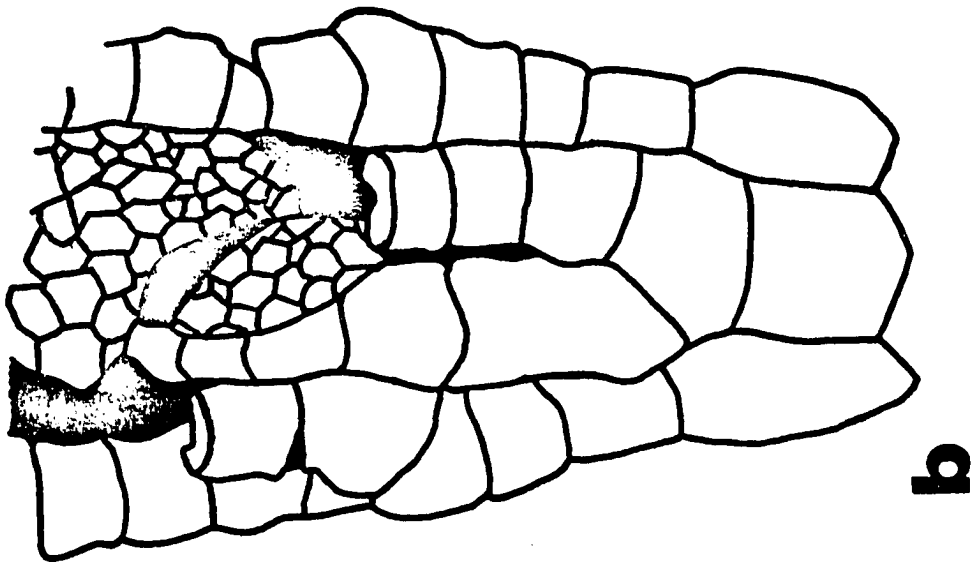
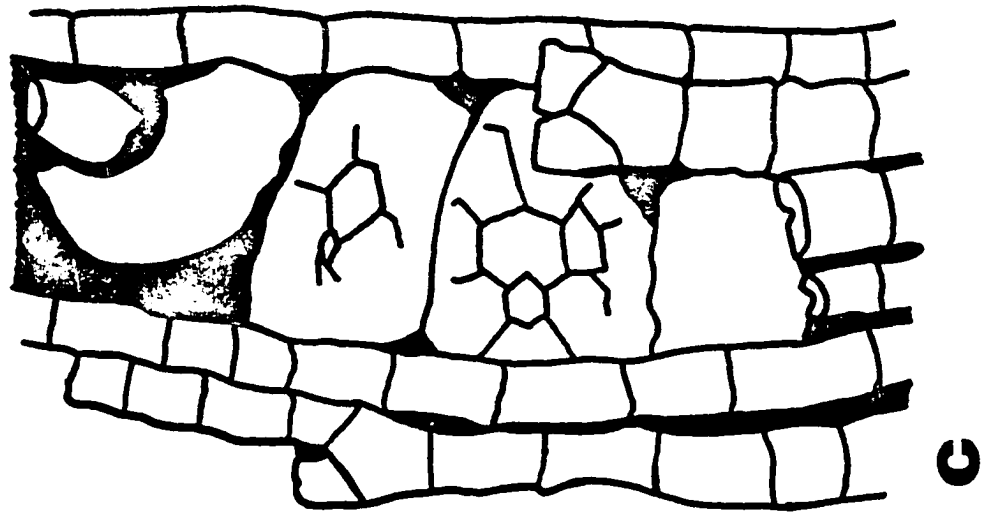
a—camera lucida drawing of a CD interray view of  
USNM S.2082b, X8.36;

b—the same from a slightly different angle, X21.50.

c—camera lucida drawing of an E ray view of USNM  
S.2082a, X21.50.

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Ohioocrinus brauni Ulrich, 1925

Pl. 10; Text-fig. 17.

1925 Ohioocrinus brauni Ulrich, p. 90, Text-figs. 7b-c.

Primary type material—USNM S. 2082a (Ulrich's Text-fig. 7b) and S.2082b (Ulrich's Text-fig. 7c) are syntypes of O. brauni. USNM S.2082b (Pl. 10, figs. 1-3; Text-fig. 17) is herein designated lectotype and USNM S.2082a (Pl. 10, figs. 4-6; Text-fig. 17) lectoparatype of O. brauni. Both are Maysvillian from Madison, Indiana.

Diagnosis—Ohioocrinus with nearly isotomous branching, i.e., with the arms and armlets of about the same width.

Description—O. brauni has arms with three or four branches per arm and three to four (commonly four?) Br per division series. Br variability is apparently smaller than in O. laxus. Arms and armlets are about the same size, but armlets (given off on alternate sides beginning with the first abradially or away from the ray) continue unbranched to the tips of the arms.

Occurrence—Maysvillian. O. brauni is known from only two specimens from the Fairview Formation at Madison, Indiana.

Discussion—O. brauni, while differing from O. laxus, may not really be distinct; it is conceivable that specimens referred to O. brauni might be juveniles of O. laxus. This will remain uncertain, however, until our knowledge of ontogeny of O. laxus approximates that known for Cincinnati-

crinus varibrachialus, Cincinnatiocrinus pentagonus, and Ectenocrinus simplex is known for species of Ohioocrinus. O. brauni arose from C. varibrachialus by elongation, inflation, and coiling of the anal sac, either directly, or with O. laxus as intermediary.

## Subfamily Atopocrininae (new herein)

Diagnosis—Cincinnatiidae with a conical (less steeply than in the Cincinnatiidae) dorsal cup; with unequal-sized compound RR (in the C and E rays) with the C ray R somewhat shorter and the E ray R somewhat taller than the nearly equal-sized fused RR (in the A, B, and D rays); and with the anal series as an armlike branch off the C ray  $IBr_1$  (termed brachianal by Moore, 1962).

Genus Atopocrinus Lane, 1970

1970      Atopocrinus Lane, p. 14.

Type species—Atopocrinus priscus Lane, 1970 by original designation (p. 14)—Whiterockian of Utah.

Because Atopocrinus is at present the only genus in the Atopocrininae, the generic diagnosis is the same as for the subfamily.

Description—Atopocrinus has equidimensional, pentagonal BB that expand distally. The E ray sR extends nearly to the distal margins of the A and B ray IBrr<sub>2</sub>. The C ray IBr<sub>1</sub> (brachianal) has a truncated left shoulder to support X<sub>1</sub>; succeeding IBrr are narrower and rest on the remaining distal edge of the IBr<sub>1</sub>. There are two arms in the A and B rays, but branching in the C, D, and E rays is unknown. The A and B ray IBrr are as wide as the underlying RR (the A and B ray IBrr are quite low rectangles), but the C and E (and apparently D) ray IBrr are much narrower (the C and E ray IBrr are low rectangles, but are nearly square) than the underlying RR. The IBrr and one or two most proximal IIBrr lack armllets; the next ten or so Brr, however, have armllets given off from every Br on alternate sides, with the first given off as an inner branch; succeeding Brr have armllets given off one or both sides of each Br. Where there are two armllets per Br, they are offset to give the appearance of derivation from an

alternating heterotomous condition by fusion of two adjacent Brr. Armlet facets on the oral surfaces of the arms are connected to the ambulacral groove by oblique rooves that join the ambulacral groove alternately (Text-fig. 18c). The stem is circular, pentapartite with radial pentameres, and has a proximal portion that tapers rapidly distally (as in members of the Homocrininae).

Occurrence—Whiterockian. Atopocrinus is known from a single specimen from the M zone (of Hintze, 1951) of the Kanosh Shale near Ibex, Utah.

Discussion—Among inadunates, branching of the anal series off the third radial plate of the C ray, rather than off the first or second, is a rarity. The only other known inadunate with this C ray plate arrangement is Peniculocrinus Moore, 1962. However, Atopocrinus differs from Peniculocrinus in having compound RR in two rays rather than in all five. Possession of an anal series as a branch off the C ray IBr<sub>1</sub> (brachianal) is a primitive feature and supports the view that the anal series originated as a C ray arm branch that came to be modified and incorporated into the calyx.

Atopocrinus's branching in the distal portions of the arms is unique among disparids and appears to have been derived from an alternating heterotomous condition by fusion of adjacent Brr in sets of two. Derivation from

alternating heterotomous is not only supported by food groove configuration of bipinnulate Brr but also by arm ontogeny (unbranched--alternating heterotomous--bipinnulate Brr).

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Text-fig. 18. Atopocrinus priscus.

All are of USNM 165240 after Lane (1970).

a—E ray view, X2.83;

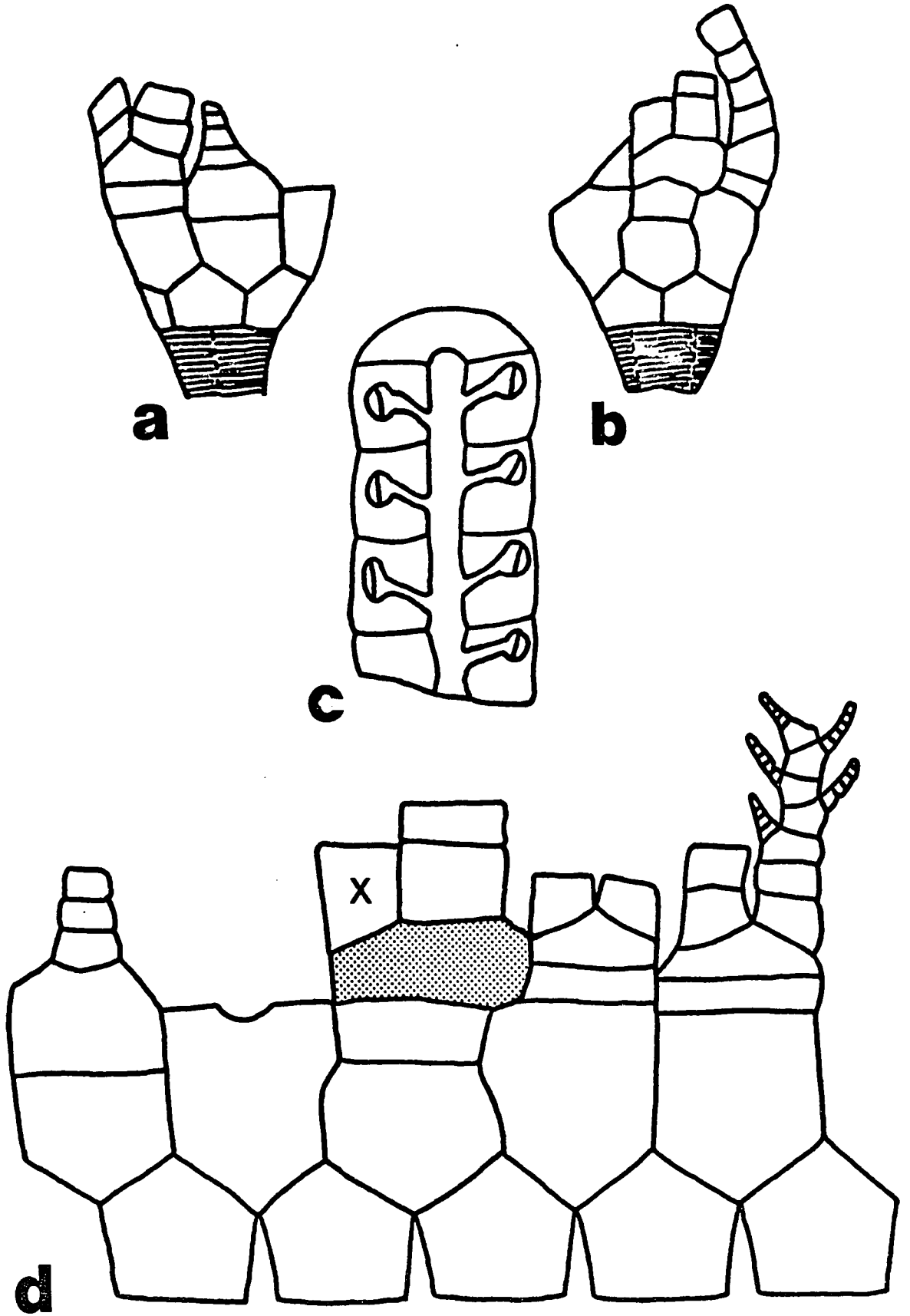
b—C ray view, X2.83;

c—ventral view of arm, X15;

d—exploded diagram, X4.25.

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Atopocrinus priscus Lane, 1970

Pl. 2; Text-fig. 18.

1970 Atopocrinus priscus Lane, p. 15; p. 8, Text-  
fig. 2f-j; p. 11, Pl. 1, figs. 4-6.

Primary type material—The holotype and only known specimen of A. priscus is USNM 165240.

Because A. priscus is presently the only known species of Atopocrinus, the specific diagnosis, description, occurrence, and discussion are the same as for the genus.

## Superfamily Homocrinacea Kirk, 1914

(nom. transl. ex Homocrinidae Kirk, 1914)

Diagnosis—Disparid inadunate crinoids with a steeply conical dorsal cup having undivided RR in two rays (in the A and D rays) and compound RR in three rays (in the B, C, and E rays).

Description—The homocrinacean dorsal cup has five symmetrically or four asymmetrically and one symmetrically pentagonal BB, about equal in size. The distal left corner of the C ray sR and the distal right corner of the D ray R are truncated to accommodate  $X_1$ , which is a branch off the C ray. Succeeding XX are quadrangular and backed by numerous small polygonal plates to form a tubular (and armlike) anal sac (this is unknown in Ibexocrinus but known to varying degree in other homocrinaceans). Each of the five RR supports a series of quadrilateral IBrr.  $IBr_1$  articulates with the underlying R by imobile suture (and is thus fixed) along its entire proximal surface.

Discussion—Kirk (1914) erected the family Homocrinidae for Homocrinus. Kirk was of the opinion that, while Homocrinus is related to the Heterocrinidae, especially to Ectenocrinus (this was, of course, prior to Ulrich's, 1925, transferral of Ectenocrinus to the Homocrinidae), the Heterocrinidae could not house Homocrinus. Jaekel (1918, p. 54), perhaps still suffering under the mis-

conception that Homocrinus was dicyclic, added his new genera Nassoviocrinus, Jahnocrinus, and Ascocrinus (all dicyclic and none closely related to Homocrinus). Ulrich (1925) added Ectenocrinus Miller, 1889 and his new genera Drymocrinus, Daedalocrinus, and Sygcaulocrinus. Drymocrinus is considered as a junior synonym of Ectenocrinus. Lane (1970, p. 12) added his new genus Ibexocrinus. Ubaghs (1953) elevated Kirk's family Homocrinidae to superfamily Homocrinacea. The superfamily Homocrinacea as now envisioned, then, contains Homocrinus, Daedalocrinus, Ectenocrinus, Ibexocrinus, and Sygcaulocrinus.

Homocrinaceans are morphologically similar to cincinnaticrinaceans. Homocrinaceans and cincinnaticrinaceans have steeply conical cups, similar arm size and shape, and similar placement of  $X_1$  (except for Atopocrinus); homocrinaceans have three compound RR (in the B, C, and E rays) and only two fused RR (in the A and D rays); Ectenocrinus, Ibexocrinus, and Sygcaulocrinus have alternating heterotomous branching as do the Cincinnaticrinacea (except Isotomocrinus, which has isotomous branching).

Homocrinaceans occur in Whiterockian to Niagaran rocks of western, central, mideastern, and eastern United States and mideastern Canada. They have been found in Edenian and Maysvillian strata in the tristate Ohio-Kentucky-Indiana

area (around Cincinnati); in Shermanian and Edenian rocks of northwestern New York; in the Edenian of southern Pennsylvania; in Kirkfieldian to Edenian rocks of the Ottawa-St. Lawrence lowland of Canada; in Richmondian strata of Iowa; in Whiterockian strata of Utah; and in Niagaran rocks of New York.

Family Homocrinidae Kirk, 1914

Because this is the only family of the Homocrinacea, familial characters are the same as for the superfamily. Two subfamilies are envisioned here. The subfamily Homocrininae contains Homocrinus, Ectenocrinus, Ibexocrinus, and Sygcaulocrinus. The subfamily Daedalocrininae is erected to accommodate Daedalocrinus, which is somewhat removed, morphologically and presumably phylogenetically, from other homocrinids.

Subfamily Homocrininae Kirk, 1914

(nom. transl. ex Homocrinidae Kirk, 1914)

Diagnosis—Homocrinidae with equal-sized compound RR (in the B, C, and E rays) somewhat taller than the equal-sized fused RR (in the A and D rays) and with a round column that tapers rapidly distally just below the dorsal cup.

Description—Members of the subfamily Homocrininae have  $Ibrr_1$  that taper distally and  $IBrr_2$  that expand slightly distally. The column is round with a pentagonal lumen and tapers rapidly distally just below the calyx.

(Ibexocrinus is an exception to both statements. Ibexocrinus has rectangular  $IBrr_1$  and  $IBrr_2$ , and the column of Ibexocrinus, while round, tapers more gradually than in other Homocrininae.).

Discussion—Apparently, members of the Homocrininae have a point of columnal generation at the base of the rapidly tapering proximal portion of the column rather than at the base of the dorsal cup, the common location of columnal addition (aside from distal insertion). It appears that a trend in Homocrininae is to incorporate proximal columnals into the calyx. This feature is undeveloped in Ibexocrinus, the oldest of the Homocrininae; well-developed in Ectenocrinus; and best-developed in Sygcaulocrinus and Homocrinus, the youngest of the Homocrininae.

Members of the Homocrininae occur in Whiterockian to Niagaran rocks of western, central, mideastern, and eastern United States and mideastern Canada. They have been found in Edenian and Maysvillian strata around Cincinnati; in Shermanian and Edenian rocks of northwestern New York; in the Edenian of southern Pennsylvania; in Edenian rocks of the Ottawa-St. Lawrence lowland of Canada; in Richmondian strata of Iowa; in Whiterockian strata of Utah; and in Niagaran rocks of New York.

Genus Homocrinus Hall, 1852

- 1852 Homocrinus Hall, p. 185 (partim).
- 1859 Homocrinus Hall, Hall, p. 102 (partim).
- 1880 non Homocrinus Hall, Wachsmuth & Springer, p. 77,  
Text-fig. 6.
- 1886 non Homocrinus Hall, Wachsmuth & Springer, p. 144.
- 1889 Homocrinus Hall, Miller, p. 255 (partim).
- 1893 non Homocrinus Hall, Bather, p. 101.
- 1900 non Homocrinus Hall, Bather, p. 178.
- 1900 non Homocrinus Hall, Wachsmuth, p. 155.
- 1907 non Homocrinus Hall, Slocum, p. 289.
- 1913 non Homocrinus Hall, Springer, p. 217.
- 1914 Homocrinus Hall, Kirk, p. 476.
- 1925 Homocrinus Hall, Ulrich, p. 94.
- 1944 Homocrinus Hall, Moore & Laudon, p. 145.
- 1962 Homocrinus Hall, Moore, p. 7, Text-fig. 1—8;  
p. 10; p. 11, Text-fig. 3—4.

Type species—Homocrinus parvus Hall, 1852 by subsequent designation of Miller (1889, p. 255), although this fact had been muddled for some time.

Diagnosis—Homocrininae with tall (about twice as tall as broad and about as tall as the RR), symmetrical, and similarly shaped BB; with the five rays unbranched; and with proximal columnals short, of about equal height.

Description—Specimens belonging to the genus Homocrinus are minute (height of the dorsal cup is less than two and one-half millimeters—commonly about one and three-fourths millimeters). The BB are tall, about one-half the height of the dorsal cup. The A and D ray RR are fused; the B, C, and E ray RR are slightly taller and compound, divided into iRR and sRR of about equal size. The anal structure beyond  $X_1$  is unknown but is presumably similar to other homocrinids, cincinnaticrinids, and related forms (i.e., the anal series is probably an armlike branch off the C ray).

According to Kirk (1914, p. 477), each of the five arms has a food groove roofed over by an alternating biseries of tiny cover plates. The  $IBrr_1$  articulate along their entire proximal surfaces with the underlying RR and are apparently fixed; they are shaped like inverted truncated cones and are shorter than succeeding Brr; the  $IBrr_1$  are about as broad as tall. Succeeding IBrr are about twice or more as tall as broad and shorten somewhat distally; they are wider at the articulations than at the middles of the plates.

The column tapers rapidly in a distal direction just below the cup. Kirk (1914, p. 477-478) related that just distal to the tapering portion is an area in which two sizes of columnals alternate and that this alternating

portion grades distally into an area with columnals of uniform size. Specimens examined in connection with this study show a round column that gradually enlarges distally below the rapidly tapering portion with all columnals observable approximately equal in size to their neighbors.

Occurrence—Niagaran. Homocrinus is known from the Rochester Shale around Lockport, New York (according to Ringueberg, 1888, p. 269 from the top of the lower third of the Rochester Shale).

