BULLETINS OF AMERICAN PALEONTOLOGY

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STUDIES IN PALEONTOLOGY AND STRATIGRAPHY

Dedicated to
Kenneth E. Caster,
Professor of Geology, University of Cincinnati
on his 45th year of teaching.

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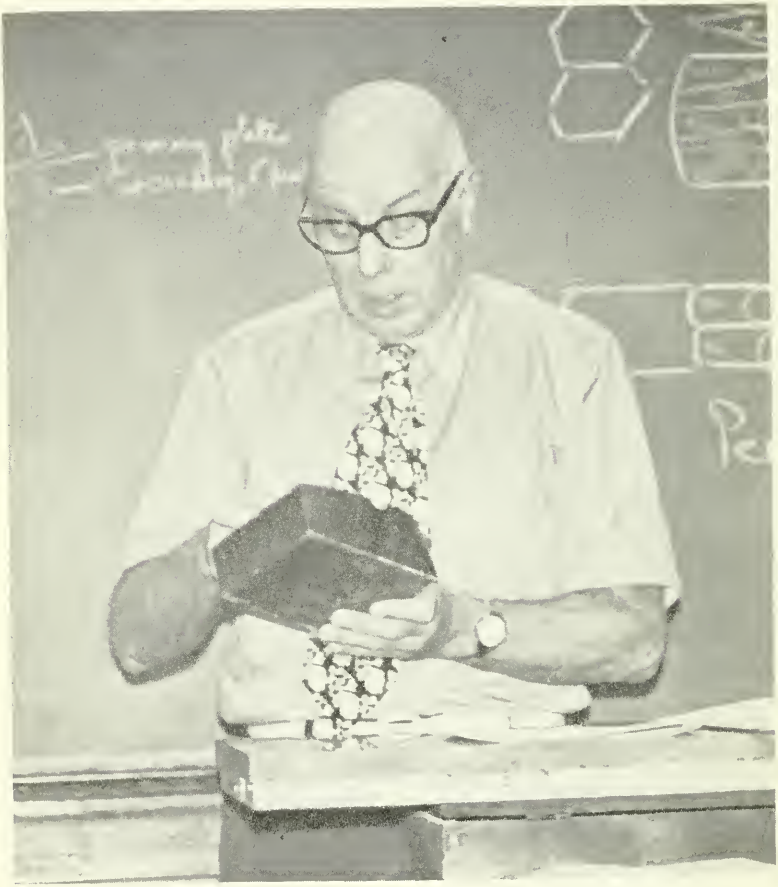

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STUDIES IN PALEONTOLOGY AND STRATIGRAPHY

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This book is affectionately dedicated to

KENNETH E. CASTER

by his former students

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STUDIES IN PALEONTOLOGY AND STRATIGRAPHY

KENNETH EDWARD CASTER

"Paleontology is an art as well as a science."

Kenneth Caster is a complex man. Raised and educated in upstate New York, and Pennsylvania, he blends the resourcefulness and craftsmanship of the Yankee pioneers of his part of this country with the imagination and analytical mind of the scientist and the wit and sophistication of a man of letters and international travel. Those who have learned from him have come away inspired, aware not only of their science but also of the breadth of man's other finer endeavors, such as art and literature, and of nature's riches. Few scientists combine the penetrating intelligence, rapid comprehension of detail, stamina, and enthusiasm for life to permit themselves simultaneously to become both masters of their chosen fields and broadly authoritative throughout the arts, humanities, and other sciences as well.

Born in New Albany, Pennsylvania, in 1908, Kenneth Caster grew up in Ithaca, New York. There he received his early education and at Cornell University, his A.B. in 1929, M.S. in 1931, and Ph.D. in 1933. Even before entering college, Kenneth came under the influence and inspiration of J. C. Bradley, entomologist, and E. Laurence Palmer, natural historian, both of Cornell University. In his early college years, Caster's interest was entomology. However, as a senior, even while serving as an assistant in entomology to Bradley, his interest was diverted toward the work of G. D. Harris, paleontologist and stratigrapher in the Department of Geology at Cornell University. Harris, although a specialist in Tertiary mollusks, recognized the need for continuing work in the mid-Paleozoic rocks of Pennsylvania and New York and there directed Caster's attention. The result was Caster's study of the faunas and stratigraphy of the Upper Devonian and Lower Carboniferous of southwestern New York and northwestern Pennsylvania, his doctoral dissertation, his early publications, and his continuing interest in that part of the geologic column.