Discussion—The nature of Homocrinus was mistakenly thought to be dicyclic until Kirk's (1914) restudy of Homocrinus. Thus, in the synonymy, all pre-1914 references were to Homocrinus as being dicyclic; those with partim were with H. parvus (monocyclic) as type, while those with non were with a dicyclic type species (and with H. parvus at most only listed as an included species). From 1914 to the present, references have been to Homocrinus as monocyclic with H. parvus as type (and only) species.

Hall (1852, Paleontology of New York, vol. 2) included in his new genus Homocrinus two new species, H. parvus (p. 185, Pl. 41, figs. 1a-c) and H. cylindricus (p. 186, Pl. 41, figs. 2a-c, 3a-c), and two species described by Hall in the first volume of the Paleontology of New York (1847), Poteriocrinus alternatus (p. 83) and P. gracilis (p. 84). In 1859 Hall added two new species (both

dicyclic), Homocrinus scoparius (p. 102, Pl. 1, figs. 1-9) and H. proboscidualis (p. 138, Pl. 85, figs. 24-25).

Wachsmuth and Springer (1880, p. 77-78) attempted to make H. scoparius type species of Homocrinus:

"The typical specimens which Hall used for description were most unsatisfactory, that of H. parvus being evidently a very young individual, while those of H. cylindricus are very imperfectly preserved. In Hall's corrected list of New York fossils he seems to have given up both Dendrocrinus and Homocrinus, as he groups the species of both under Poteriocrinus [no such reference has been located; indeed, Hall, 1859a, p. 82, listed H. parvus and H. cylindricus in unaltered fashion]. In 1861 [1859b], however, he described two new species under Homocrinus, from good specimens. They are not Poteriocrinus, for they have no pinnulae, nor Cyathocrinus, for they have an extra intercalated plate above the basals; nor Dendrocrinus for that plate is not radial; but their affinities are the closest with the latter, with which they agree in all principal characters. We [Wachsmuth and Springer] therefore regard Homocrinus as a subgenus under Dendrocrinus [dicyclic]...with Homocrinus scoparius Hall [dicyclic] as type...."

However, designation of H. scoparius Hall, 1859 as type

species of Homocrinus Hall, 1852 is not allowable under article 69 of the Code (Stoll, et al., 1964), for H. scoparius is not one of the (four) originally included nominal species.

In 1889 Miller (p. 255) listed H. parvus as type species of Homocrinus, and this is accepted as legitimate designation of the type species. Later, Bather (1893, p. 101), rejected H. parvus as type species:

"There is certainly nothing in the description or figures of H. parvus to show that it is congeneric with H. cylindricus, and it seems very doubtful to what genus it belongs; it is therefore better to ignore this species, at all events until it has been properly described, and not take it, as Mr. S. A. Miller has done, for the type-species of the genus."

Bather then suggested that H. cylindricus be considered type species of Homocrinus.

It is apparent that, until Kirk's (1914) revision of Homocrinus, the genus was considered to be dicyclic, largely because three different species (H. parvus, monocyclic; H. cylindricus, dicyclic; and H. scoparius, dicyclic) were considered the type by various authors, and because the monocyclic nature of H. parvus was not known (in fact, twenty dicyclic species have, mostly

before 1914, been referred to Homocrinus, and only one monocyclic species, H. parvus, has ever been included). Kirk, applying the convention of page priority, chose H. parvus as type species (apparently Kirk did not consider Miller's, 1889, listing of H. parvus as the type adequate, perhaps because no one after Miller, 1889, and before Kirk, 1914—e.g., Bather, 1893, had either) and illustrated the monocyclic nature of H. parvus. He erected the new dicyclic genus Lasiocrinus with H. scoparius as type for some of the dicyclic forms formerly referred to Homocrinus. Kirk berated some authors' choice (e.g., Wachsmuth and Springer's, 1880) of a species not included among those in the original description of the genus for the type and farsightedly argued for the need for rules in paleontology to restrict "...the powers of subsequent writers in revising the original author's conception of the genus...." (Kirk, 1914, p. 474). Kirk's (1914) work caused H. parvus to be accepted as the type and put an end to over fifty years of confusion of the nature of Homocrinus.

The diminutiveness of H. parvus has led some crinoid specialists (e.g., Wachsmuth and Springer, 1880) to view specimens attributed to H. parvus as juveniles of some other species with a radically different adult form. However, many specimens, all tiny, have been found; no

gradation in morphology away from the common Homocrinus parvus form has been observed, and no morphologically reasonable potential adult is known from the same strata. It appears that adults of H. parvus are minute.

Homocrinus differs from other Homocrininae mainly in having five unbranched arms and taller BB. As (Kirk, 1914, p. 479) suggested, Homocrinus would make a good ancestor for cincinnaticrinids (Kirk said heterocrinids); it would also be a good ancestor for homocrinids. However, its age (Niagaran) precludes its being anything but a successor to known homocrinids and cincinnaticrinids. Probably Homocrinus was a precursor of haplocrininitids (Devonian), which have similar structure in the radial circlet and unbranched arms, and pisocrinids (Silurian-Devonian), which have modified homocrinid cup structure and unbranched arms.

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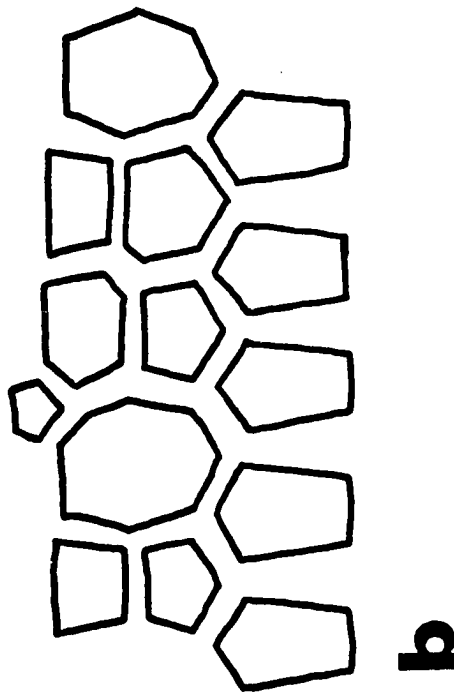
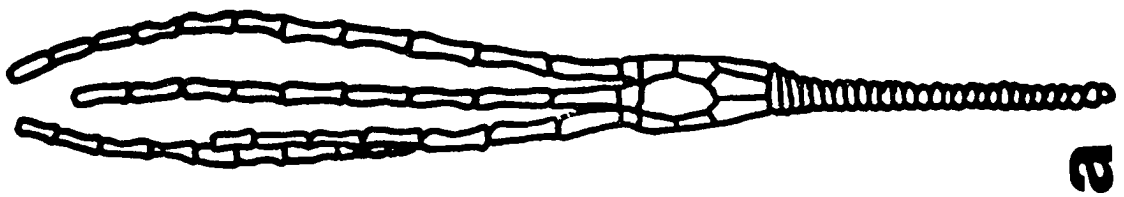
Text-fig. 19. Homocrinus parvus.

a—A ray view, X12 (after Kirk, 1914);

b—exploded diagram (after Kirk, 1914).

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Homocrinus parvus Hall, 1852

Pl. 11; Text-fig. 19.

- 1852 Homocrinus parvus Hall, p. 185, Pl. 41, figs. 1a-f; Kirk, 1914, Pl. 42, figs. 6-7.
- 1914 Homocrinus parvus Hall, Kirk, p. 476, Pl. 42, figs. 1-5, 8; Ulrich, 1925, p. 93, Text-figs. 10a-b (mislabelled 10a-a); Moore & Laudon, 1943, Pl. 1, figs. 4a-b; Moore & Laudon, 1944, Pl. 53, figs. 4a-e.
- 1920 Homocrinus parvus Hall, Springer, Pl. 4, fig. 22 (an illustration of Lecanocrinus nitidus with H. parvus entangled among its arms).
- 1944 Homocrinus parvus Hall, Moore & Laudon, Pl. 52, fig. 7.

Primary type material—AMNH 1705a, b, and c (all from the Rochester Shale, Lockport, New York) are syntypes of H. parvus. 1705a (Pl. 11, figs. 1-2) is herein designated lectotype and 1705b and c (Pl. 11, figs. 3-4) lectoparatypes of H. parvus Hall, 1852.

Because H. parvus is at present the only known species of Homocrinus, the specific diagnosis, description, occurrence, and discussion are the same as for the genus.

Genus Ectenocrinus Miller, 1889

- 1847 Heterocrinus Hall, p. 278 (partim).
- 1850 Heterocrinus Hall, D'Orbigny, p. 24 (partim).
- 1857 Heterocrinus Hall, Pictet, p. 329 (partim).
- 1857 Heterocrinus Hall, Billings, p. 271.
- 1859 Heterocrinus Hall, Billings, p. 48.
- 1866 Heterocrinus Hall, Hall; p. 14; Hall, 1872, p. 210, (partim).
- 1873 Heterocrinus Hall, Meek, p. 1 (partim).
- 1879 Heterocrinus Hall, Zittel, p. 358 (partim).
- 1880 Heterocrinus Hall, Wachsmuth & Springer, p. 68 (partim).
- 1886 Heterocrinus Hall, Wachsmuth & Springer, p. 205; Cumings, 1908, p. 713.
- 1886 Stenocrinus Wachsmuth & Springer, p. 207 (partim).
- 1889 Ectenocrinus Miller, p. 242; Cumings, 1908, p. 712.
- 1889 Heterocrinus Hall, Miller, p. 252 (partim).
- 1893 Heterocrinus Hall, Bather, p. 25.
- 1900 Ectenocrinus Miller, Bather, p. 146, fig. 58—3.
- 1900 Heterocrinus Hall, Wachsmuth, p. 152.
- 1900 Ectenocrinus Miller, Wachsmuth, p. 152.
- 1902 Heterocrinus Hall, Jaekel, p. 1100.
- 1910 Heterocrinus Hall, Grabau & Shimer, p. 50 (partim).
- 1911 Ectenocrinus Miller, Springer, p. 26.

- 1913      Heterocrinus Hall, Springer, p. 212.
- 1913      Ectenocrinus Miller, Springer, p. 212 (partim).
- 1918      Heterocrinus Hall, Jaekel, p. 86.
- 1924      Ectenocrinus Miller, Slocum, p. 337.
- 1925      Ectenocrinus Miller, Ulrich, p. 94; Moore,  
            1962, p. 11, Text-fig. 3—2a.
- 1925      Drymocrinus Ulrich, p. 96; Moore, 1962, p. 11,  
            Text-fig. 3—6.
- 1925      Heterocrinus Hall, Fritz, p. 10 (partim).
- 1943      Ectenocrinus Miller, Moore & Laudon, p. 27,  
            Text-fig. 3.
- 1944      Ectenocrinus Miller, Moore & Laudon, p. 145.
- 1944      Drymocrinus Ulrich, Moore & Laudon, p. 145.
- 1962      Ectenocrinus Miller, Moore, p. 7, Text-fig.  
            1—6; p. 10.
- 1962      Drymocrinus Ulrich, Moore, p. 10.

Type species—Heterocrinus simplex Hall, 1847 by original designation (Miller, 1889, p. 242).

Diagnosis—Homocrininae with short (about half as tall as broad) BB; one symmetrically pentagonal B (in the BC interray) and four asymmetrically pentagonal BB; with five rays bifurcating isotomously to form ten arms; and with proximal columnals short, of about equal height.

Description—Ectenocrinus has short, irregularly pentagonal BB; BB that underlie a compound R and a simple

R have one sloping upper side (under the compound R) and one horizontal upper side (under the fused R); a single B (in the BC interray) underlies two compound RR (in the B and C rays) and has two sloping upper sides. The compound RR (in the B, C, and E rays) are inverted pentagons, divided into a taller sR and shorter iR; compound RR are slightly taller than fused RR, which are tall rectangles. The distal left corner of the C ray sR and distal right corner of the D ray R are truncated to accommodate the armlike anal series.  $X_1$  is an inverted, nearly parallel-sided, pentagon that supports a series of rapidly tapering distally XX backed by numerous small polygonal plates to form a tube.

Ectenocrinus has two IBr in each ray.  $IBr_1$  is a low rectangle nearly twice as broad as high;  $IBr_1$  articulates along its entire proximal surface with the underlying R and is fixed.  $IBr_2$  is a pentagonal axillary supporting two arms (to form a total of ten arms) with alternating heterotomous branching with the first armlets given off away from the ray.

Occurrence—Kirkfieldian or Shermanian to Richmondian. Ectenocrinus is known from the Kope and Fairview Formations (Edenian and Maysvillian at Cincinnati) in the Ohio-Kentucky-Indiana tristate area; from the "Trenton limestone", Trenton Falls, New York, Ottawa, Ontario, and

Montreal, Quebec; and from the Maquoketa Formation (Richmondian?) of Iowa. In addition, Ulrich (1925, p. 95) reported a few specimens from the Curdsville formation (Kirkfieldian?) of central Kentucky, but this report requires verification.

Discussion—Ectenocrinus is the genus that for over half a century was confused with Heterocrinus (see discussion of Cincinnatiocrinus varibrachialis, p. Two species, E. simplex and E. geniculatus, are recognized. H. geniculatus is the type species of Drymocrinus Ulrich, 1925, but the differences between H. geniculatus and E. simplex appear to be specific rather than generic. Drymocrinus, then, is a junior synonym of Ectenocrinus. Ectenocrinus may have been the progenitor, directly or indirectly, of all homocrinids, although Ibexocrinus or Daedalocrinus could have served this function.

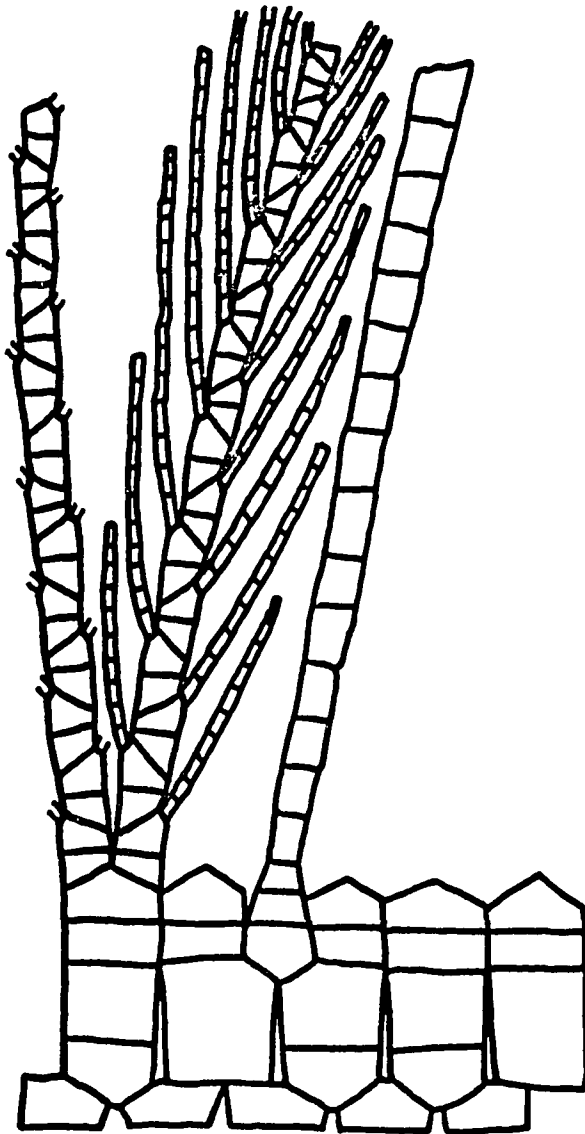
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Text-fig. 20. Exploded diagram of Ectenocrinus simplex  
(after Ulrich, 1925).

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- Ectenocrinus simplex (Hall), 1847  
Pls. 12-14 ; Text-fig. 20.
- 1847 Heterocrinus simplex Hall, p. 280, Pl. 76,  
figs. 2a-d; Cumings, 1908, p. 720.
- 1857 Heterocrinus simplex Hall, Billings, p. 271.
- 1859 Heterocrinus canadensis Billings, p. 48, Pl.  
4, figs. 5a-d.
- 1871 Heterocrinus simplex Hall, Hall, Pl. 1, figs.  
11-12; Hall, 1872, Pl. 5, figs. 11-12.
- 1873 Heterocrinus simplex Hall, Meek, p. 7, Pl. 1,  
figs. 4a-b, 5a-b; Cumings, 1908, Pl. 4, figs.  
10, 10a; Grabau & Shimer, 1910, p. 502, Text-  
fig. 1814; Moore & Laudon, 1943, Pl. 1, figs.  
5a-b; Moore & Laudon, 1944, Pl. 53, figs.  
8a-b; Moore, 1962, Pl. 1, fig. 2a.
- 1873 Heterocrinus simplex var. grandis Meek, p. 9,  
Pl. 1, figs. 6a-b, 7a-c; Grabau & Shimer,  
1910, p. 502, Text-fig. 1814; Moore, 1962,  
Pl. 1, figs. 2b-c.
- 1909 Ectenocrinus canadensis (Billings), Wood, p. 22.
- 1910 Heterocrinus simplex Hall, Grabau & Shimer, p. 502.
- 1914 Ectenocrinus grandis (Meek); Foerste, p. 124,  
Pl. 1, figs. 8a-d.
- 1924 Ectenocrinus raymondi Slocum, p. 337, Pl. 29,  
figs. 5-9.

1925        Ectenocrinus simplex (Hall), Ulrich, p. 95,  
               Text-fig. 11; Moore & Laudon, 1944, Pl. 52,  
               fig. 7.

1926        Ectenocrinus raymondi Slocom, Thomas  
               and Ladd, p. 14, Pl. 2, fig. 2.

Primary type material—AMNH 656/2a, b, c, d, e, f, g,  
 and h are syntypes. 656/2a (Hall, 1847, Pl. 76, figs.  
 2a and d; herein Pl. 12, figs. 1-2) is herein designated  
 lectotype and 656/2 b, c, d, e, f, g, and h lectoparatypes  
 of Heterocrinus simplex Hall, 1847.

Diagnosis—Ectenocrinus having straight arms made up  
 of numerous syzygal pairs, each pair composed of an armlet-  
 bearing epizygal above articulating syzygally below with a  
 hypozygal.

Description—E. simplex, as well as having the generic  
 (Ectenocrinus) features of two Brr in the IBr series, has  
 two Brr in each succeeding series. Diagonal sutures,  
 alternating in direction of slope, separate each division  
 series, with an armlet (pinnule) given off at the highest  
 part of every second Br (hypozygal). The armlets are not  
 visible when the arms are folded tightly together, which  
 is commonly the case (presumably for the same reason that  
 cincinnaticrinacean arms are usually folded—see cincin-  
 naticrinacean discussion, p. 50). Young (small) E. simplex  
 have tall Brr, while older (larger) individuals have

shorter Brr. Apparently Brr are first secreted as tall quadrilateral ossicles which then grow faster laterally than vertically and so get proportionally shorter.