While still a graduate student at Cornell, Caster served as Harris' "right hand man" in the post of Instructor of Paleontology. Upon receiving his doctoral degree, and after his marriage to the gracious Anneliese, Kenneth moved rapidly through the positions of Instructor of Geology and Paleontology at Cornell, and Assistant Head of Science at the New York State Normal School at Geneseo. He arrived at the University of Cincinnati in 1936 as Instructor in Geology and Curator of the Geology Museum and rose steadily to his present position of Professor of Geology (1952) and Fellow of the Graduate School. Additionally, he held visiting professorships at Potsdam State College (1936), Universidade de São Paulo, Brazil (1944-47), Escuela Nacional de Minas, Colombia (1948), University of Virginia Biological Station (1955), University of Tasmania (1956-57), University of California at Berkeley (1962), University of Cologne, Germany (1964), and University of Southern California (1966, 1970).

Kenneth's society memberships, activities, and even honors and distinctions are too numerous to list fully. He was recipient of the Derby Medal at the Brazilian Geological Survey Centennial (1952) and of the Gondwana Medal at the Geological Survey of India Centennial (1956). He has received Guggenheim and Fulbright Fellowships for travel and study in South America, Africa, Australia, and New Zealand and grants from the National Research Council, Geological Society of America and National Science Foundation for study of Upper Ordovician, Devonian, and Mississippian faunas and stratigraphy. He is a fellow or has been an executive officer of ten of the 38 societies and foundations of which he is a member, including the presidency of the Cincinnati MacDowell Society (1964-66), Paleontological Society (1960), and twice the presidency of the Paleontological Research Institution.

To find the source of Caster's success and acclaim, we must scan the impressively long list of his publications. Their subjects span most of geological time and touch upon almost all animal phyla. At first glance, there seems to be no general systematic or chronologic organization to the papers. It quickly becomes apparent that the papers are divided into vaguely defined periods. Like the paintings of Picasso, Caster's papers are arranged into periods reflecting his changing interests: the Devono-Mississippian Period, by extension, the Austral Hemisphere Period, the Sponge Period, the Jellyfish Period, the Merostome Period, the Continental Drift Period and the Echinoderm-Carpoid Period. The papers may also be organized by theme. Some, as the Devono-Mississippian faunal and stratigraphic studies and the South American studies, are comprehensive attacks upon large and widely known geological problems. Others, as the merostome and carpoid papers, began with serendipity, the chance discovery of fossils out of place in time or of such exceptional preservation as to shed new light upon their groups. The succession of papers in this category are Caster building upon a foundation largely laid by Caster. Underlying all of the papers is excellence and imagination — excellence in comprehension and presentation, and imagination in finding and exposing the unique qualities of each subject. Moreover Caster dared to be unconventional. The demonstration of facies in his early work, at that time a novel and even unpopular concept, has become a classic in American stratigraphy. His eloquent insistence over many years that continental drift is "a topic at least worthy of consideration" has finally been justified.

These bare facts, however, do not reveal the man behind the name Caster. It is in Kenneth's other interests that his personality is revealed. Kenneth is a man of art; he and Anneliese regularly have attended musical and theater productions in Cincinnati where Kenneth is a trustee of the Playhouse in the Park. Kenneth delights in literature. The Casters' handsome home displays not only the artifacts and handicrafts which are mementos of their global travels, but also endless bookshelves housing their non-scientific collection. Kenneth's spacious office and anteroom at the University contain one of the finest private paleontological libraries in the world. His correspondence is voluminous and international. From this, as a secondary benefit, he adds to his extensive stamp collection. Caster's humor and tolerance of students' humor is legendary, as witnessed by his degree from the "University of the State of Collapse", his charter membership in the "Lipalian Research Foundation", his "Agawana Medal", and his perseverance under the stare from the bronze bust of Ernst Haeckel placed high atop a bookcase in his office. Kenneth is generous with his time and information. Years ago, there clustered about him a band of dedicated, enthusiastic, amateur, fossil collectors who organized to become the Dry Dredgers.

In return for patient instruction, he has received from them some of the finer specimens in the Geology Museum. Both Kenneth and Anneliese are warm, generous, and hospitable. The frequent gatherings of graduate students at their home and their continuing concern for students has resulted in a binding, life-long *esprit de corps*. Not only Kenneth's mastery of paleontology, his outstanding teaching and research, but also his magnetic personality have drawn generations of students to Cincinnati.

LA CASA EN CLIFTON HEIGHTS

El homenaje a un científico que llega a los 45 años de vida, no sólo de sobresalientes trabajos de investigación, sino de enseñanza universitaria para cuyo desempeño feliz se necesita una vocación casi monacal, no puede ser más merecido y oportuno.