Distal to the rapidly tapering proximal part (a homocrininan character), the column of Ectenocrinus simplex shows a columnar gradation similar in some respects to that of Cincinnatiocrinus varibrachailus. Just below the the rapidly tapering portion of the column, columnals are short and nearly equal in size to the few adjacent columnals on either side. The column enlarges gradually distally, and the section of equal-sized short columnals grades into a zone with columnals of two different sizes: smaller (shorter and narrower) columnals alternating with larger (taller and broader) columnals (Pl. 13, fig. 3)

The column is tripartite with the trimeres of each columnal disposed in the following manner: one occupies the EA and AB interrays, another lies in the BC interray and the C ray, and the third occupies the D ray and the DE interray (Text-fig. 21). Each trimere is in optical continuity; therefore, the trimeres are apparently not derived from a pentameric condition by fusion of two sets of two plates (such derivation is obvious in the basal circlets of many crinoids having only three BB as well as blastoids). Derivation from a pentameric condition by fusion of two sets of two pentameres is also precluded

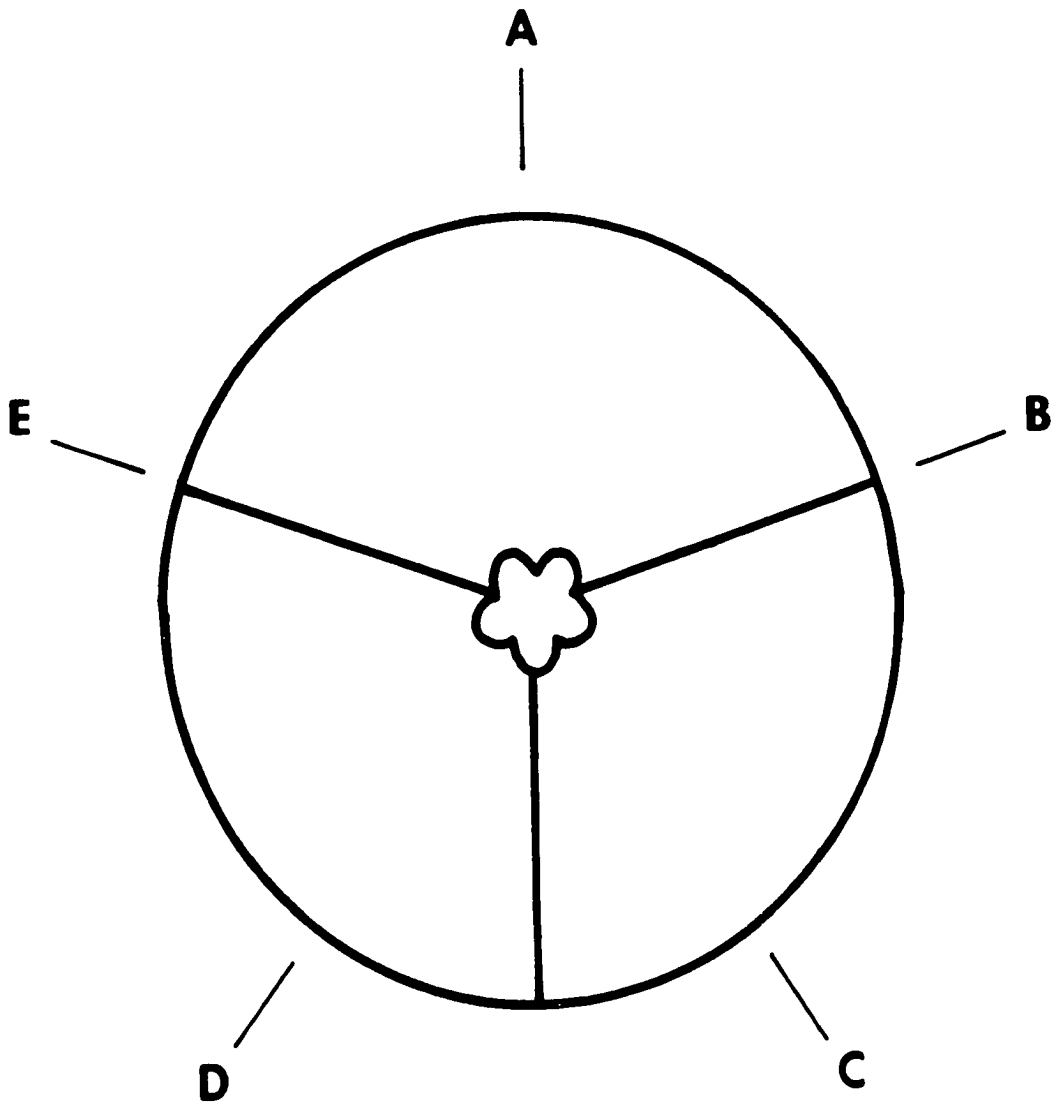
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Text-fig. 21. Disposition of trimeres and lobes of the axial canal in Ectenocrinus simplex. Rays are lettered A, B, C, D, and E. With intertrimeric sutures in the B ray, CD interray, and E ray, E. simplex has trimeres disposed as follows: one occupies the EA and AB interrays, another lies in the BC interray and C ray, the third occupies the D ray and DE interray. Although E. simplex has trimeres, its axial canal has five lobes, all directed interradially.

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by the unique disposition of the inter-trimeric sutures. One is interrarial (in the CD interrarry) and two are rarial (in the B and E rays) (in monocyclic crinoids with pentapartite columns, interpentameric sutures are all interrarial, whereas in dicyclic and pseudomonocyclic crinoids with pentapartite columns, all interpentameric sutures are rarial). The axial canal in Ectenocrinus simplex, however, is pentalobate with the lobes directed interrarially (Text-fig. 21).

Occurrence—Kirkfieldian or Shermanian to Richmondian. E. simplex is known from the Kope and Fairview Formations around Cincinnati; the Trenton limestone around Ottawa and Montreal and at Trenton Falls, New York; the Martinsburg Formation of southern Pennsylvania; and the Maquoketa Formation at Clermont, Iowa. Hall (1847, p. 280) described Heterocrinus simplex from "...the soft shaly portions of the Blue limestone of Ohio at Cincinnati, equivalent in position to the Hudson-river group of New York." Billings (1857, p. 271-273) described specimens he found in the "Trenton limestone, Ottawa and Montreal" as H. canadensis, which is now a junior synonym of E. simplex. Wood (1909, p. 23) reported E. canadensis (Billings) from the "...lower part of Trenton formation [at] Frankfort, Kentucky." Slocom and Foerste (1924, p. 337-339) described E. raymondi, a junior synonym of E. simplex,

from the lower part of the Maquoketa Formation at Clermont, Iowa. Additionally, numerous good specimens are known from the Kope Formation around Cincinnati and the Martinsburg Formation of southern Pennsylvania (especially from Swatara Gap).

Discussion—Small Ectenocrinus simplex and lichenocrinid bases are a common association, and juvenile E. simplex probably have a lichenocrinid holdfast. However, because Cincinnatiocrinus varibrachialus and E. simplex usually occur together (in the Kope), nothing definite can be said of the E. simplex holdfast. In these occurrences, however, there are holdfasts that differ from those that can probably be referred to C. varibrachialus in two respects: they are somewhat larger (with diameters of about four to five mm as opposed to two to two and one-half mm) and the plates of the polyplated upper wall are well demarcated (unlike the C. varibrachialus holdfast which is obscurely plated).

It appears that in adult E. simplex new columnals are added at the base of the rapidly tapering proximal column and intercalated distally, for the smallest (cup height of 1.4 mm) individual has a rapidly tapering portion—as do all others (the largest has a cup height of 7.0 mm). A growth zone, similar to that at the base of the cup in most disparids, some distance below the cup (at the base of the rapidly tapering portion of the column) is a feature

common to homocrinids and apparently unique among disparids. Evidently, a trend in homocrinids is to incorporate a few proximal columnals into the calyx. The interradi-  
lumen extensions suggest that Ecternocrinus simplex is a true monocyclic crinoid, but the strange trimeric distribution suggests both monocyclicism and pseudomonocyclicism.

The taxonomic splitting of E. simplex (as shown in the synonymy) was largely due to lack of awareness of population variation during the classical period of paleontology. Billings (1857, p. 273) reported that his specimens were conspecific with Heterocrinus simplex:

"I had drawn up the description of our Canadian specimens as above, under the impression that they were of a species different from that of the Hudson River Group [H. simplex]. But having since seen Professor Hall's collection, I now believe that ours are identical. .... Should, however, it hereafter be found that ours is different from the Hudson River species, I beg that it may be called H. Canadensis...."

Hall (1847, p. 280) had incorrectly described the proximal part of the column of H. simplex as pentagonal (it is really round), and Billings (1859, p. 48-49) used the Canada specimens' having round columns as the differentium

between Heterocrinus canadensis and H. simplex. Meek (1873, p. 9-10) described H. grandis as a subspecies of H. simplex; the subspecies was reported to be larger than H. simplex with shorter Brr than in H. canadensis. Slocom (1924, p. 337-339) described Ectenocrinus raymondi as like E. grandis but with shorter Brr, more slender pinnules, and transverse grooves on the dorsal sides of the arms. Size of the crown and height of Brr are poor taxobases, for individuals grow larger and Brr grow faster laterally than vertically, so that older individuals have proportionally shorter Brr than younger individuals. The transverse grooves in the single specimen (CFM UC24701) of E. raymondi may be a unique feature, but E. raymondi is considered to be conspecific with E. simplex.

E. simplex probably gave rise to E. geniculatus with addition of a third Br in each division series and geniculation of the arms; E. simplex may have given rise to Sygcaulocrinus typus with heightening of the BB, heightening and fusion of the three most proximal columnals, and addition of Brr in each division series; and perhaps E. simplex produced Homocrinus parvus with heightening of the BB and elimination of branching.

Ectenocrinus geniculatus (Ulrich), 1879

Pls. 14-16.

- 1879      Heterocrinus geniculatus Ulrich, p. 16, Pl. 7,  
          figs. 13, 13a-c.
- 1925      Drymocrinus geniculatus (Ulrich), Ulrich, p.  
          96, Text-figs. 12a-b; Moore & Laudon, 1944,  
          Pl. 52, fig. 7.
- 1925      Drymocrinus manitouliensis Foerste, p. 101, Pl.  
          7, fig. 7.
- 1925      Drymocrinus sp. Foerste, Pl. 7, fig. 2.

Primary type material—The holotype (and that specimen figured by Ulrich, 1879, Pl. 7, fig. 13) is UCGM 36313. A natural mold of the holotype is USNM 42219a. USNM 42219b, c, d, e, f, g, h, i, j, k, and l and CFM UC8829 are paratypes. All are lowest Edenian at Cincinnati.

Diagnosis—Ectenocrinus with geniculate (zig-zag) arms and two to four IIBr and higher (more commonly two or three than four).

Description—E. geniculatus has IBrr<sub>1</sub> that taper distally and IBrr<sub>2</sub> that expand slightly distally. The IBrr<sub>1</sub> are shaped like upright, truncated cones. Thus, the junction of the IBrr<sub>1</sub> and IBrr<sub>2</sub> forms a constriction in the crown that marks the position of the tegmen, above which the arms become free. The IBr and higher axillaries expand noticeably distally. Whereas the armlets in E.

simplex are usually concealed when the arms are folded together (which is usually the case), the armllets in Ectenocrinus geniculatus are obvious in folded specimens for the zig-zag nature of the arms reveals them.

The column is round and expands gradually distally. Near the cup, the columnals are short, but they become gradually taller distally until they are nearly as tall as wide (Pl. 15, fig. 6). Ulrich (1925, p. 96) reported that the column is quinquepartite, but this has not been verified (the nature of the column is difficult to determine from specimens in the type suite; the column is probably pentapartite, as Ulrich said, but may be tripartite, as in E. simplex). The axial canal is pentalobate with the five lobes directed interradially.

Occurrence—Edenian. At the base of the Kope Formation in the immediate Cincinnati vicinity. Sheguiandah Formation northeast of Tamarack Point and at St. Hyacinthe in the Manitoulin Island (in Lake Huron) area of Canada.

Discussion—Ulrich (1925, p. 96) described the column of E. geniculatus as being cirrose and illustrated it (p. 96, Text-fig. 12b) as being profusely so. One of the paratypes (USNM 422191) has numerous appendages that resemble cirri but are apparently broken armllets lying along its column (none appear to be attached to the column). No specimen examined for this report possesses either cirri

or attachment sites for cirri, and the column of Ectenocrinus geniculatus is evidently not cirrose.

Ulrich (1925, p. 96) also described the anal sac as like that of Ectenocrinus (E. simplex) but wider and with "...a series of thin quadrate plates on either side of the median series." Available evidence, however, indicates that E. geniculatus has an anal sac like that of E. simplex (a series of facing XX backed by numerous small polygonal plates).

E. geniculatus was probably a short-lived offshoot from E. simplex that gave rise to no successors. Such evolution would have required only geniculation of the arms and slight increase in number of Brr in the IIBr, and higher, division series.

Genus Ibexocrinus Lane, 19701970 Ibexocrinus Lane, p. 12.

Type species—Ibexocrinus lepton Lane, 1970 by original designation (p. 12).

Diagnosis—Homocrininae with symmetrically pentagonal BB about as tall as wide and equal in size; with five rays bifurcating isotomously to form ten arms; and with proximal columnals short, of about equal height.

Description—Ibexocrinus has compound RR divided about equally into iRR and sRR. The anal tube, aside from the first two XX, is unknown but is probably like that of Ectenocrinus. Each ray apparently has two IBrr, with isotomous branching on the IBrr<sub>2</sub>. IBr<sub>1</sub> is a low rectangle nearly twice as broad as high articulating with the underlying R along its entire distal surface. IBr<sub>2</sub> is a pentagonal axillary supporting two equal-sized arms. Succeeding branching is alternating heterotomous with the first armlets on the outside (or abradially). In subsequent division series there are six to nine IIBrr and higher. The stem is round and expands only slightly proximally just below the dorsal cup; it is pentapartite with radial pentameres.

Occurrence—Whiterockian. Ibexocrinus is known from a single specimen from the M zone (of Hintze, 1951), Kanosh Shale, near Ibex, Utah.

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Text-fig. 22. Ibexocrinus lepton.

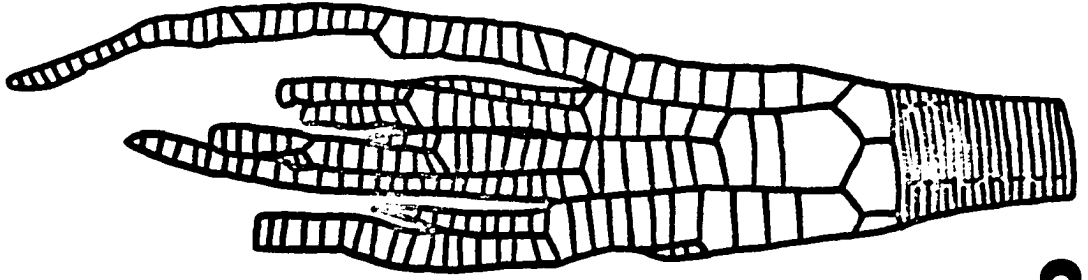
USNM 165249 (both after Lane, 1970).

a—CD interray view, X10.5;

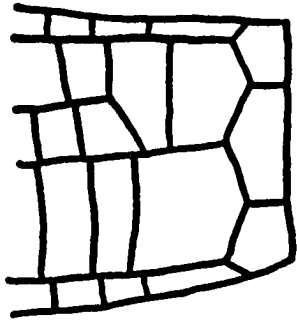
b—A ray view, X5.6.

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**b**



**a**

Ibexocrinus lepton Lane, 1970

Pl. 16, figs. 4-6; Text-fig. 22.

1970 Ibexocrinus lepton Lane, p. 13; p. 8, Text-  
figs. 2b-c; p. 11, Pl. 1, fig. 1.

Primary type material—The holotype and only known specimen of Ibexocrinus lepton Lane, 1970 is USNM 165239.

Because I. lepton is presently the only known species of Ibexocrinus, the specific diagnosis, description, occurrence, and discussion are the same as for the genus.

Genus Sygcaulocrinus Ulrich, 1925

- 1925      Sygcaulocrinus Ulrich, p. 98.  
 1944      Sygcaulocrinus Ulrich, Moore & Laudon, p. 145.  
 1962      Sygcaulocrinus Ulrich, Moore, p. 11, Text-  
           figs. 3—7a-b (b is Ulrich, 1925, p. 93,  
           Text-fig. 10b).

Type species—Sygcaulocrinus typus Ulrich, 1925 by original designation (Ulrich, 1925, p. 99).

Diagnosis—Homocrininae with tall BB, about one and one-half times as tall as broad; with one symmetrically pentagonal B (in the BC interray) and four asymmetrically pentagonal BB; with five rays bifurcating isotomously to form ten arms; and with proximal columnals inflated, greatly taller than adjacent (mor distal) columnals.

Description—Sygcaulocrinus has irregularly pentagonal BB; BB that underlie a compound R and a simple R have one steeply sloping upper side (under the compound R) and one nearly horizontal upper side (under the fused R). A single B (in the BC interray) underlies two compound RR and has two sloping upper sides. The compound RR (in the B, C, and E rays) are inverted pentagons, divided into a taller sR and a shorter iR; compound RR are taller than fused RR, but unlike Homocrinus and Ibexocrinus, which have the proximal points of the RR even (at the same level of the cup) and the distal edges of the

compound RR higher, or Ectenocrinus, which has compound RR with the distal edges higher and the proximal points lower than those of the fused RR, the distal edges of all RR in Sygcaulocrinus are even, and the proximal points of the compound RR are lower than the proximal points of the simple RR. Only  $X_1$  of the anal series is known; it is an inverted, distally tapering pentagon inserted into the notch formed by the truncated shoulders of the C and D ray RR.

Sygcaulocrinus has two IBrr in each ray.  $IBr_1$  articulates along its entire proximal surface with the underlying R and tapers somewhat distally.  $IBr_2$  is a pentagonal axillary supporting two arms. Branching and number of Brr per division series beyond this isotomous division is unknown except for USNM 89876 (the holotype of S. typus).

The most distinctive feature of Sygcaulocrinus is the "exploded" nature of the proximal columnals. The most proximal columnals (usually three) are wider and higher than distally adjacent columnals. As in other Homocrininae, this proximal portion of the column tapers distally. The column is evidently round, although it is unknown beyond (distal to) the first five or six most proximal columnals.

Occurrence—Richmondian. Maquoketa Formation from Fort Atkinson, Iowa.

Discussion--Ulrich (1925, p. 98-99) described and illustrated a number of features for Sygcaulocrinus that cannot be verified from known specimens: 1) a tripartite column, 2) alternating heterotomous branching, 3) three to six IIBrr and higher, and a tiny  $X_1$  lying in a similar-sized notch at the junction of the C and D ray RR. The author has been unable to establish the tripartite nature of the column, and only the holotype exhibits branching or number of Brr beyond the IBr axillaries, but number of IIBrr and branching pattern is difficult to determine from this specimen. However,  $X_1$  and the proximal column has been observed in a number of specimens.  $X_1$ , and the notch formed by the truncated corners of the C and D ray RR, seems to be quite a bit larger than Ulrich reported (Ulrich probably described  $X_1$  as minute because  $X_1$  of the holotype has been rotated and only the northeast corner of the plate juts through sediment enclosing it.

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Text-fig. 23. Sygcauloocrinus typus.

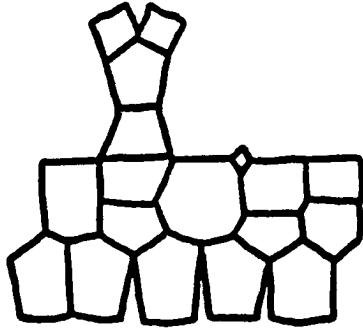
a—exploded diagram (after Ulrich, 1925);

b—camera lucida drawing of USNM 89876, D ray view, X4;

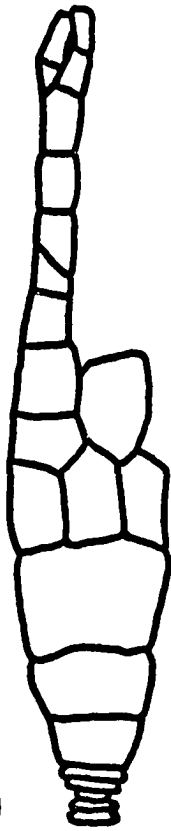
c—D ray view, X about 3 (after Ulrich, 1925).

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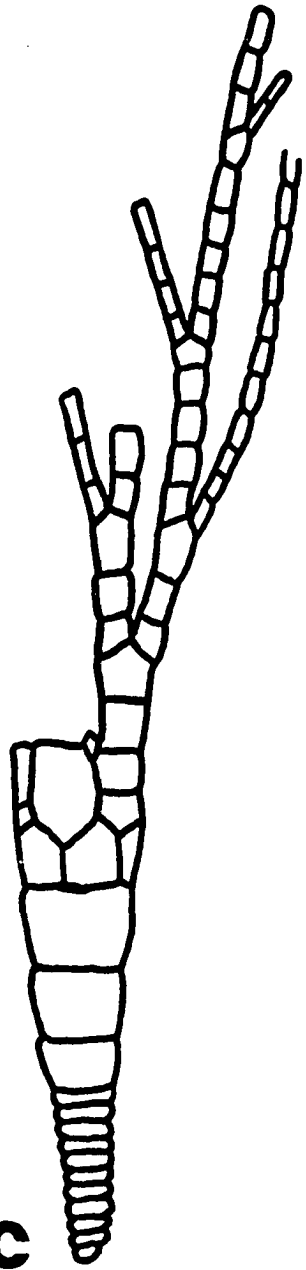
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**a**



**b**



**c**

Sygcaulocrinus typus Ulrich, 1925

Pl. 17; Text-fig. 23.

1925 Sygcaulocrinus typus Ulrich, p. 90, Text-figs. 10a-b (? mislabelled 10b-b); Moore & Laudon, 1944, Pl. 52, fig. 7.

1926 Ectenocrinus elongatus Thomas & Ladd, p. 12, Pl. 2, figs. 3-8, Pl. 5, figs. 3-4.

Primary type material—The holotype of S. typus Ulrich, 1925 is USNM 89876.

Because S. typus is presently the only known species of Sygcaulocrinus, the specific diagnosis, description, occurrence, and discussion are the same as for the genus.

## Subfamily Daedalocrininae (new herein)

Diagnosis—Homocrinidae with the dorsal cup made up of strongly interlocking RR; with the compound RR somewhat taller than the fused RR, except for the B ray R, which, although compound, is the same height as the fused RR; with five rays bifurcating isotomously to form ten arms after which branching is endotomous; and with a pentagonal column without a proximal tapering portion.