Hay sinembargo, fuera de la parte científica, la parte humana que es en realidad la que aglutina en un todo coherente, la vida misma del hombre. Quien esto escribe ha tenido el privilegio de la amistad de Kenneth y Ana Caster por más años de los que pueda recordar y desea rememorar en estas cortas líneas, la trayectoria del hogar de los Caster como un lugar siempre abierto para los numerosos paleontólogos y geólogos americanos y extranjeros conocidos a lo largo de los extensos viajes de los Caster por Sur América, Africa, Australia, Europa, etc. — Aquella casona de Cincinnati ha llegado a ser una especie de Embajada diplomática sin el pesado aspecto oficial usual, y sí con una incomparable y acogedora llaneza que rememora la hospitalidad de los tiempos coloniales norteamericanos.

Como uno de los paleontólogos extranjeros que se ha acogido muchas veces al techo protector y hospitalaria de Kenneth y Ana, me atrevo a hacerme vocero de los muchos otros visitantes científicos multinacionales, al pedir a los espíritus protectores de la Paleontología y sus cultores, permitan que en los muchos años por venir, el hogar de Clifton Heights y sus dueños, sigan siendo el lugar obligado de peregrinación bajo la sombra del añoso Gingko, árbol más que apropiado para proteger el hogar de un paleontólogo, en su doble carácter de árbol sagrado y fósil viviente.

G. Botero-Arango.
Medellín, Colombia

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INTRODUCTION

The idea of a Caster *Festschrift* occurred to us in the summer of 1972, as a way of honoring Kenneth Caster's scholarship in paleontology and stratigraphy, and the fact that he has had over 50 graduate students more than half of whom obtained their Ph.D. degrees at the University of Cincinnati. We felt that an anniversary publication would be appropriate as 1974 would be his 45th year of teaching. We first approached his charming wife Annie, and Katherine VanWinkle Palmer, his longtime friend and editor of the publications of the Paleontological Research Institution, and received enthusiastic support for the project.

To raise money to publish this book we decided to approach K.E.C.'s present and former students, friends, paleontological and faculty colleagues, the Department of Geology at the University of Cincinnati, and the Dry Dredgers, an organization of collectors of fossils in and around Cincinnati, Ohio. The response to our request was overwhelming and in short order we had funds enough to go ahead with the Caster volume. A list of all monetary contributors follows this introduction.

With the full cooperation of Katherine Palmer, it was decided to publish the book as a volume of the Bulletins of American Paleontology. This seemed especially appropriate because Ken was a student of G. D. Harris, who founded the Bulletins and the Paleontological Research Institution, and because K. E. C. and his students have published extensively in the two series of the Paleontological Research Institution.

The scope of paleontology at Cincinnati is broad as is shown by the contributed papers assembled here. The subjects include, biogeography, biostratigraphy, functional morphology, descriptive morphology, ontogeny, paleoecology, phylogeny, and systematics. The animal groups discussed are: anthozoans, asteroids, brachiopods, bryozoans, cephalopods, crinoids, edrioasteroids, gastropods, limulids, machaeridians, ostracodes, pelecypods, trilobites, and ichnofossils. Stratigraphically, the papers span the geologic column from the Cambrian to the Cretaceous, with special concentration in the lower and middle Paleozoic.

K. E. C. has worked with famous colleagues at Cincinnati and elsewhere and has written many publications, but we like to think that he is best known for the large number of students who have studied with him and learned from him at Old Tech (the building which houses the Department of Geology at the University of Cincinnati). Ken Caster's personality, his thorough understanding of the field, his great ability as a teacher, the University's large collection of fossils, and the fact that Cincinnatian rocks abound with fossils, all contribute to attracting fledgling students of paleontology to Cincinnati. Once there, students first get a solid background in systematics before passing on to other aspects of paleontology.

Early in the project it was decided to limit the scientific contributions in this book to Ph.D. students of K. E. C.; 19 of his students were able to contribute papers. Of those by several writers only the senior author was a student of Caster. So, Ken, for better or worse, you have only yourself to blame for what follows, for none of us would have gotten this far without your help and personal blessing. Many thanks!