Because this is a monogeneric subfamily, other features are discussed under Daedalocrinus.

Genus Daedalocrinus Ulrich, 1925

- 1925      Daedalocrinus Ulrich, p. 97.  
 1944      Daedalocrinus Ulrich, Moore & Laudon, p. 145.  
 1962      Daedalocrinus Ulrich, Moore, p. 10.

Type species—Daedalocrinus kirki Ulrich, 1925 by original designation (p. 97), although it is a junior subjective synonym of Heterocrinus bellevillensis Billings, 1883.

Because the genus Daedalocrinus is presently the only known member of the subfamily Daedalocrininae, the generic diagnosis is the same as for the subfamily.

Description—Daedalocrinus has equi-dimensional, symmetrically pentagonal BB of about equal size. The arms are long and have numerous branches; each arm has as many as ten armllets. Armllets are unbranched and extend to the arm tips. The genus has three to five IBrr per ray (apparently four is most common). Like members of the Cincinnaticrininae, number of Brr in each division series appears to be variable, both among different rays in single individuals and among the same rays in different individuals. Branching beyond the IBr axillaries is quite variable with armllets given off from every third to seventh Br. That is, a single specimen might have an arm with five IIBrr, three IIIBrr, and seven IVBrr.

The column is also like that of members of the cincinnaticrininae. It is pentapartite with radial pentameres, has a pentagonal lumen with interradian angles, and is pentagonal proximally, with gradation distally from pentagonal to round.

Occurrence—Kirkfieldian. Daedalocrinus is known from the Hull crinoid beds of Belleville and Kirkfield, Ontario. Billings (1883, p. 50) described Heterocrinus bellevillensis from the "Trenton limestone" at Belleville, Ontario (= Hull beds); Ulrich (1925, p. 97) reported its, and another species' (D. kirki, considered a junior synonym of D. bellevillensis), occurrence in the "Lower Trenton crinoid beds", Kirkfield, Ontario (= Hull crinoid beds at Kirkfield, Ontario, where it is evidently fairly common).

Discussion—Daedalocrinus was described by Ulrich (1925, p. 97) for inadunates with a conical cup with three compound and two fused RR and with ten arms branching endotomously (a feature noted by Billings, 1883, p. 50 for H. bellevillensis). Ulrich (1925) placed Daedalocrinus in the Homocrinidae.

In some respects, Daedalocrinus resembles crinoids not in the Homocrinidae. It has endotomous branching like Geraocrinus, an anomalocrinid, and a column and variable number of Brr per division series like members of the Cincinnaticrininae.

Springer (1911, p. 27) reported that Kirkfield material in the United States National Museum collection makes it evident that Heterocrinus bellevillensis has a convoluted anal sac, which confirms its referral (by Springer) to Ohiocrinus. Ulrich (1925, p. 97-98), using the same material as Springer had, described the anal sac as large and balloon-shaped. The author has examined a number of well-preserved specimens in the Kopf collection (at the University of Cincinnati) and has perused the USNM cincinnaticrinids and homocrinids, types and non-types (although not looking specifically to solve this problem), but has not found evidence to corroborate Springer's or Ulrich's observations (indeed, only one of the at least twelve syntypes of Daedalo-  
crinus kirki has been located). A note (in Springer's or Ulrich's handwriting) accompanying USNM S.2141 lists twelve specimens collected from Kirkfield, Ontario in 1905 by Edwin Kirk. However, M. W. Moodey has added—on March 16, 1934—the comment that she has "located only what is in this tray [USNM S.2141].").

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Text-fig. 24. Daedalocrinus bellevillensis.

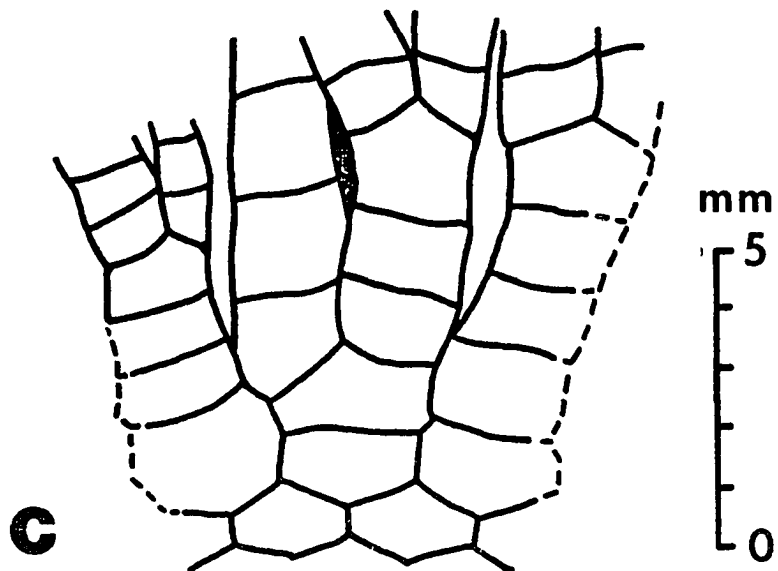
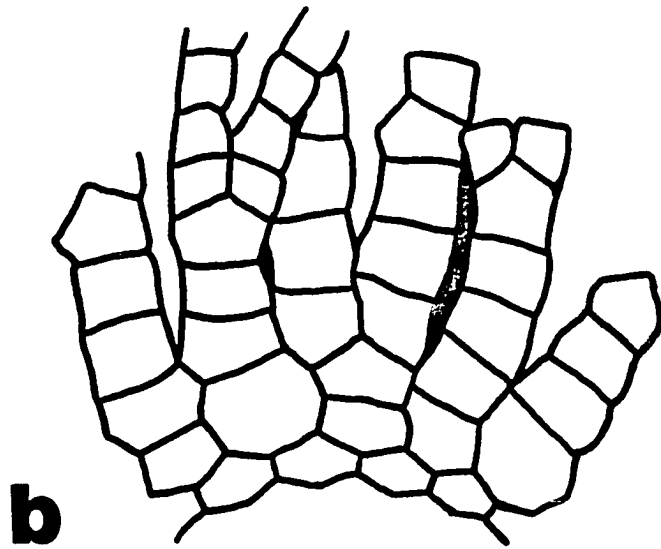
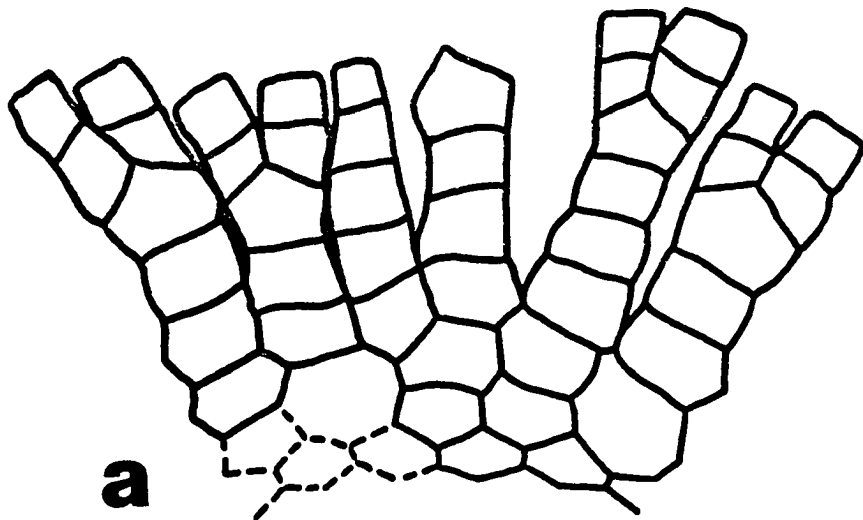
a—exploded diagram of UCGM K.36696a,

b—exploded diagram of UCGM K.36696b,

c—exploded diagram of the posterior side of the proximal part of the crown of USNM S.2141 (lecto-type of Daedalocrinus kirki, a junior synonym of Heterocrinus bellevillensis).

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Daedalocrinus bellevillensis (Billings), 1883

Pl. 18; Text-fig. 24.

- 1883 Heterocrinus bellevillensis Billings, p. 49,  
three figures (neither numbered or lettered)  
on a single unnumbered plate.
- 1900 Heterocrinus bellevillensis Billings, Bather,  
p. 146, Text-fig. 58—2.
- 1911 Ohiocrinus bellevillensis (Billings), Springer,  
p. 26.
- 1925 Daedalocrinus kirki Ulrich, p. 97; p. 98, Text-  
figs. 13a-c.
- 1944 Daedalocrinus kirki Ulrich, Moore & Laudon, Pl.  
52, fig. 11.

Primary type material—GSC 1439 is the holotype of Heterocrinus bellevillensis Billings, 1883. USNM S.2141, the only known of Ulrich's syntypes (and luckily the best), is herein designated lectotype of Daedalocrinus kirki Ulrich, 1925, a junior synonym of D. bellevillensis.

Because D. bellevillensis is at present the only known species of Daedalocrinus, the specific diagnosis, description, and occurrence are the same as for the genus.

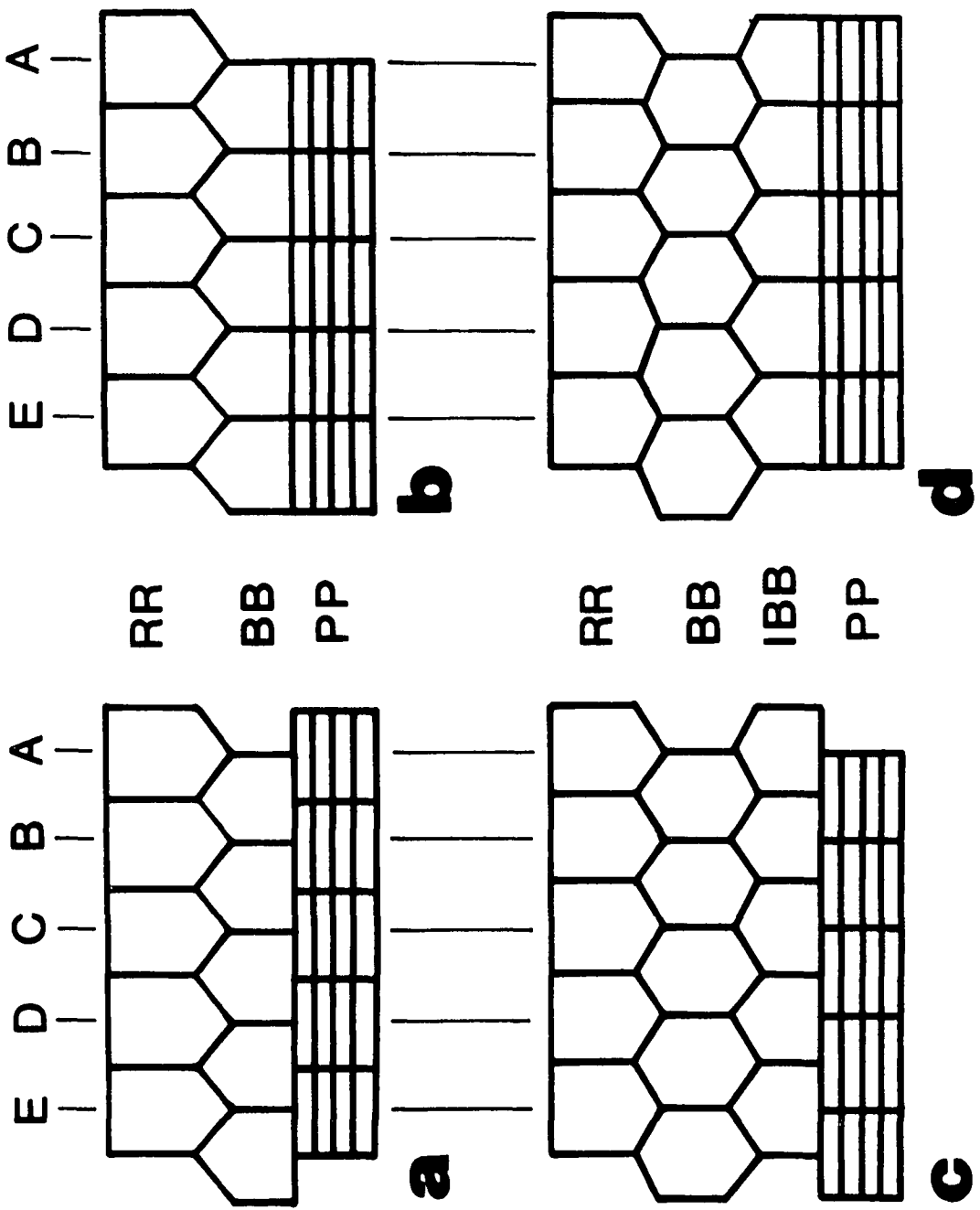
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Text-fig. 25. Relationship of dorsal cup plates and column pentameres in monocyclic, pseudomonocyclic, dicyclic, and pseudodicyclic crinoids. a) monocyclic, b) pseudomonocyclic, c) dicyclic, and d) pseudodicyclic. Rays are lettered A, B, C, D, and E. RR = radials; BB = basals; IBB = infrabasals; and PP = pentameres. Normally, pentameres of the column alternate in position with the lowest circlet of cup plates (i.e., monocyclic and dicyclic—a and c); however, crinoids that have lost or added IBB (pseudomonocyclic and pseudodicyclic—b and d) have column pentameres directly underlying the lowest circlet of cup plates.

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## Remarks on morphology

The disposition of pentameres in the columns of Cincinnatiocrinus, Dystactocrinus, Isotomocrinus, Ohioocrinus, Atopocrinus, Ibexocrinus, and Daedalocrinus shows that they are true monocyclic (as opposed to pseudomonocyclic) crinoids. Monocyclic crinoids have radial pentameres and column angles and interrarial lumen angles, while dicyclic and pseudomonocyclic (monocyclic demonstratably derived from dicyclic by loss of IBB) crinoids have interrarial pentameres and column angles and radial lumen angles (Text-figs. 25 and 26). These crinoids (Table 6) have pentapartite columns and pentagonal lumens with the pentameres disposed radially and the lumen angles disposed interradi ally.

The radial disposition of pentameres in pentapartite columns and points in pentagonal columns and the interrarial nature of the angles of pentagonal to star-shaped lumens agree with the "law of Wachsmuth and Springer", which is, in Wachsmuth and Springer's (1885, p. 229) words:

" 1. In species with underbasals [IBB], whenever the the column is pentangular, its longitudinal angles are directed interradi ally, the sides and columnar cirrhi radially; on the contrary, in species with basals only, those angles are radial, the sides of the column and the cirrhi interradi ally.

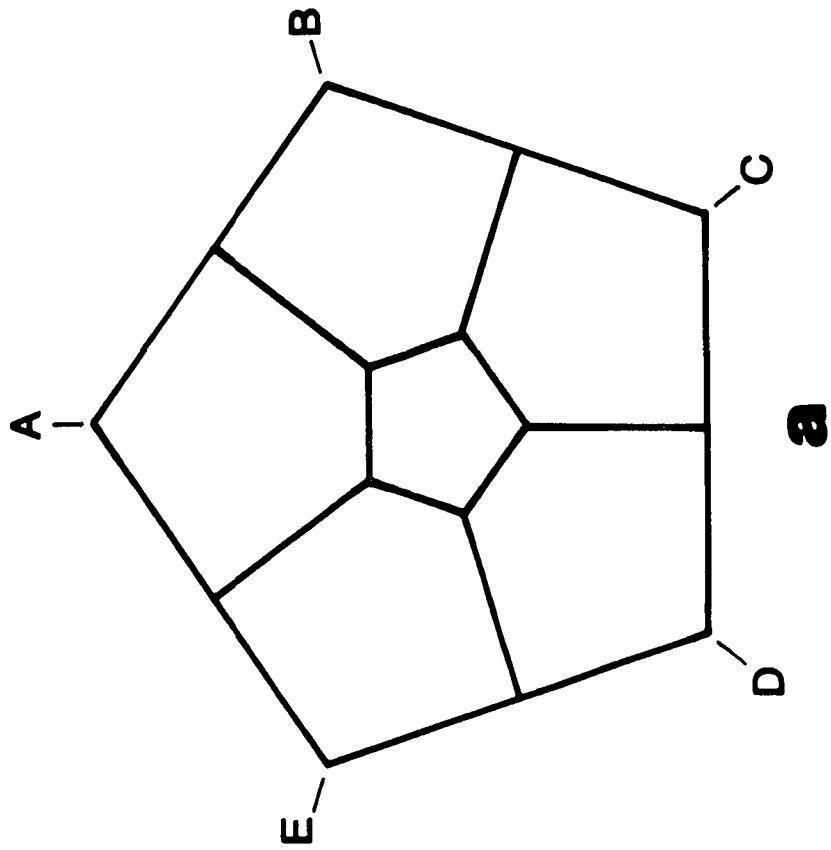
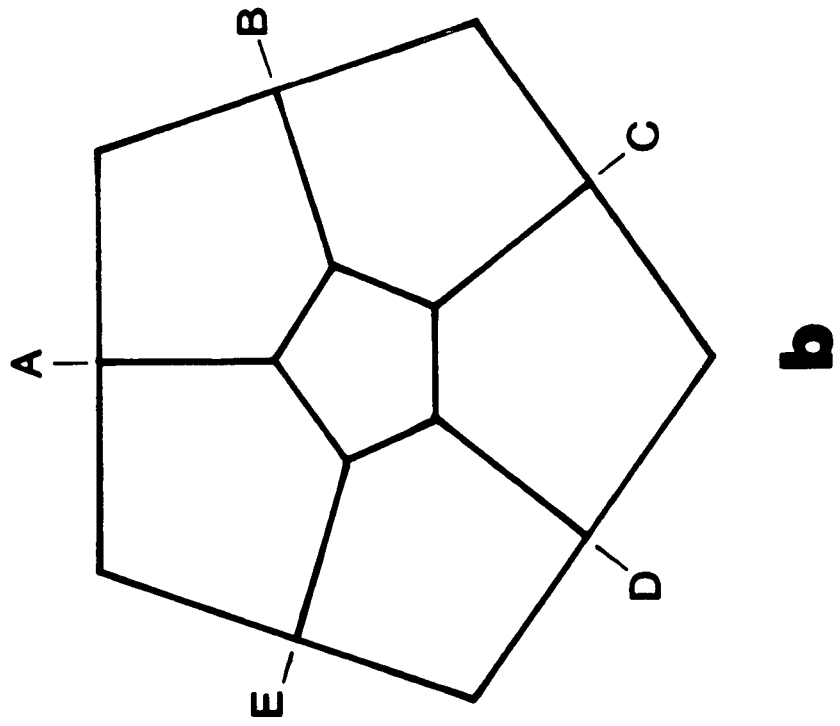
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Text-fig. 26. Disposition of pentameres, interpentameric sutures, column angles, and lumen angles in crinoids. a) monocyclic and pseudocyclic (with radial pentameres and column angles and interrational sutures and lumen angles) and b) dicyclic and pseudomonocyclic (with interrational pentameres and column angles and radial sutures and lumen angles). Rays are lettered A, B, C, D, and E.

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2. When there are underbasals and the column is pentapartite, the five sections of the column are radial [this is a mistake, it should read interradi-], the longitudinal sutures interradi- [should read radial], the radiation along the axial canal radial; but the opposite is the case when basals only exist." That is, in dicyclic (and pseudomonocyclic) crinoids with pentagonal-pentapartite columns, column angles and pentameres are interradi- with radial column sides, cirri, angles or extensions of the axial canal, and sutures between pentameres, while monocyclic crinoids have radial column angles and pentameres and interradi- column sides, cirri, axial canal extensions, and inter-pentameric sutures (Text-fig. 26). Although Wachsmuth and Springer (1885; 1886) admitted that the presence or absence of IBB is important in crinoid classification, they used this only as a familial (and lower) taxobasis, and then inconsistently (Wachsmuth and Springer included seven monocyclic families, two dicyclic families, and one family with monocyclic and dicyclic members in the Camerata; two dicyclic families in the Articulata; two monocyclic and two dicyclic families in their branch Larviformia of the Inadunata; and six monocyclic families, three dicyclic families, and one both monocyclic and dicyclic family in their branch Fistulata of the Inadunata—Table 2).

## Class Pelmatozoa Leuckart, 1848

## Subclass Crinoidea Miller, 1821

## Order Paleocrinoidea Wachsmuth

## Suborder Camerata Wachsmuth &amp; Springer, 1885

Family	Reteocrinidae-----	monocyclic and dicyclic
"	Rhodocrinidae-----	dicyclic
"	Glyptasteridae-----	dicyclic
"	Melocrinidae-----	monocyclic
"	Actinocrinidae-----	monocyclic
"	Platycrinidae-----	monocyclic
"	Hexacrinidae-----	monocyclic
"	Acrocrinidae-----	monocyclic
"	Barrandeocrinidae-----	monocyclic
"	Eucalyptocrinidae-----	monocyclic

## Suborder Articulata Wachsmuth &amp; Springer, 1885

Family	Ichthyocrinidae-----	dicyclic
"	Crotalocrinidae-----	dicyclic

## Suborder Inadunata Wachsmuth &amp; Springer, 1885

## Branch Larviformia Wachsmuth &amp; Springer, 1886

Family	Haplocrinidae-----	monocyclic
"	Symbathocrinidae-----	monocyclic
"	Cupressocrinidae-----	dicyclic
"	Gasterocomidae-----	dicyclic

## Branch Fistulata Wachsmuth &amp; Springer, 1886

Family	Hybocrinidae-----	monocyclic
"	Heterocrinidae-----	monocyclic
"	Anomalocrinidae-----	monocyclic
"	Belemnocrinidae-----	monocyclic
"	Cyathocrinidae-----	dicyclic
"	Poteriocrinidae-----	dicyclic
"	Encrinidae-----	dicyclic
"	Astylocrinidae-----	monocyclic and dicyclic
"	Catilloocrinidae-----	monocyclic
"	Calceocrinidae-----	monocyclic

Table 2. Monocyclic-dicyclic breakdown of the classification of Wachsmuth and Springer (1885; 1886).

Bather (1900, p. 104-105) expanded the "law of Wachsmuth and Springer":

"If the crinoid have a monocyclic base the [nerve] cords that pass to the basals join one another in a ring immediately surrounding the chambered organ, the lobes of which in this case correspond with the basals, i.e. are interradiar. If the base be dicyclic, the ring forms a commissure at the level of the centres of the basals; and from these points the cords again fork towards the adjacent infra-basals, where they join in another ring round the chambered organ, the lobes of which in this case correspond with the infrabasals, i.e. are radial.... The so-called "law of Wachsmuth & Springer"...is ...applicable only to pentagonal stems or lumens, and even then liable to exceptions...; but by attending (as is here done) chiefly to the relations of the axial cords, we shall have a surer guide for discrimination between monocyclic and dicyclic crinoids in the many doubtful cases that occur."

Bather (1899; 1900), using monocyclic versus dicyclic as the highest taxobasis for crinoid classification, divided the class Crinoidea into two subclasses, Monocyclica and Dicyclica. Bather implied, however, morphologic proximity of members of the two subclasses,

Class Crinoidea Miller, 1821

Subclass Monocyclica Bather, 1899-----monocyclic

Order Inadunata

" Adunata

" Camerata

Suborder Melocrinoidea

" Batocrinoidea

" Actinocrinoidea

Subclass Dicyclica Bather, 1899-----dicyclic

Order Inadunata

Suborder Cyathocrinoidea

" Dendrocrinoidea

Order Flexibilia

Grade Impinnata

" Pinnata

Order Camerata

Table 3. Monocyclic-dicyclic breakdown of the classification of Bather (1899; 1900).

if not phylogenetic relationship, by including in each of his two subclasses an order Inadunata and an order Camerata (Table 3).

Jaekel (1918—Table 4) and Moore and Laudon (1943—Table 5) arrived at a classificatory position intermediate between Wachsmuth and Springer's (1885; 1886) and Bather's (1899; 1900) by using monocyclic versus dicyclic as an ordinal taxobasis. Moore and Laudon (1943) divided Paleozoic crinoids into the three subclasses Inadunata, Flexibilia (dicyclic), and Camerata; in the Inadunata were placed the monocyclic Disparata (= Disparida) and the dicyclic Cladoidea (= Cladida), and in the Camerata were placed the monocyclic Monobathra and the dicyclic Diplobathra. According to Moore and Laudon (1943, p. 7-9) Bather's (1899; 1900) view of a primary monocyclic-dicyclic crinoid schism seems to be supported by a number of lines of evidence: 1) throughout their known history (Ordovician to Permian) the easily differentiated Flexibilia show a dicyclic structure, 2) the Disparida form a cohesive group based on criteria unrelated to the monocyclic nature of the dorsal cup, and 3) all blastoids are monocyclic. These lines of evidence point to basal, and infrabasal, circlet stability in the dorsal cup. But evidence for a primary schism along monocyclic-dicyclic lines is balanced (Moore and

## Class Crinoidea Miller, 1821

## Subclass Eocrinoidea

## Subclass Cladocrinoidea Jaekel, 1894

## Order Monocyclica-----monocyclic

## Suborder Tetramera

" Disjuncta

" Pentamera

" Miomera

## Order Dicyclica-----dicyclic

## Suborder Tetramera

" Pentamera

## Subclass Pentacrinoidea Jaekel, 1894

## Order Fistulata Wachsmuth &amp; Springer, 1886---dicyclic

## Suborder Cyathocrinites

" Dendrocrinites

" Merocrinites

" Barycrinites

" Rhenocrinites

" Poteriocrinites

## Order Articulata

## Suborder Typica-----dicyclic

" Libera

" Compacta-----monocyclic

## Order Articulosa Jaekel, 1894-----dicyclic

## Suborder Taxocrinites

" Calpiocrinites

" Lecanocrinites

" Ichthyocrinites

## Order Reducta-----dicyclic

## Order Turbata-----monocyclic

## Suborder Heterocrinites

" Calceocrinites

" Triacrinites

" Symbathocrinites

## Order Costata-----monocyclic

## Suborder Hybocrinites

" Hyocrinites

Table 4. Monocyclic-dicyclic breakdown of the classification of Jaekel (1918).

Class Crinoidea Miller, 1821

Subclass Inadunata Wachsmuth & Springer, 1885

Order Disparata-----monocyclic

Order Cladoidea-----dicyclic

Suborder Cyathocrinoidea Bather, 1899

" Dendrocrinoidea Bather, 1899

Subclass Flexibilia Zittel, 1879-----dicyclic

Order Taxocrinoidea Springer, 1913

Order Sagenocrinoidea Springer, 1913

Subclass Camerata Wachsmuth & Springer, 1885--- dicyclic

Order Diplobathra-----dicyclic

Order Monobathra-----monocyclic

Table 5. Monocyclic-dicyclic breakdown of the classification  
of Moore and Laudon (1943).

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Table 6. Disposition of pentameres, column angles, and lumen angles in members of the Cincinnaticrinacea and Homocrinacea. A question mark denotes information unknown; a dash denotes information lacking (*i.e.*, those with dashes have round columns). <sup>1</sup>E. simplex has a trimerous, rather than pentamerous, column with trimeres disposed as follows: one occupies the EA and AB inter-rays; a second lies in the BC interray and C ray; and the third occupies the D ray and DE interray (Text-fig. 20).

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	pentameres	column angles	lumen angles
<u>G. varibrachialus</u>	radial	radial	interradial
<u>C. pentagonus</u>	radial	radial	interradial
<u>D. constrictus</u>	radial	radial	interradial
<u>I. tenuis</u>	radial	radial	interradial
<u>O. laxus</u>	radial	radial	interradial
<u>O. brauni</u>	radial	radial	interradial
<u>A. priscus</u>	radial	—	?
<u>H. parvus</u>	?	—	?
<u>E. simplex</u>	trimeres <sup>1</sup>	—	interradial
<u>E. geniculatus</u>	?	—	interradial
<u>I. lepton</u>	radial	—	?
<u>S. typus</u>	?	—	?
<u>D. bellevillensis</u>	radial	radial	interradial

Table 6. Disposition of pentameres, column angles, and lumen angles in members of the Cincinnaticrinacea and Homocrinacea.

Laudon, 1943, p. 7-9) by evidence for numerous episodes of derivation of monocyclic from dicyclic (or vice versa): 1) the subclass Camerata contains both monocyclic and dicyclic forms and is a strict phylogenetic unit with numerous structural peculiarities linking dicyclic and monocyclic (this is especially true of Ordovician camerates with similarity of radial median ridges, depressed interbrachial areas, CD interray features, and arm structure), 2) in Ordovician camerates there is diminution of IBB to a point of disappearance, and 3) dicyclic camerates seem to represent homeomorphic offshoots from a number of different, and distantly related, monocyclic camerate lines.

Ubaghs (1953, p. 666-671) discussed the base of the dorsal cup in crinoids and illustrated phylogenetic possibilities (evolution of monocyclic to dicyclic, or vice versa) with a number of examples drawn from his and others' (Yakovlov, 1930; Kirk, 1937; Wachsmuth and Springer, 1897; Bather, 1900, 1917; Wilson, 1916; Beyrich, 1871; and Springer, 1920) experience.

It is obvious that evolution of true monocyclic to true dicyclic, or vice versa, requires more than addition or loss of IBB. Rotation of the calyx 36° in every dicyclic to monocyclic lineage would be required, and that is no mean feat. Obviously, disposition of

pentameres in crinoid genera deserves more attention with discernment of pseudomonocyclism (and pseudodicyclism, if it is a reality). Perhaps a primary dichotomy in crinoids along monocyclic (and pseudodicyclic) versus dicyclic (and pseudomonocyclic) lines does exist, as Bather imagined.

Morphological examination of cincinnaticrinaceans and homocrinaceans helps to delineate familial and generic taxobases applicable to them, and presumably to other crinoids. Relatively good familial characters appear to be: number and arrangement of simple versus compound RR and dorsal cup shape. Thus, the superfamily Cincinnaticrinacea is diagnosed as disparids with a conical dorsal cup having undivided RR in the A, B, and D rays and compound RR in the C and E rays, while homocrinaceans have a conical dorsal cup with fused RR in the A and D rays and compound RR in the B, C, and E rays. These characters have been used at the familial level for some time, and most inadunate families are defined in similar terms.

Good generic characters appear to be: branching type and column morphology. Similar branching and column morphology occur in various crinoids that are considered to be only distantly related and must be treated as independent acquirements. Configuration of

the tegmen is probably one of the better familial and generic taxobases, except that the tegmen is poorly known or unknown in many inadunates (e.g., the tegmen of Cincinnatiocrinus is really the only one known of the Cincinnatiocrinacea and Homocrinacea).

Good specific features are shapes of cup plates, although care must be taken, for cup plates change shape somewhat during ontogeny (less so than Brr, though).

Phylogenetically the armlike anal series in all Cincinnatiocrinaceans and homocrinaceans supports the common view that the anal series was derived from an arm. Although constancy in number of Brr per division series is the case in homocrinaceans and most other crinoids, in Cincinnatiocrinaceans it appears to be an unattained evolutionary endpoint toward which Cincinnatiocrinaceans evolve.

## APPENDIX

The following portion of the dissertation, while representing a significant part of the author's Ph.D. research, is included here as an appendix. It has already been written up as a separate paper and has been submitted to and accepted by the Journal of Paleontology for publication in its June 1974 issue. It is presented here in that form.

## PRESUMED MYZOSTOMID INFESTATION OF AN ORDOVICIAN CRINOID

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ABSTRACT—New information, from study of deformed columns of the Late Ordovician crinoid Heterocrinus juvenis Hall, 1866, lends support to the hypothesis (proposed by Graff, 1885) that perforated swellings in fossil crinoid columns are myzostomid (annelid) galls. Oval calcium-phosphatic rings, occurring both on column surfaces and inside column galls, resemble Recent encysted myzostomes in size, shape, and orientation. These resemblances, coupled with the similarity of fossil swellings to Recent myzostome galls and the abundance of Recent crinoid infestation by myzostomes (these two lines of evidence were the basis for Graff's hypothesis), provide substantial, although inconclusive, support for the myzostomid affinities of perforated swellings in the columns of fossil crinoids.

## INTRODUCTION

Crinoid specialists are familiar with swellings in fossil crinoid columns; these swellings are wide-ranging (geographically and stratigraphically) and, although relatively rare in most crinoid deposits, are occasionally found in surprising abundance. It has been known for some time (Phillips, 1836; Milne-Edwards and Haime, 1850-1854; Rofe, 1869; Young, 1876, 1878; and Etheridge, 1876, 1880) that some column swellings have been caused by encrusting corals, bryozoans, and brachiopods. However, one type of swelling, differing from those associated with organisms living on crinoids as a substrata by being barrel-shaped and pierced by a central perforation (Pl. 1, figs. 2-4, 7, 10-12, 16, and 19), has remained somewhat problematic.

Perforated column swellings were first described by Ure (1793, p. 324), who believed they were caused by puncture (represented by the central hole) of the column. Miller (1821) figured swollen columns and attributed them to healing after loss of cirri (p. 69). Etheridge (1880) serially-sectioned perforated swellings and described the geometry of the interior cavity. In a questionable allusion to an internal parasite, he considered the sparry calcite infilling "the object" that had dwelt within the stem. Etheridge, however, neglected a black, crescentiform body—probably the true remains of the parasite—

occupying part of the cavity. Graff (1885), who worked on the Challenger Myzostomida (1884, 1887) and was therefore familiar with the extensive infestation of Recent crinoids by these annelids, recognized the similarities of fossil stem swellings and Recent myzostome galls. (Myzostomes are peculiar polychaete annelids, abundantly, and almost exclusively, parasitic on Recent crinoids. Most are ectoparasites that steal food from the ambulacra, but a few are endoparasites that form reproductive galls in crinoid arms and pinnules, e.g. Text-figs. 1-2). This external similarity of skeletal deformation led Graff to suggest that perforated swellings in fossil crinoid columns are attributable to myzostomids. Although numerous references, since 1885, to myzostomid swellings in fossil crinoid columns have been made, they added no new information. The purpose of this paper is to illustrate gall morphology (internal and external) and associated parasitic remains in a species of Late Ordovician crinoid. Graff's myzostome hypothesis is reexamined in light of this new information.

This study was facilitated by the discovery that perforated swellings are common in Heterocrinus juvenis Hall, 1866 (Heterocrinus with column diameter near the dorsal cup nearly equal to that of the cup) from a starfish and crinoid "pocket." The abundance of such swellings permitted acidizing and serial-sectioning for detailed

study. The pocket had scattered crinoid columns and calyces and starfish in a thin (0.5 to 4.0 mm), argillaceous limestone that graded vertically into a lens made up largely of columns. The echinoderm occurrence was found at N39°34', W84°45'30" in an intermittent stream flowing into the southwest side of Acton Lake (in Hueston Woods State Park), about 100 yards (1 yd. = 0.91 meters) southwest of the end of Fourmile Road, as located on the College Corner, Ohio quadrangle (USGS 7.5' series) map. These strata are of Richmondian age and are probably assignable to the Liberty formation (stratigraphic occurrence is between Liberty beds near the top of the dam spillway and lowest Whitewater beds above the lake, fide J. K. Pope, personal communication, October 1972). Specimens are deposited in the University of Cincinnati Geological Museum with UCGM numbers.

Remains of the parasite, in the form of calcium-phosphatic rings (determined by W. H. Blackburn, University of Kentucky with a Jarrell-Ash Laser Microprobe II), occur in three ways: 1) on the surfaces of associated, but unaffected, columns; 2) near the exterior ends of the sediment-filled perforations; and 3) within the galls at the inner ends of the cavities. Study of the gall interior was accomplished by acidizing (in dilute acetic) and recovering the residues, by thin-sectioning, and by serial-sectioning (with a Croft Parallel Grinder, with cellulose acetate sheet peels taken at 0.05mm intervals).

## EXTERNAL FEATURES

Galls in Heterocrinus juvenis are barrel-shaped expansions of the column, involving only a few columnals, around single central holes (Pl. 1, figs. 2-4, 7, 10-12, 16, and 19). Malformation ranges from slight (Pl. 1, fig. 3) to about one and one-half the normal diameter of the column (Pl. 1, fig. 7). Obliteration of sutures (by fusion) between columnals occurs in a few large galls (Pl. 1, figs. 2 and 7). The oval, outward-flaring, central perforations are relatively consistent in size regardless of the sizes of their respective galls. In all but a few galls the longest diameter of the opening is perpendicular to the axial canal of the column.

On the surfaces of unaffected parts of the columns are oval, translucent, amber-brown rings of apatitic composition (Pl. 1, figs. 6, 22, and 23) with concentric lamellae (growth lamellae?). The longest diameter (length) of the rings ranges from 1.0mm to 2.0mm and is roughly perpendicular to the axial canal of the column; the shortest diameter (height) ranges from 0.7mm to 1.3mm and is parallel to the axial canal; length to height ratios range from 1.1 to 2.4 (Table 1). Near the openings of the cavities of many (13 of 51) of the galls there are phosphatic rings with similar shape and orientation (Pl. 1, figs. 16 and 19) but somewhat smaller size (Table 1).

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Table 1—Measured values for phosphatic rings. Length is number of millimeters perpendicular to the column axis; height is number of millimeters parallel to column axis.

<sup>1</sup>longest diameter (length) inclined at about 30°  
from normal

<sup>2</sup>longest diameter inclined at about 20° from normal

<sup>3</sup>orientation unknown but assumed to be as others.

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A) surface			
specimens	length	height	l/h
UCGM 41491	1.5	0.7	2.1
UCGM 41492	1.5	0.8	1.9
UCGM 41472a	1.5	0.7	2.1
b	1.3	0.7	1.9
c	1.5	0.7	2.1
d	1.5	0.7	2.1
e	2.0	1.2	1.7
UCGM 41473a	1.5	0.7	2.1
b	1.5	0.7	2.1
c	1.5	0.7	2.1
UCGM 41475	1.9	1.3	1.5
UCGM 41476	1.0	0.7	1.4
UCGM 41477a	1.3	1.2	1.1
b	1.7	0.7	2.4
UCGM 41478	1.2	0.9	1.3
UCGM 40597	1.4	0.9	1.6
UCGM 41502i	1.2	0.8	1.5
ave.	1.5	0.8	1.8
σ	0.2	0.2	0.4

B) specimens in openings			
UCGM 41474a	1.1	0.6	1.8
b	1.1	0.7	1.6
c	1.0	0.9	1.1
UCGM 41481	1.3	1.2	1.1
UCGM 41502d	0.8	0.4	2.0
UCGM 41485	1.2	0.7	1.7
UCGM 41486	1.3	0.8	1.6
UCGM 41488	1.1	0.9	1.2
UCGM 41489	1.0	0.7	1.4
UCGM 41490	1.0	0.7	1.4
ave.	1.1	0.8	1.5
σ	0.1	0.2	0.3

C) specimens inside galls			
UCGM 41498	0.8	0.4	2.0
UCGM 41499	1.0	0.6	1.7
UCGM 41497 <sup>1</sup>	1.1	0.5	2.2
UCGM 41487 <sup>2</sup>	1.0	0.7	1.4
UCGM 41495a	1.3	1.1	1.2
b <sup>3</sup>	0.8	0.4	2.0
UCGM 41496	1.3	0.6	2.2
UCGM 41494	1.1	0.5	2.2
UCGM 41493 <sup>1</sup>	1.1	0.5	2.2
UCGM 41479	1.3	1.0	1.3
UCGM 41480	1.3	0.8	1.6
ave.	1.1	0.7	1.8
σ	0.2	0.2	0.4

## INTERNAL FEATURES

Cylindrical sediment-filled cavities or passageways, about 1.5mm in diameter, extend from the openings toward the axial canals of the columns (most end short of the canals) along the line of fusion of two adjacent pentameres of the five forming each columnal (Pl. 1, fig. 15). Some have inner expansions to form inner chambers. The cavities are filled with sediment (microcrystalline calcite, clay minerals, and broken-up crinoid stereom), either completely (Pl. 1, figs. 14 and 20) or partially, with the innermost part filled by sparry calcite (Pl. 1, figs. 21, and 25-29). The space now occupied by sparry calcite was probably void (of solid material) at death of the parasites and subsequently during diagenesis received calcitic infilling. Some galls have no internal phosphatic material, but most acidized or sectioned galls have solitary rings at the sediment-sparry calcite interface (Pl. 1, figs. 21, 25, 28, and 29) or at the sediment-stereom interface (Pl. 1, figs. 5, 8, 13, and 24). These rings have the same orientation as those on the surface but differ in shape and size. The internal rings have either their upper and lower edges folded toward the exterior or their lateral edges folded toward the interior (or a combination) so that they are saddle-shaped (Pl. 1, figs. 13 and 18; compare Text-figs. 3-4). They are also smaller (length of 0.8mm to 1.3mm, height of 0.4mm to 1.1mm, and with length to height ratios of 1.2 to 2.2—Table 1).

The Mann-Whitney U test (a distribution-free alternative to the "Student" T test—Siegel, 1956, pp. 116-127) was used to compare the distributions of length, height, and length/height of surface specimens (sample A), specimens near the cavities' openings (sample B), and specimens inside cavities (sample C) two distributions at a time (Table 1 has the measured values). (Distributions were first checked for normality, following the method by Jones, 1969, and were found to be non-normal. Thus, distribution-free statistics had to be used.) A one-tailed test was used and the directional alternate hypothesis ( $H_1$ ) was that the measured values of length, height, and length/height were greater for sample A (for B-C comparisons a non-directional two-tailed test was made). For A-B length, A-B height, A-C length, and A-C height,  $H_0$  (the Null hypothesis) was rejected at alpha = 0.05, and for B-C length, B-C height, A-B length/height, A-C length/height, and B-C length/height  $H_0$  was accepted at alpha = 0.05. Thus, length and height of sample A are significantly greater than length and height of sample B and sample C, while there appear to be no significant differences between length and height of B and C or between any two of the three groups of length/height.