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STRATIGRAPHY AND PALEOECOLOGY OF CARBONIFEROUS CORALS, LISBURNE GROUP, BROOKS RANGE, ARCTIC ALASKA

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ABSTRACT

The Carboniferous Lisburne Group of arctic Alaska contains coral faunas ranging in age from Osagean (Early Mississippian) to Atokan (Middle Pennsylvanian). Osagean beds have a small fauna of solitary and tabulate corals. Meramecian and lowermost Chesterian beds contain a large fauna of *Ekvasophyllum* spp., *Faberophyllum* spp., *Diphyphyllum venosum* Armstrong, *D. klawockensis* Armstrong, *D. nasorakensis* Armstrong, *Lithostrotion (Siphonodendron) dutroi* Armstrong, *L. (S.) sinuosum* (Kelly), *L. (S.) warreni* Nelson, *L. (S.) lisburnensis* Armstrong, *Lithostrotion reiseri* Armstrong, *Lithostrotionella niakensis* Armstrong, *L. banffensis* (Warren), *L. mclareni* (Sutherland), *L. birdi Armstrong, L. pennsylvanica* (Shimer), *Thysanophyllum astraeiforme* (Warren), *T. orientale* Thomson, *Sciophyllum lambarti* Harker and McLaren, and *S. alaskaensis* Armstrong. Corals, rare in younger Chesterian beds, are *Lithostrotionella* aff. *L. mclareni* (Sutherland), *Lithostrotion (S.) ignekensis* Armstrong, *Syringopora* spp., and occasional solitary corals. Pennsylvanian (Atokan) beds of the Lisburne Group contain *Lithostrotionella wahooensis* Armstrong, *Corwenia jagoensis* Armstrong, a thick-walled syringoporoid, and *Michelinia* sp.

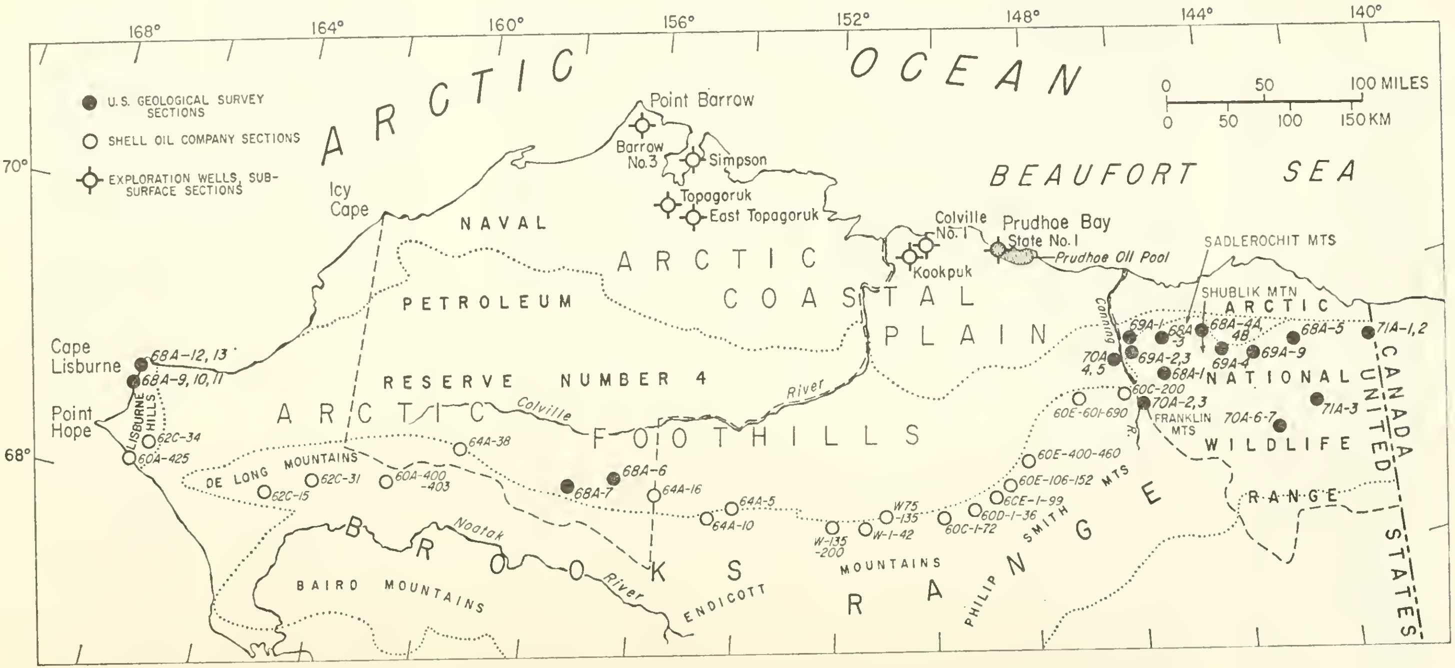
Preliminary studies of the lithostrotionoids indicate that the Lisburne Group can be divided into eight coral-assemblage zones. The zones in ascending order are: Meramecian, 4 zones: *Lithostrotion (S.) dutroi* Armstrong, *L. reiseri* Armstrong, *Lithostrotionella mclareni* (Sutherland), and *Sciophyllum lambarti* Harker and McLaren; Meramecian-Chesterian transition, 1 zone: *Lithostrotion (S.) lisburnensis* Armstrong; Chesterian, 2 zones: *Lithostrotionella* aff. *L. mclareni* (Sutherland) and *Lithostrotion (S.) ignekensis* Armstrong; Atokan, 1 zone: *Corwenia jagoensis* Armstrong.