#### DISCUSSION

Recent crinoids are susceptible to extensive infestation by parasites and commensals. Clark (1921, pp. 613-687)

described numerous organisms for which Recent crinoids serve as hosts: tunicates, decapods, isopods, amphipods, copepods, ostracods, barnacles, ophiuroids, gastropods, juvenile pelecypods, polyzoans, polychaetes (mostly, but not exclusively, myzostomes), hydroids, corals, sponges, dinoflagellates, ciliates, sporozoans, and foraminiferans. Of these, only the cysticolous myzostomes seem a reasonable cause for the perforated swellings in fossil crinoid columns.

Myzostomes are small (0.1mm to 10mm, modified polychaete annelids with saucer-shaped bodies (elongate to a varying degree) possessing ten pairs of marginal sensory projections (for accounts from which this, and the following, biologic information is taken see Hyman, 1955, pp. 115-117 or, for more detail, Graff, 1884, pp. 1-26). On the ventral side are five pairs of parapodia arranged in two semicircles with four pairs of suckers in the intervals between the parapodia (Text-fig. 2). Each parapodium is armed with a hook apparatus extensible by complicated musculature radiating from a thick, central muscle mass. Mouth and anus are on the ventral surface near opposite ends of the body.

Myzostomes are hermaphroditic with organs of both sexes present but with one set of sex organs usually dominant. They are parasitic on Recent echinoderms (chiefly crinoids) and have four general life habits

(the first two ectoparasitic, the last two endoparasitic):  
1)most run freely over the host and gather food from the ambulacra and mouth; 2)some attach themselves more or less permanently to arms and pinnules where they steal food from the ambulacra; 3)a few inhabit the digestive tract or gonads; and 4)others form cysts or galls, reminiscent of galls produced by insects in plants, in the arms and pinnules (cysticolous myzostomes).

One, two, or three individuals are found together in Recent galls, and it is likely that self-fertilization can occur. In most encysted forms two individuals are present, one dominantly male and one dominantly female. The female deposits eggs, which the male fertilizes. The larvae abandon the gall through the opening to the exterior. After the larvae have lost their ciliated coat, they associate in pairs and bore their way into arms or pinnules, which causes the arm or pinnule to swell. The gall appears to serve as an area for insuring fertilization and success of the embryo and larva in its early stages. Hyman (1955, p. 118) implied that cysticolous forms occur at greater depths than free-living forms. Figures derived from rather scanty data gathered by Clark (1921, pp. 658-675) show that free-living forms have been found from about 5 to 2500 meters deep with an average depth of about 390 meters. The encysted forms are found from depths of 115 meters to 1150 meters with an average depth of about

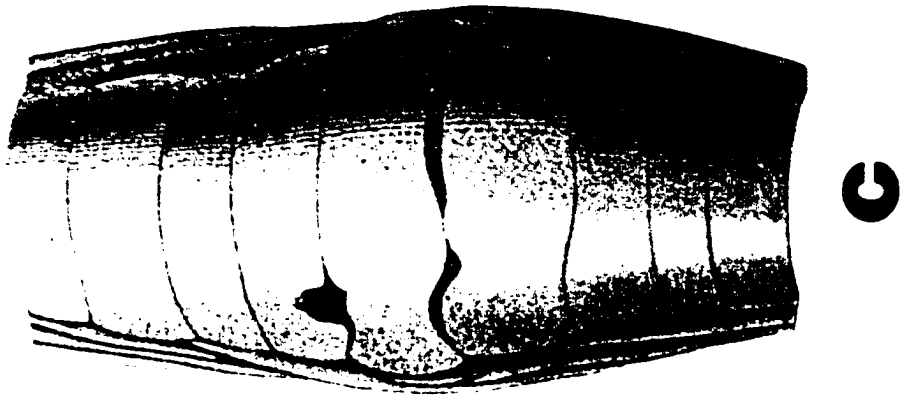
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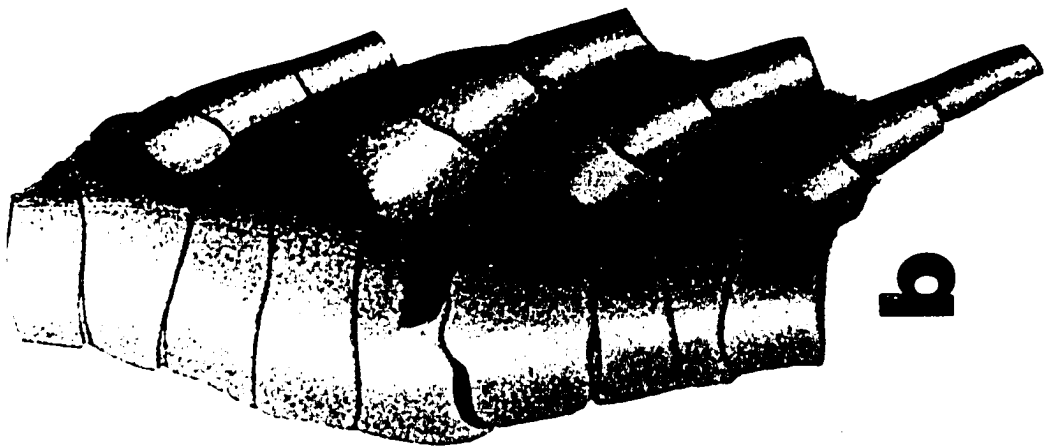
Text-fig. 1—Three views of a gall formed by Myzostomum pentacrini Graff in an arm of Pentacrinus alternicirrus Carpenter. In B the myzostome is visible through the external opening. All X2.0. Modified from Graff (1884, Pl. 11, fig. 9).

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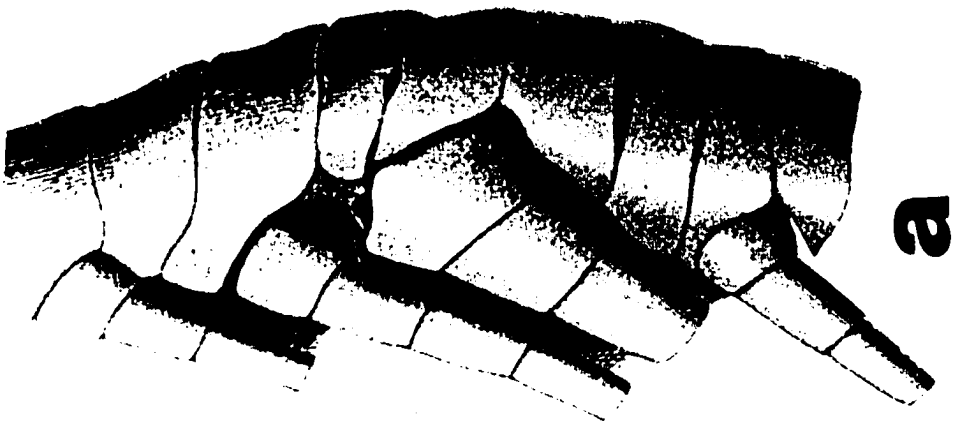
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**c**



**b**



**a**

640 meters. Based on available information, correlation of water depth and encysted forms seems not to be high. However, such studies as Stummer-Traunfels (1908), Boulenger (1916), Fauvel (1936), and Hartman (1966) indicate a higher incidence of encysted forms in Antarctic waters, and better data may show that cysticolous myzostomes tend to be more abundant in deep and/or cold waters.

The similarities between Recent myzostome galls (Text-fig. 1) and fossil column swellings (Pl. 1, figs. 2-4, 7, 10-12, 16, and 19) provide support for the myzostomid hypothesis, although the occurrence of galls only in arms and pinnules, and not columns, of Recent crinoids (stalked and free-living) is an apparent contradiction. The extent of myzostome infestation of Recent crinoids, however, supports the idea that these structures are myzostomid galls. These two lines of evidence are not new, for they form the basis for the myzostomid hypothesis proposed by Graff in 1885 and subsequently accepted.

The remains (?) of the parasite that caused swellings in the columns of Heterocrinus juvenis lends support to Graff's hypothesis, but not without concomitant problems. The most damaging piece of evidence to the fossil myzostomid hypothesis is that no myzostome is reported to have hard parts other than the five pairs of tiny hook apparatuses. Perhaps the rings represent a replacement of

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Text-fig. 2—Myzostomum deformatum Graff, 1884. a, ventral view; b, dorsal view; c, cross-section through the posterior half of the body; a and b X6.0, c X8.0. From Graff (1884, Pl. 12, figs. 1 and 7).

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soft parts by apatite. If the rings on the surfaces of the columns, in the gall openings, and inside the galls are remnants of the same organism (this appears to be a fairly safe assumption), then what remains of the parasite appears to have been flexible during life. Certainly, a better case for preservation of soft parts could be made for myzostomes inside the columns (in a microenvironment away from scavengers and oxygen-rich waters) than for those on the surface of the columns. Another problem is raised by the surface rings being larger than rings inside the galls (although similarity of length/height ratios adds support for conspecificity). Based on the life cycle of Recent cysticolous myzostomes, the reverse would be more acceptable; smaller individuals on the surface could then be interpreted as recently settled juveniles in the initial stages of burrowing.

The phosphatic rings do show resemblance to Myzostomum deformatum Graff, 1884 (Text-fig. 2). Size (length) is similar—0.8mm to 2.0mm for the fossil rings versus 3mm for M. deformatum. Both have an oval shape in plan view (most myzostomes do) and the same orientation, i.e. longest diameter perpendicular to the axis of the column (of the arm or pinnule for M. deformatum) with shortest diameter parallel to that axis. In addition, according to Graff (1884, p. 63) all encysted myzostomes have their lateral (= upper and lower) edges folded dorsally toward

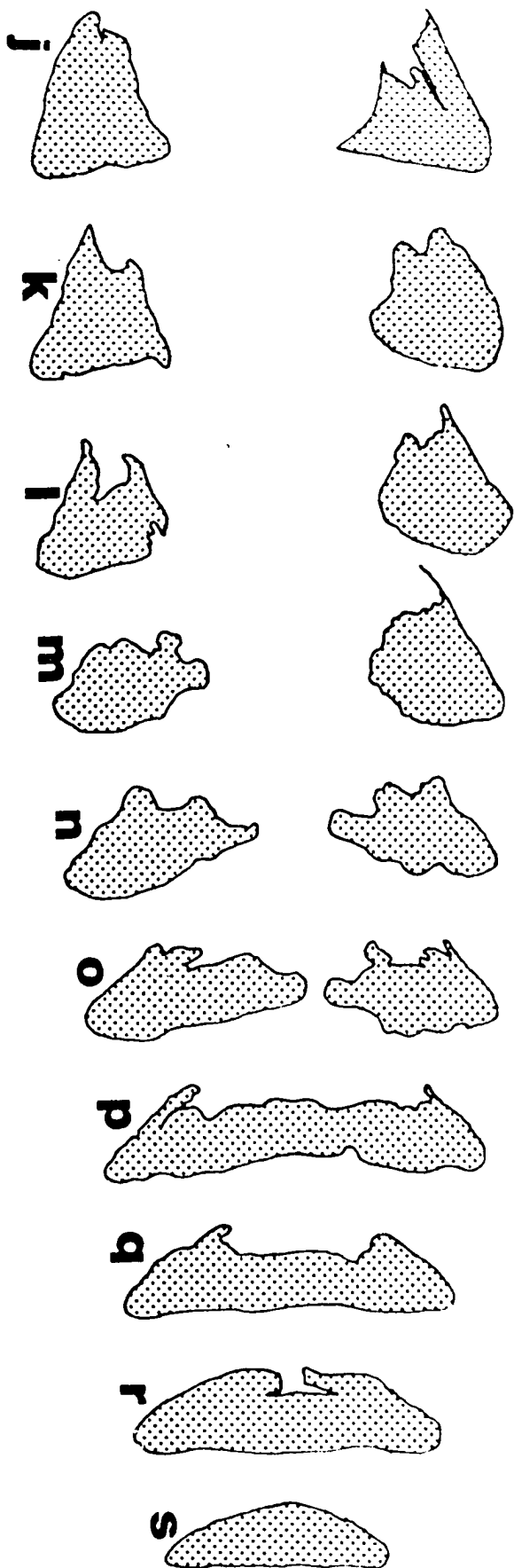
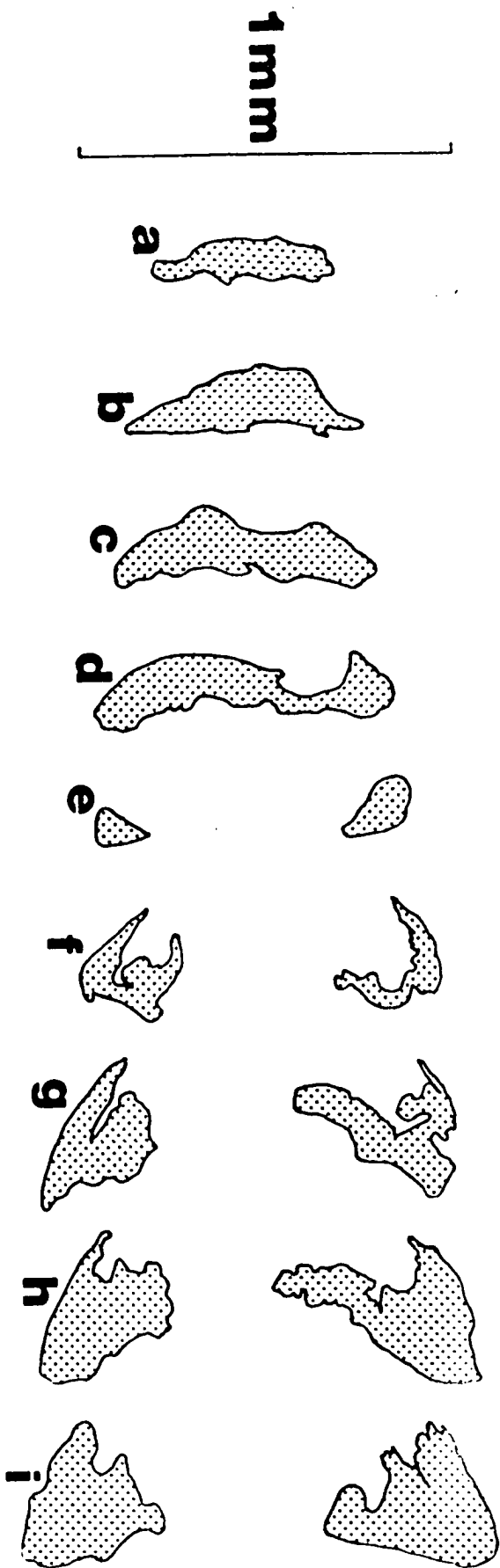
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Text-fig. 3—A phosphatic ring (UCGM 41480) from the interior of a gall in the column of Heterocrinus juvenis (transverse sections of column). Camera lucida drawings from peels of serial sections at 0.05mm intervals. The axial canal of the column would be centered about 1.5mm (at actual magnification) to the right of each lettered section and would extend perpendicular to the plane of the section. The opening of the cavity would be about 0.9mm to the left.

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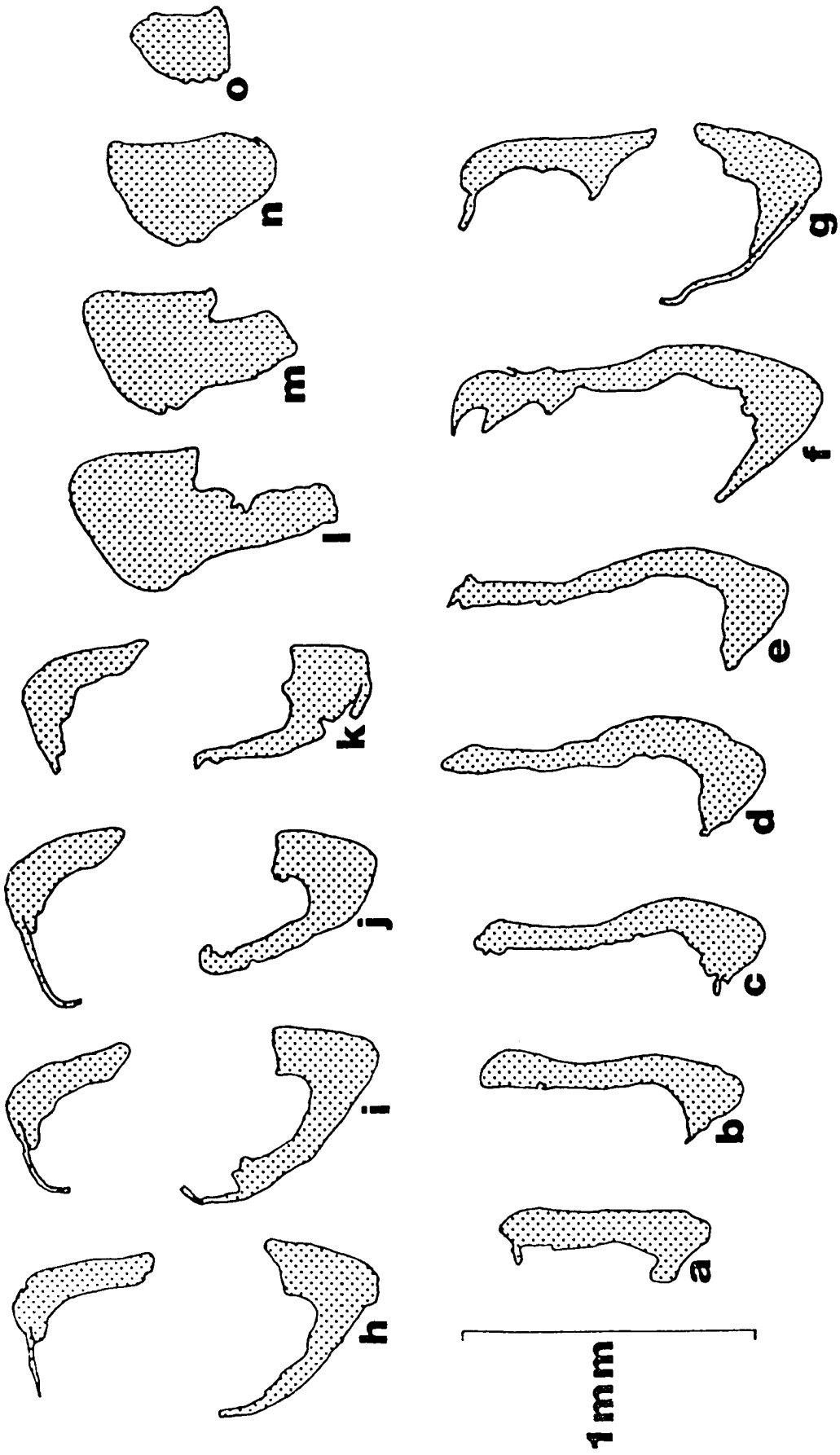
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Text-fig. 4—A phosphatic ring (UCGM 41479) from the interior of a gall in the column of Heterocrinus juvenis (transverse sections of column). Camera lucida drawings from peels of serial sections at 0.05mm intervals. The axial canal of the column would be centered about 1.3mm to the right of each lettered section and would extend perpendicular to the plane of the section. The opening of the cavity would be about 0.7mm to the left.

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the opening (exterior) of the gall (e.g. Text-figs. 2b-c); the same seems to be true of the phosphatic rings (Text-figs. 3-4 and Pl. 1, figs. 5, 8, 13, 17, and 18). In galls formed by Myzostomum deformatum two nearly equal-sized individuals are always found (Graff, 1884, p. 64), although other encysted species commonly have only one per gall. Some Recent species form galls which are inhabited by a tiny male and a female 50-100 times larger. In one swellings (UCGM 41495) what appear to be two individuals of nearly equal size have been found; all others examined internally have one or none.

In short, although these new lines of evidence, in addition to Graff's (1885) observations, suggest myzostomid affinities for the swellings of Heterocrinus juvenis (and presumably other fossil crinoids), the hypothesis that perforated swellings in fossil crinoid columns are myzostomid galls remains unproven. Indeed, the new evidence raises more problems than it solves.

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## EXPLANATION OF PLATE 1

All figures are of dorsal cups and columns of Heterocrinus juvenis or parasites found in or on H. juvenis columns. Figures 1-5, 7-13, 16-19, and 23-24 are photographs of whitened specimens. Figures 6, 15, and 22 are of specimens under benzol alcohol. Figures 14, 20-21, and 25-29 are transmitted light photomicrographs.

Fig. 1—DE interray view of calyx and proximal column.

1—UCGM 41500, X1.5.

2—Portion of column with four perforated swellings (two on opposite side). UCGM 41474, X1.75.

3—UCGM 41490, X1.75.

4—UCGM 41484, X2.0.

5—Ventral view of phosphatic ring (partially covered by undissolved crinoid stereom) acidized from within gall. Axial canal of column would extend vertically up and down page centered medially about 1mm over ring (above the page). UCGM 41495a, X14.0.

6—Dorsal view of surface ring. Axial canal of column extends vertically up and down page centered medially about 2.5mm below ring (below the page). UCGM 41475, X9.5.

7—UCGM 40593, X1.75.

8—Lateral (= upper or lower) view of phosphatic ring (also figured in 5 and 13). Pillar on which

ring rests is undissolved sediment filling cavity; opening to exterior is represented by lowermost edge of sediment. Axial canal would be centered about 1mm above ring and would extend perpendicular to page. UCGM 41495a, X14.0.

9—CD interray (anal) view of calyx and portion of column. UCGM 41501, X1.0.

10—UCGM 41489, X2.0.

11—Portions of two columns with ten galls (openings four of the ten are not visible). Made up in part of portions of column figured as 3 (rotated 180°), 4 (rotated 180°), 10 (rotated 80°), 12, 16, and 19. X0.75.

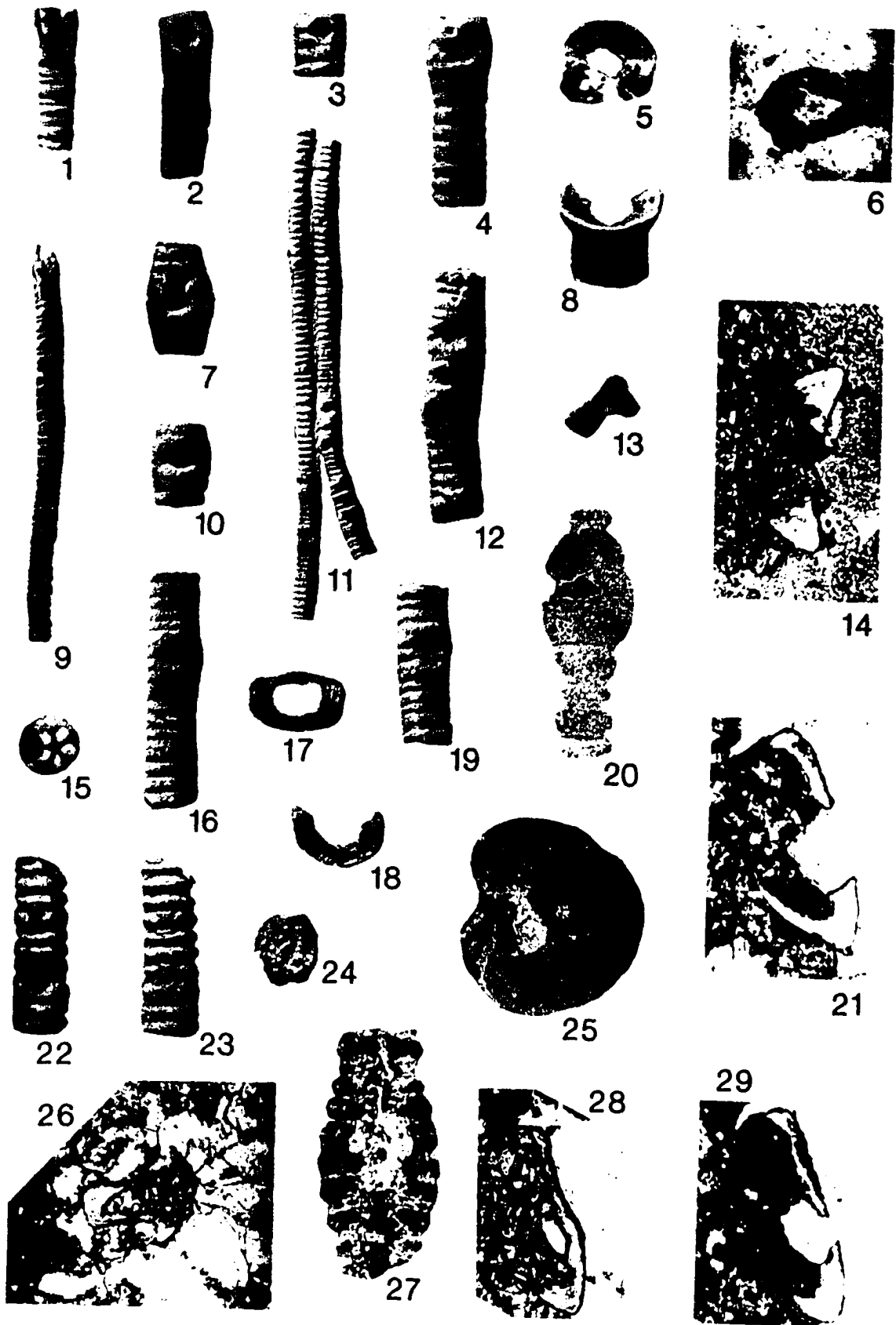
12—UCGM 41502d, X2.0.

13—View of right end (anterior or posterior?) of UCGM 41495a, as figured in 5 and 8. Axial canal would be about 1mm above ring extending horizontally across page. X14.0.

14—Acetate peel from cross-section of gall (= transverse section of column) with phosphatic ring at interface of sediment-filled cavity and stereom of column. Axial canal of column is 0.8mm off to right (from right edge of figure) extending perpendicular to page; opening of cavity is 0.7mm off to left (from left edge of figure). Corresponds to Text-fig. 3i. UCGM 41480, X2.0.

- 15—End view of disarticulated columnal (= transverse section of column). UCGM 41482, X2.0.
- 16—UCGM 41488, X2.0.
- 17—Ventral view of phosphatic ring acidized from inside gall. Axial canal would extend vertically up and down page centered medially about 1.25mm over ring (above the page). UCGM 41478, X14.0.
- 18—Lateral (upper or lower) view of the same phosphatic ring. Axial canal would be centered about 1.25mm above ring and would extend perpendicular to page; opening of cavity to exterior would be about 1mm directly below ring. UCGM 41478, X14.0.
- 19—UCGM 41486, X2.0.
- 20—Acetate peel from cross-section of gall (longitudinal section of column). UCGM 40595, X3.0.
- 21—Acetate peel from cross-section of gall (= transverse section of column) with ring at interface of sediment-filled cavity and sparry calcite. Axial canal is about 0.9mm off to right extending perpendicular to page; opening is about 0.7mm off to left. Corresponds to Text-fig. 4h. UCGM 41479, X30.0.
- 22—Three complete and two partial rings on surface of column. UCGM 41472, X2.0.
- 23—Same, X2.0.

- 24—Ventral view (?) of phosphatic ring acidized from same gall as was UCGM 41495a (figs. 5, 8, and 13). UCGM 41495b, X14.0.
- 25—Acetate peel from cross-section of gall (= transverse section of column) with phosphatic ring (corresponding to Text-fig. 4b) at sediment-sparry calcite interface of cavity. UCGM 41479, X6.75.
- 26—Enlargement of fig. 27 (UCGM 41497). X20.0.
- 27—Thin section of gall with phosphatic ring in sparry calcite portion of cavity (= longitudinal section of column). UCGM 41497, X3.5.
- 28—Acetate peel from cross-section of gall (= transverse section of column) with phosphatic ring at sediment-sparry calcite interface of cavity. Axial canal is 0.9mm off to right extending perpendicular to page; opening is 0.7mm off to left. Corresponds to Text-fig. 4f. UCGM 41479, X30.0.
- 29—Same. Corresponds to Text-fig. 4g. UCGM 41479, X30.0.



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Plates 1-18.

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Plate 1. Unrecognizable species.

fig. 1—lectotype (designated herein) of Heterocrinus heterodactylus Hall, 1847, AMNH 1116/3, from Snake Hill, Saratoga Co., New York, X2.27.

2—latex cast of above, X2.27.

3—lectoparatype of H. heterodactylus, AMNH 1116/2, from Boonville, New York, X0.85.

4—lectoparatype of H. heterodactylus, AMNH 1116/1, from Pulaski, New York, X0.85.

5—lectoparatype of H. heterodactylus, AMNH 1116/1, from Pulaski, New York, X0.85.

6—lectoparatype of H. heterodactylus, AMNH 1116/1, from Pulaski, New York, X0.85.

7—holotype of Heterocrinus exilis Hall, 1866, AMNH 1176/1, from Cincinnati, Ohio, X1.13.

8—holotype of H. exilis, AMNH 1176/1, CD interray view, X3.39.

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Plate 2. Unrecognizable species (figs. 4-8) and Atopocrinus priscus (figs. 1-3).

fig. 1—holotype of Atopocrinus priscus Lane, 1970, USNM 165240, E ray view, from Ibex, Utah, X2.83.

2—same, C ray view, X2.83; photographed under ethanol.

3—same, C ray view, X2.83.

4—latex cast of holotype of Heterocrinus? gracilis Hall, 1847, AMNH 1117, from Snake Hill, Saratoga Co., New York, X2.27.

5—supposed holotype of Heterocrinus juvenis Hall, 1866, AMNH 1173/1, D ray view, purportedly from Lebanon, Ohio, X5.10.

6—holotype of Columbicrinus crassus Ulrich, 1925, USNM 89826, A ray view, from Columbia, Tennessee, X2.83.

7—same, CD interray view, X2.83.

8—holotype of Ohiocrinus exilis Foerste, 1914, USNM 78718, from Rogers Gap, Kentucky, X2.83.

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Plate 3. Cincinnatiocrinus varibrachialus.

- Fig. 1—holotype of Cincinnatiocrinus varibrachialus and the specimen figured by Meek, 1873, Pl. 1, figs. 1a-b, as Heterocrinus heterodactylus, UCGM 3871; C ray view; from the Kope Formation at Cincinnati, Ohio; X1.13.
- 2—same; X3.39.
- 3—MU 959a; from the Kope Formation, Cincinnati, Ohio; X3.39.
- 4—paratype of C. varibrachialus, UCGM 405751; AB interray view; the tegmen is visible just over the  $IBrr_1$  as are the anal backing plates on  $X_1$ ; from locality 4 (Text-fig. 10); X3.97.
- 5—same; oral view; X7.93.
- 6—UCGM 40580; CD interray view; from locality 1; X5.10.
- 7—UCGM 42674; from the Kope Formation, Newport, Kentucky; X4.52.
- 8—UCGM 36287; from Trenton Falls, New York; X3.39.
- 9—UCGM 40580; CD interray view; X15.30.
- 10—UCGM 6562; from the Kope Formation, Rapid Run Creek, Cincinnati, Ohio; X2.23.
- 11—UCGM 2021a; A ray view; from the Kope Formation, Cincinnati, Ohio; X3.39.
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Plate 4. C. varibrachialus.

(all are paratypes; all are X3.39; and all are from locality 5—Text-fig. 10)

Fig. 1—UCGM 40555, C ray view.

2—UCGM 40497, C ray view.

3—same, E ray view.

4—UCGM 40555, E ray view.

5—UCGM 40500, A ray view.

6—same, CD interrayer view.

7—UCGM 40502, E ray view.

8—UCGM 40531, A ray view.

9—same, CD interrayer view; photographed under ethanol.

10—same, E ray view.

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Plate 5. C. varibrachialus.

(all were photographed under ethanol)

Fig. 1—UCGM 40579; A ray view; from locality 1 (Text-fig. 10); X10.18.

2—same; D ray view; X10.18.

3—UCGM 40580; B ray view; from locality 1; X10.18.

4—same; DE interray view; X10.18.

5—UCGM 40578; A ray view; from locality 1; X10.18.

6—same; D ray view; X10.18.

7—UCGM 40582; A ray view; from locality 1; X10.18.

8—same; CD interray view; X10.18.

9—UCGM 40583BU; B ray view; from locality 1; X10.18.

10—UCGM 40568; C ray view; from locality 4; X6.23.

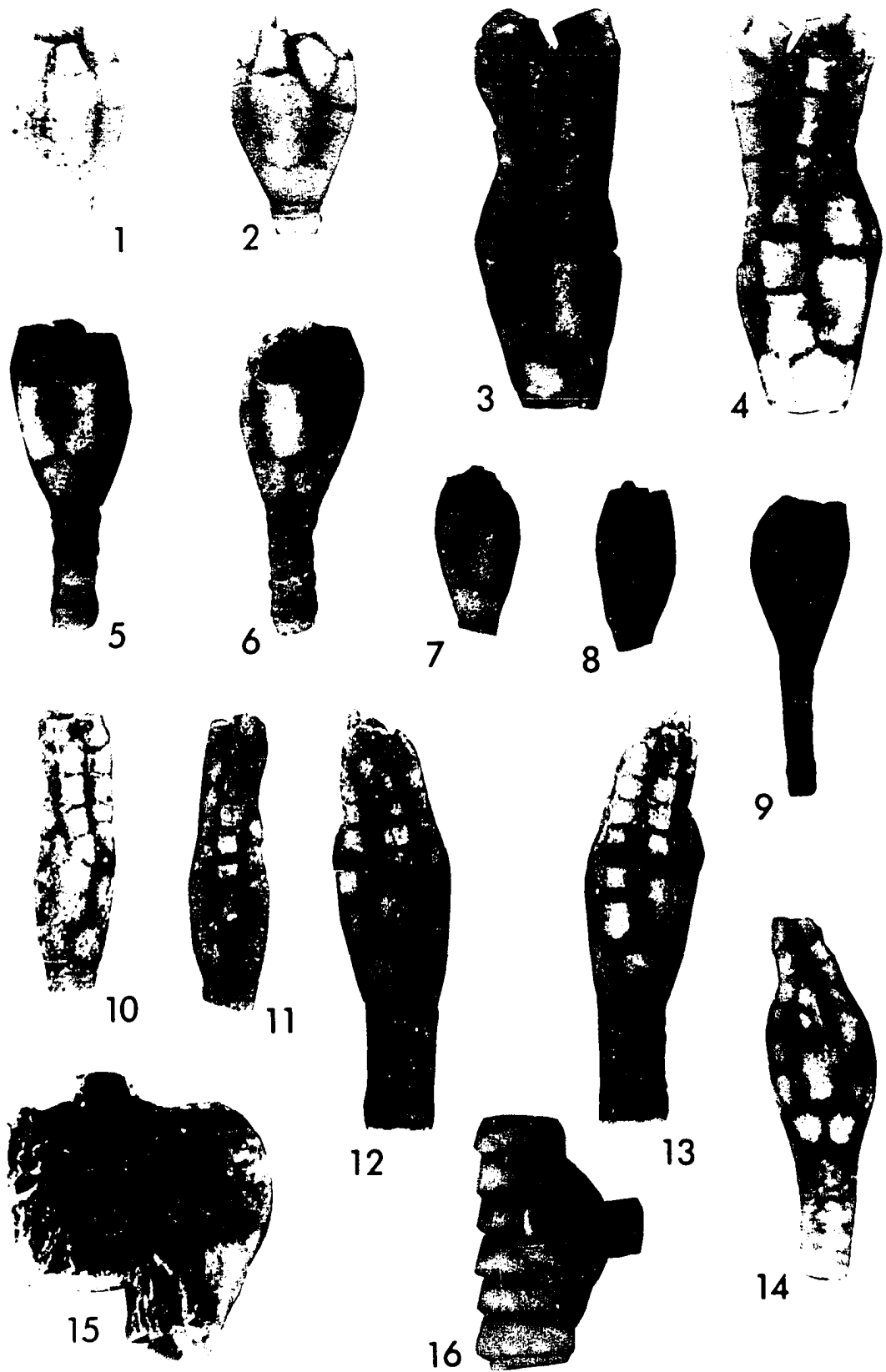
11—same; E ray view; X6.23.

12—UCGM 40569; B ray view; from locality 4; X6.23.

13—same; DE interray view; X6.23.

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Plate 6. Cincinnatiocrinus pentagonus.

Fig. 1—lectotype of Heterocrinus pentagonus Ulrich, 1882,  
YPM 24801; EA interray view; from the Fairview  
Formation, Cincinnati, Ohio; X2.27.

2—UCGM 17626; BC interray view; from the Grant Lake  
Formation?, Lebanon, Ohio; X2.27.

3—UCGM 6559a; A ray view; from the Bull Fork Formation,  
Westwood, Cincinnati, Ohio; X2.27.

4—UCGM 11609; CD interray view; from the Fairview  
Formation, Fairview Heights, Cincinnati, Ohio; X2.27.

5—lectoparatype of H. pentagonus, YPM; CD interray  
view; from the Fairview Formation, Cincinnati,  
Ohio; X2.27.

6—UCGM 41501; D ray view; from the Bull Fork Formation,  
Hueston Woods State Park, Ohio; X1.13.

7—UCGM 6450c; D ray view; from the Bull Fork Formation,  
Clarksville, Ohio; X2.27.

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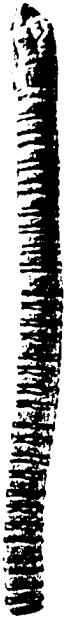
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Plate 7. Dystactocrinus constrictus.

Fig. 1—UCGM 42675; B ray view; from Cincinnati, Ohio; X1.70.

2—same; DE interray view.

3—UCGM 6542; A ray view; Cincinnati, Ohio; X1.70.

4—UCGM 6424; Cincinnati, Ohio; X1.70.

5—HMCZ 2165, holotype of D. constrictus; B ray view;  
Frant Lake Formation, Cincinnati, Ohio; X2.27.

6—same; C ray view; X2.27.

7—same; DE interray view; X2.27.

8—UCGM 42676; A ray view; Grant Lake Formation,  
Ft. Mitchell, Kentucky; X1.13.

9—USNM 89827 (holotype of Atyphocrinus corryvillensis,  
a junior synonym of D. constrictus); EA interray  
view; Grant Lake Formation, Cincinnati, Ohio; X1.70.

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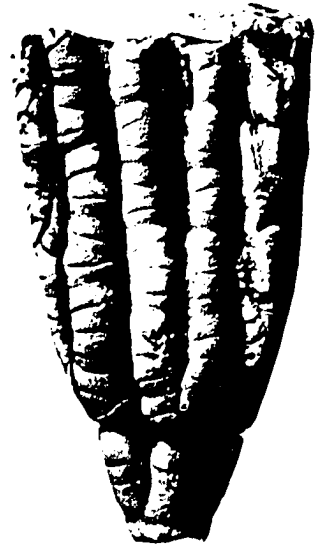
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Plate 8. Isotomocrinus tenuis.

(1-4 and 6-7 are from Kirkfield, Ontario, while 5 is from Ottawa, Ontario)

Fig. 1—holotype of Isotomocrinus typus Ulrich, 1925 (a junior synonym of I. tenuis), USNM S.2077a; D ray view; X6.23.

2—paratype of I. typus, USNM S.2077b; CD interray view; X6.23.

3—paratype of I. typus, USNM S.2077c; AB interray view; X6.23.

4—USNM S.2077a-c; X1.70.

5—lectotype of I. tenuis, GSC 1438; EA interray view; X3.39.

6—UCGM K.42677; AB interray view; X1.70.

7—UCGM K.42678; CD interray view; X1.70.

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Plate 9. Ohioocrinus laxus.

Fig. 1—UCGM 23048; B ray view; X1.70.

2—Ohioocrinus sp.; UCGM 6600; Fairview Formation,  
Madison, Indiana; X1.70.

3—UCGM 6545a; CD interray view; Grant Lake Formation,  
Orland Avenue, Cincinnati, Ohio; X1.70.

4—same; X5.10.

5—HMCZ 2167, holotype of Ohioocrinus laxus; CD interray  
view; Cincinnati, Ohio; X2.27.

6—UCGM 6524a; CD interray view; Cincinnati, Ohio; X2.27.

7—same; X5.10 (spiral anal sac is visible between  
arms of the C and D rays).

8—same; EA interray view; X5.10 (spiral anal sac is  
visible between arms of the E and A rays).

9—USNM 42304a (lectotype of Heterocrinus oehanus, a  
junior synonym of O. laxus); Fairview Formation,  
Cincinnati, Ohio; X1.70.

10—same; X3.39.

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Plate 10. Ohioocrinus brauni.

(both are from the Fairview Formation, Madison, Indiana)

fig. 1—lectotype of Ohioocrinus brauni Ulrich, 1925,

USNM S.2082b, CD interray view, X5.10.

2—same, X9.07; photographed under ethanol.

3—same, X18.14; photographed under ethanol.

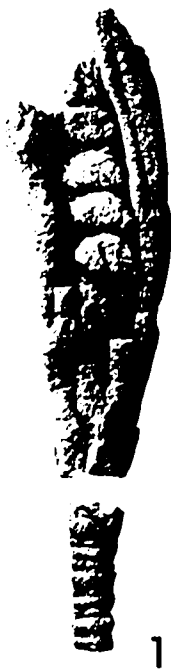
4—lectoparatype of O. brauni, USNM S.2082a, E ray  
view, X5.10.

5—same, X9.07; photographed under ethanol.