Lisburne limestones were deposited on a slowly subsiding carbonate platform and are cyclic. Colonial corals of Meramecian and Atokan age occur in carbonates associated with shallow-water shoaling facies. The paucity of corals in carbonates of Osagean, Chesterian, and Morrowan age is attributed to regional temperature or salinity changes that inhibited their growth. Carboniferous corals are not known to have formed reeflike masses in arctic Alaska, but some biostromal accumulations occur.

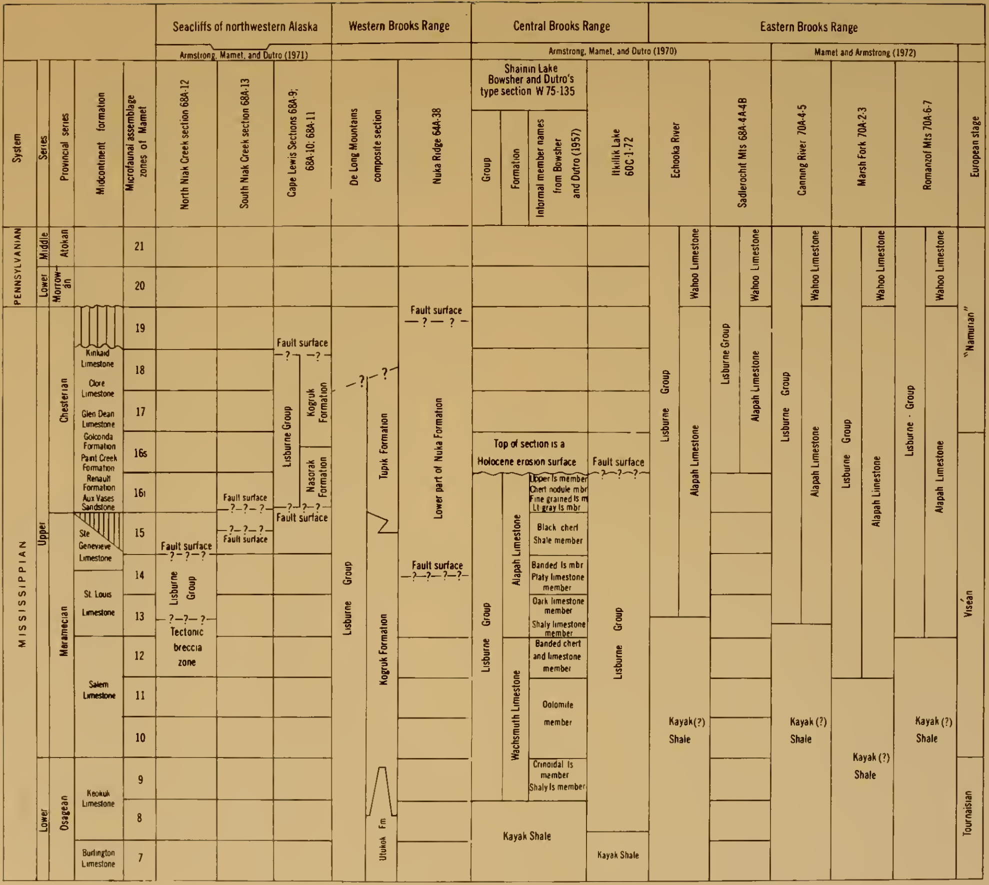
INTRODUCTION

The locations of Carboniferous outcrops in arctic Alaska are shown in Text-figure 1. Field collecting began in 1962, and laboratory studies are only partly completed; therefore, this paper is an interim report. Lisburne solitary rugose and tabulate coral faunas have not been studied and are, therefore, poorly represented in this report, which does not reflect their numerical importance in the faunas.

Thirty-six stratigraphic sections in the Brooks Range, arctic Alaska, were measured by Jacob's staff and tape. Rock and foraminiferal samples were collected every 5 to 10 feet (1.5 to 3 m). Coral collections were made throughout the section. Thin sections were



Text-figure 1.—Index map of arctic Alaska showing measured stratigraphic sections and coral localities, and the Naval Petroleum Reserve Number Four, Arctic National Wildlife Range, and Prudhoe Bay oil pool; physiographic divisions of arctic Alaska from Wahrhaftig (1965).



Text-figure 2. — Carboniferous stratigraphic correlation chart, Brooks Range, arctic Alaska.

made for carbonate microfacies and microfossil studies. The corals were studied by means of 2-inch by 3-inch oriented thin sections.

Bernard L. Mamet's microfossil identifications and zonations are used in the biostratigraphic analysis of the Lisburne Group of arctic Alaska, and the determination of the vertical ranges of its coral faunas.

I wish to express my appreciation to Irvin L. Tailleur, the party chief, summer of 1968, and Hillard N. Reiser, the party chief, summers of 1969-1971, for their generosity in supporting my Lisburne Group coral collecting and stratigraphic studies. I wish to thank the Naval Arctic Research Laboratory (Barrow), Office of Naval Research, for their logistical support of fieldwork in summers 1968-1971. Large collections of corals, Foraminifera, and thin sections used in this study were collected by Shell Oil Company geologists in 1959-1964; the collections I made in 1962 and 1964, while employed by Shell Oil Company, were given to the U.S. Geological Survey. My appreciation is given to R. E. McAdams and G. E. Burton, vice presidents of Shell Oil Company.

ARCTIC ALASKA

Bowsher and Dutro (1957) established the Kayak Shale and Lisburne Group for exposures near Shainin Lake, Endicott Mountains, and published the first major study of the Carboniferous stratigraphy and faunas. They gave (p. 3) an excellent account of the earlier history of studies and paleontology of the Carboniferous rocks of arctic Alaska. Helen Duncan (unpub. data, 1950) made the first detailed study of Lisburne corals from the Endicott Mountains. She illustrated and listed species of solitary rugose and colonial tabulate corals of Early and Late Mississippian age. She also recognized and illustrated most of the colonial lithostrotionoids that occur in the Lisburne Group.

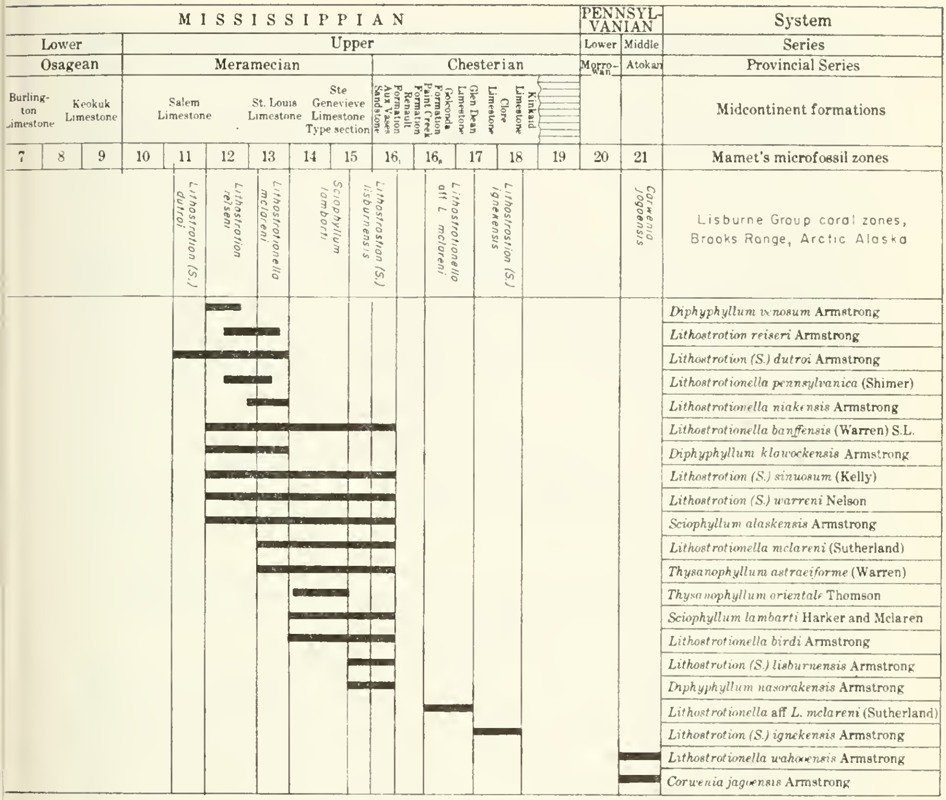
Corals are abundant in many of the Carboniferous Lisburne Group outcrops in the Brooks Range. These exposures (Text-figs. 1, 2) extend from the Canadian border on the east to the Chukchi Sea on the west. The study of the Lisburne coral faunas has been made in conjunction with detailed analyses of Lisburne Group biostratigraphy, petrology, diagenesis, and environments of deposition. The regional biostratigraphy is based on microfossil studies by Bernard L. Mamet, University of Montreal. Parts of these studies, including detailed stratigraphic description, have been published (Armstrong, Mamet, and Dutro, 1970, 1971; Armstrong and Mamet, 1970, and in press; and Mamet and Armstrong, 1972). Detailed analyses of the stratigraphy, petrography, and diagenesis of the Lisburne Group in northeastern Alaska have been made by Wood and Armstrong (in press) and in the west-central Brooks Range, by Armstrong (1970c). Armstrong (1970b, 1972a, b, 1973) published descriptions, illustrations, and stratigraphic and paleoecological analyses of the major groups of Lisburne corals.