6—same, X15.30; photographed under ethanol.

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Plate 11. Homocrinus parvus.

fig. 1—holotype, AMNH 1705a; from Lockport, New York;

X2.27.

2—same, X3.97.

3—paratypes, AMNH 1705b-c; Lockport, New York;

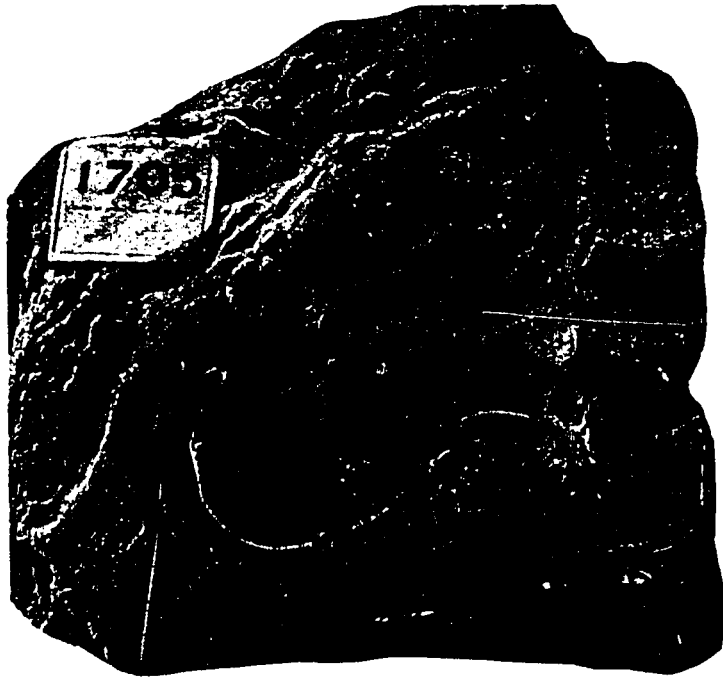
X2.27.

4—same, X3.97.

5—UCGM K.36292, from Lockport, New York, X2.27.

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Plate 12. Ectenocrinus simplex.

(all X1.70)

fig. 1—holotype of Ectenocrinus simplex (Hall), 1847,

AMNH 656/2a, A ray view, from Cincinnati, Ohio.

2—same, CD interray view.

3—paratype of E. simplex, AMNH 656/2b, CD interray view; from Cincinnati, Ohio.

4—paratype of E. simplex, AMNH 656/2c, C ray view; from Cincinnati, Ohio.

5—paratype of E. simplex, AMNH 656/2d, DE interray view; from Cincinnati, Ohio.

6—paratype of E. simplex, AMNH 656/2e, B ray view; from Cincinnati, Ohio.

7—paratype of E. simplex, AMNH 656/2f, CD interray view; from Cincinnati, Ohio.

8—same, DE interray view.

9—paratype of E. simplex, AMNH 656/2g, BC interray view; from Cincinnati, Ohio.

10—same, CD interray view.

11—SUI 3770, E ray view; from the Maquoketa Formation, Clermont, Iowa.

12—same, A ray view.

13—same, BC interray view.

fig. 14—paratype of Ectenocrinus simplex, AMNH 656/21,

AB interray view; from Cincinnati, Ohio.

15—holotype of E. raymondi Slocum, 1924 (a junior

synonym of E. simplex), CFM UC24701, BC interray

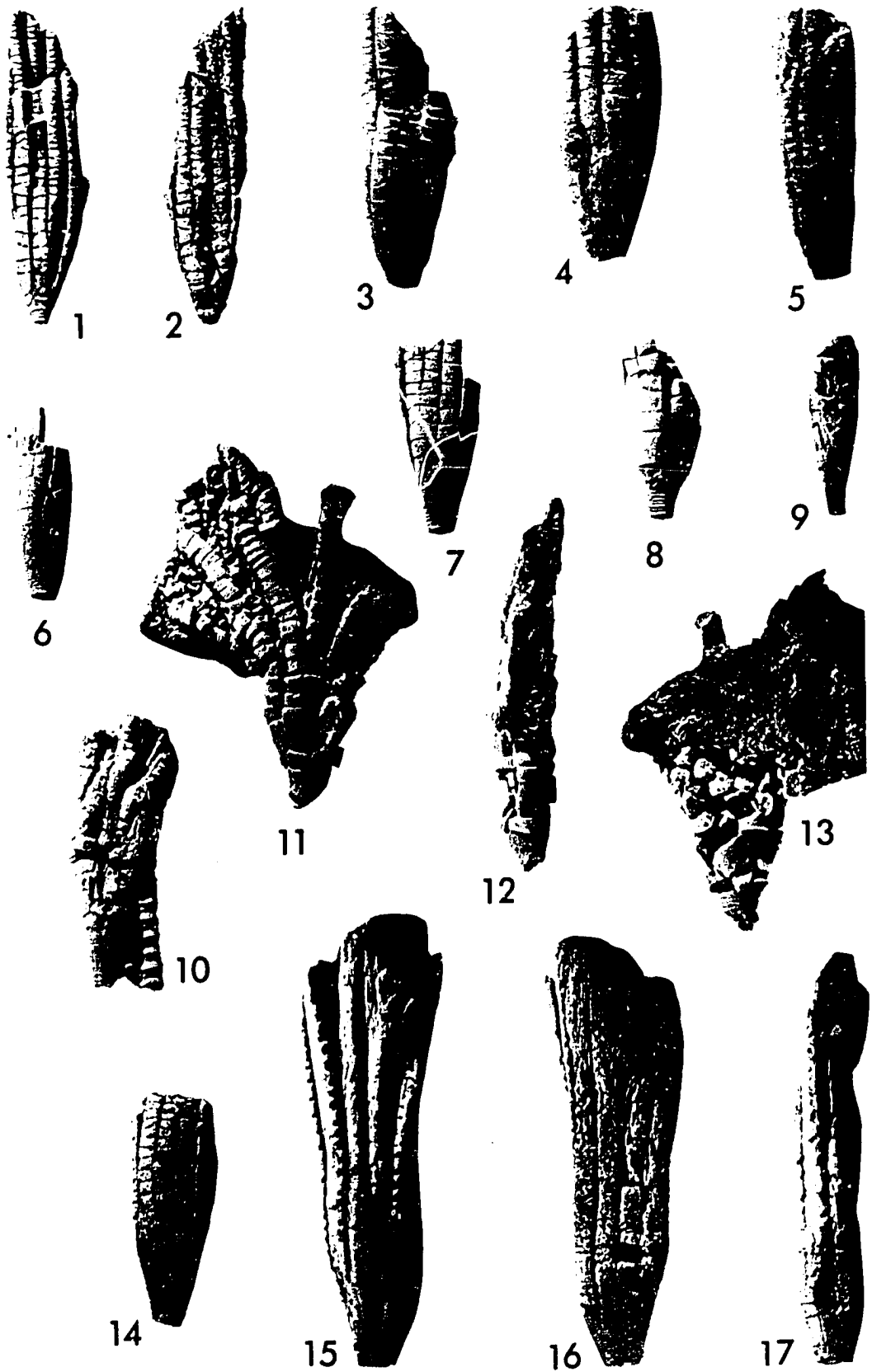
view; from the Maquoketa Formation, Clermont, Iowa.

16—same, E. ray view.

17—same, CD interray view.

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Plate 13. E. simplex.

Fig. 1—UCGM 36281a; CD interray view; from Trenton Falls,  
New York; X1.70.

2—UCGM 36281b; C ray view; Trenton Falls, New York;  
X1.70.

3—UCGM 42679; X0.57.

4—latex cast of UCGM 42680; A ray view; Martinsburg  
Formation, Swatara Gap, Pennsylvania; X1.70.

5—same; CD interray view.

6—UCGM 42681a; BC interray view; locality 2; X2.27.

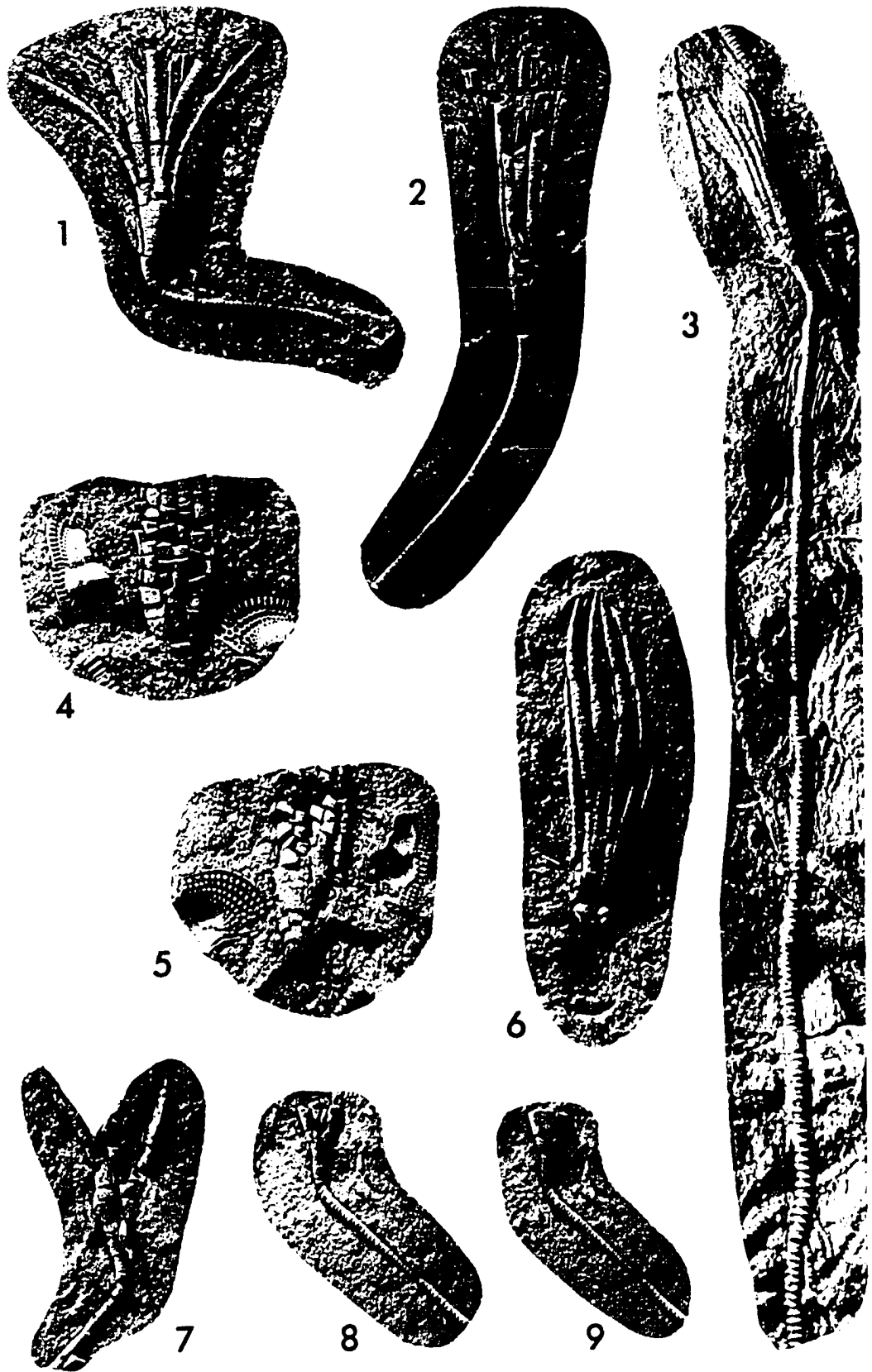
7—latex cast of Derstler 1a; BC interray view;  
Martinsburg Formation at Swatara Gap, Pennsylvania;  
X1.70.

8—latex cast of Derstler 1b; E ray view showing interior  
surfaces of B and C ray RR; X1.70.

9—same; E ray view; X1.70.

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Plate 14. E. simplex (figs. 1-7 and 9-10) and E. geniculatus (fig. 8).

(1-7 and 9-10 are latex casts of specimens from the Martinsburg Formation, Swatara Gap, Pennsylvania)

Fig. 1—Derstler 5; B ray view; X2.27.

2—Derstler 11; D ray view; X1.70.

3—Derstler 12; D ray view; X1.70.

4—Derstler 16; BC interray view; X1.70.

5—Derstler 3b; C ray view; X1.70.

6—Derstler 3a; E ray view; X1.70.

7—Derstler 5b; C ray view; X2.27.

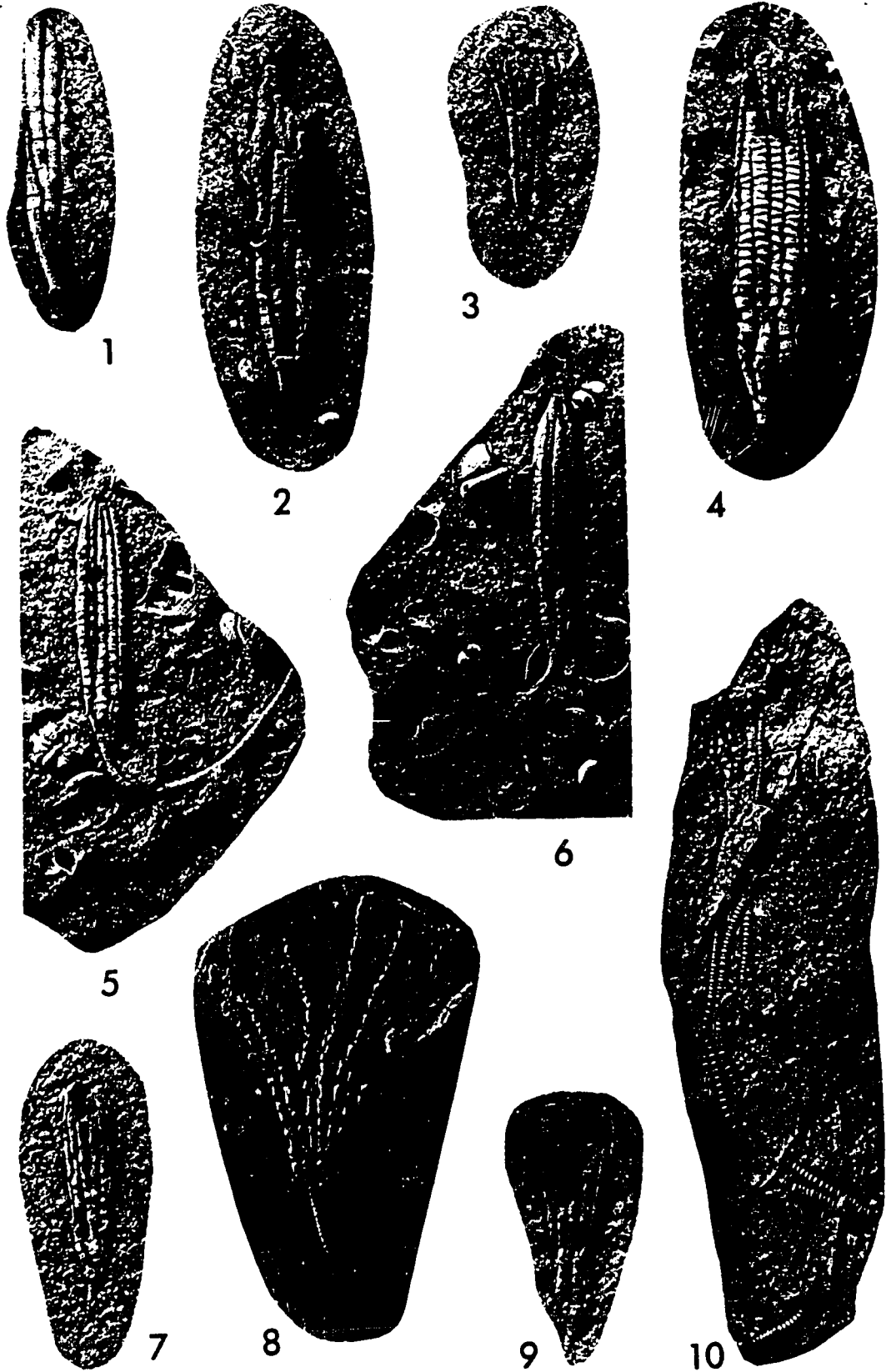
8—holotype of E. geniculatus, UCGM 36313; AB interray view; lowermost Kope Formation, Cincinnati, Ohio; X1.13.

9—Derstler 7a; D ray view; X2.27.

10—Derstler 17; X1.13.

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Plate 15. Ectenocrinus geniculatus.

(all are from the lowermost Kope Formation at Cincinnati)

fig. 1—paratype of Ectenocrinus geniculatus (Ulrich), 1879,

USNM 42219b, BC interray view, X2.27.

2—same, X4.0.

3—latex cast of USNM 42219a (which is a natural mold  
of the holotype—UCGM           ), A ray view, X1.70.

4—paratype of E. geniculatus, USNM 42219d, A ray  
view, X4.0.

5—paratype of E. geniculatus, USNM 42219k, B ray  
view, X2.27.

6—paratype of E. geniculatus, USNM 42219d, A ray  
view, X2.27.

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1



2



3



4



5



6

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Plate 16. Ectenocrinus geniculatus (figs. 1-3, 7) and  
Ibexocrinus lepton (figs. 4-6).

fig. 1—paratype of E. geniculatus, USNM 42219c, ?A ray  
view; from the lowest Kope, Cincinnati, Ohio;  
X2.27.

2—paratype of E. geniculatus, USNM 42219f, C ray  
view; from the lowest Kope, Cincinnati, Ohio;  
X2.27.

3—paratype of E. geniculatus, USNM 42219e; from the  
lowest Kope, Cincinnati, Ohio; X4.0.

4—holotype of Ibexocrinus lepton Lane, 1970, USNM  
165239, CD interray view; from Ibex, Utah; X2.83.

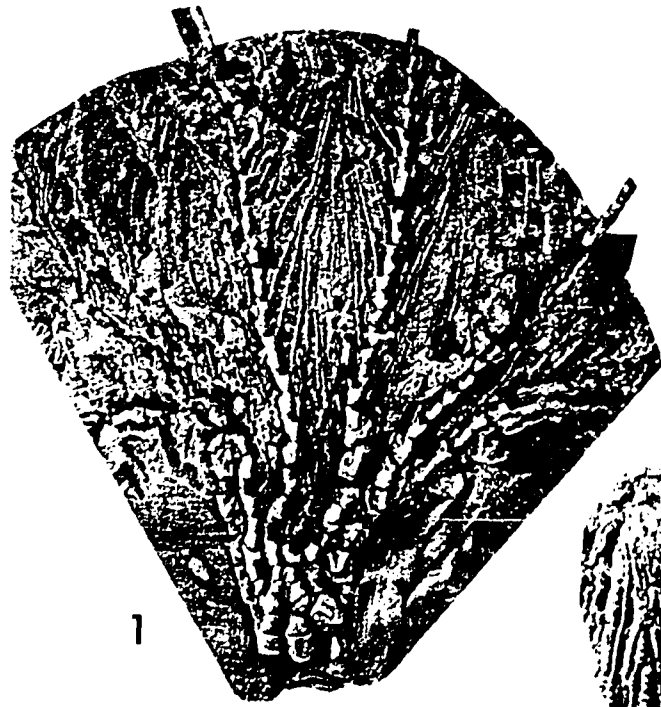
5—same, A ray view, X2.83.

6—same, CD interray view, X2.83; photographed under  
ethanol.

7—paratype of E. geniculatus, CFM UC8829; from lowest  
Kope, Cincinnati, Ohio.

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Plate 17. Sygcaulocrinus typus.

(all are from the Maquoketa Formation, Ft. Atkinson, Iowa;  
1 and 3-11 are X2.83; 2 is X4.0)

figs. 1-2—holotype of Sygcaulocrinus typus Ulrich, 1925,  
USNM 89876, D ray view.

3—lectotype of Ectenocrinus elongatus Thomas and Ladd,  
1926 (a junior synonym of S. typus), SUI 3771,  
A ray view.

4—same, CD interray view.

5—lectoparatype of E. elongatus, SUI 3772, A ray view.

6—same, E ray view.

7—lectoparatype of E. elongatus, SUI 3774, A ray view.

8—same, CD interray view.

9—SUI 37921, B ray view.

10—SUI 37923, CD interray view.

11—SUI 37922, DE interray view.

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Plate 18. Daedalocrinus bellevillensis.

(all are from Kirkfield, Ontario)

Fig. 1—UCGM K.42682; CD interray view; X2.27.

2—UCGM K.42683; A ray view; X2.27.

3—ROM 619T; E ray view; X2.27.

4—UCGM K.42684; CD interray view; X2.27.

5—lectotype of Daedalocrinus kirki Ulrich, 1925 (a junior synonym of D. bellevillensis), USNM S.2141; CD interray view; X1.70.

6—UCGM K.36696b; CD interray view; X2.27.

7—same as 5; X0.85.

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