Dunham's (1962) classification of carbonate rocks is used in this report.

BIOSTRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION OF CORALS

A preliminary zonation based on corals of the Lisburne Group and the known vertical stratigraphic distribution of the lithostrotionoid corals is shown on Text-figure 3, plotted on a geologic time scale based on Mamet's microfossil assemblage zones. *Lithostrotionella banffensis* (Warren), *Lithostrotion (S.) sinuosum* (Kelly), *L. (S.) warreni* Nelson, and *Thysanophyllum astraeiforme* (Warren) are each complex species groups which appear to have long stratigraphic ranges. Detailed morphologic studies now in progress on these fossils reveal considerable evolution in these corals from Zone 12 through Zone 16_1. An understanding of their evolution will result in new species with shorter stratigraphic ranges and better correlations within the Lisburne Group. Lithostrotionoid corals are not known in pre-Meramecian rocks of the Lisburne Group. Armstrong, Mamet, and Dutro (1970) reported that the oldest known carbonates in the central and eastern Brooks Range, based on microfossil evidence, are of earliest Keokuk (Osagean) age (Zone 8). Mamet (personal commun., 1970) reported that the oldest known carbonates in the Kogruk Formation of the De Long Mountains are also Zone 8.

Helen Duncan (*in* Bowsher and Dutro, 1957, pp. 5, 6) identified the solitary coral *"Zaphrentis" konincki s. l.* (Milne-Edwards and Haime) from the lower part of the type section of the Wachsmuth Limestone at Shainin Lake (W75-135, fig. 2) in Zone 9 (Osagean).



Text-figure 3.—Preliminary coral stratigraphic distribution and zonation of the Lisburne Group based on various species of colonial rugose corals. Some species on this chart, as *Lithostrotionella banffensis, Thysanophyllum astraeiforme, Lithostrotion (S.) warreni,* and *L. (S.) sinuosum,* are species groups which appear as shown to have long stratigraphic ranges. Detailed studies of these species groups now in progress reveal that with stratigraphic time significant morphological changes occur within each of these species groups, and new species, with shorter stratigraphic ranges, can be established.

In the east-central and eastern Brooks Range (Endicott, Philip Smith, Franklin, and Romanzof Mountains), thick sequences of from 100 to 460 m of Upper Mississippian, open marine, shallow water, platform, bryozoan-echinoderm-packstones, and wackestones contain abundant rugose colonial corals. However, these corals are also abundant in the basal transgressive phase of this facies. In the Romanzof, Franklin, and Shublik Mountains, the Meramecian shale and argillaceous limestone facies near the Kayak(?) Shale-Alapah Limestone contact commonly has an abundant lithostrotionoid coral fauna. The most common lithostrotionoid corals in the Meramecian rocks of the region are *Lithostrotionella banffensis* (Warren), *L. mclareni* (Sutherland), *L. birdi* Armstrong, *L. pennsylvanica* (Shimer), *Lithostrotion reiseri* Armstrong, *L.* (*Siphonodendron*) *warreni* Nelson, *L.* (*S.*) *sinuosum* (Kelly), *L.* (*S.*) *dutroi* Armstrong, *Thysanophyllum astraeiforme* (Warren), *Sciophyllum alaskaensis* Armstrong, *S. lambarti* Harker and McLaren, and *Diphyphyllum klawockensis* Armstrong. Associated with the lithostrotionoids are many colonies of the syringoporoid tabulate corals, individuals of *Faberophyllum* spp., and *Amplexizaphrentis* spp.

The Lisburne Group, to the west, in the Killik River (64A-5) to Mount Bupto region (68A-7), is thinner (less than 610 m thick) and is composed of dolomites, some of which were deposited in an intertidal-supratidal environment, and dolomitized shallow marine wackestones and packstones (Armstrong, 1970c). Corals are relatively rare, and those found are poorly preserved and are in the dolomitic bryozoan-echinoderm facies. Meramecian carbonate rocks at the Killik River section have yielded a small fauna of corals including *Lithostrotionella mclareni* (Sutherland), *Lithostrotion* (*S.*) *warreni* Nelson, and a few poorly preserved *Vesiculophyllum*? sp. The Mount Bupto section (68A-7) is extensively dolomitized, but colonies of *Lithostrotion* (*S.*) *sinuosum* (Kelly) (Armstrong, 1970c) are preserved in the chert.

Farther west, in the Arctic Foothills province, on Nuka Ridge, the type section of the Nuka Formation of Tailleur and Sable (1963) is now known to be composed of at least three thrust plates (Tailleur, Mamet, and Dutro, 1973), each of which is formed by rocks primarily of Mississippian age and (based on microfossils) from Meramecian (Zone 14) to Chesterian (Zone 19) in age. The Mississippian part of the Nuka Formation is formed of siltstone, arkosic sandstone and shale, and arkosic limestone. It contains a sparse fauna of solitary corals; no colonial corals are known from the Nuka Formation. The Upper Mississippian marine terrigenous shales and sandstones of the Nuka Formation was an unfavorable environment for coral growth.

Armstrong (1970b) reported a large fauna of Meramecian lithostrotionoid corals from the Kogruk Formation of the De Long Mountains. Sections 62C-15, 62C-31, and 60A-400-403 in the De Long Mountains indicate that the Kogruk Formation was deposited in an open marine environment on a subsiding shelf on which carbonate deposition and subsidence were in near equilibrium. These sections clearly show that the Meramecian corals of the Kogruk Formation are most abundant in specific rock types. The lithostrotionoid corals are common in bryozoan-echinoderm packstones and ooid packstones adjacent to ooid grainstones and well-sorted crinoid grainstones.

The Kogruk coral fauna is *Lithostrotion* (*S.*) *sinuosum* (Kelly), *L.* (*S.*) *warreni* Nelson, *Lithostrotionella mclareni* (Sutherland), *L. niakensis* Armstrong, *L. birdi* Armstrong, *L.* aff. *L. banffensis* (Warren), *Thysanophyllum astraeiforme* (Warren), *T. orientale* Thomson, *Sciophyllum lambarti* Harker and McLaren, and *S. alaskaensis* Armstrong. Also associated with the lithostrotionoids are the solitary coral *Faberophyllum* spp. and abundant syringoporoid corals.

Armstrong, Mamet, and Dutro (1971) listed a Meramecian (Zone 13) coral fauna from the base of section 68A-12. This incomplete section, in a structurally complex terrain, is exposed on a sea cliff in the northwestern Lisburne Hills. This location yielded the oldest known lithostrotionoid fauna in the Lisburne Hills region.

The corals collected from the base of section 68A-12 are: *Lithostrotion* (*S.*) *warreni* Nelson, *Lithostrotionella banffensis* (Warren), *L.* aff. *L. banffensis* (Warren), *L. niakensis* Armstrong, and syringoporoids.

South of this location, a large fauna of corals (similar to fauna from 68A-9 listed below) were found in the highest beds (68A-13) of the Nasorak Formation, with a foraminiferal fauna which indicates that they are in a transition zone between beds of Meramecian and Chesterian (Zones 15-16_1) age.

A few miles to the south at Cape Lewis (68A-9-11), a large fauna of lithostrotionoid corals was collected from Nasorak beds of early Chesterian age (Zone 16_i).

The coral faunas from both sections (68A-9 and 68A-13), and from the Nasorak Formation at Cape Thompson, are similar and contain the following: *Lithostrotion* (*S.*) *sinuosum* (Kelly), *L.* (*S.*) *warreni* Nelson, *L.* (*S.*) *lisburnensis* Armstrong, *Lithostrotionella banffensis* (Warren), *Lithostrotionella* sp., *L. mclareni* (Sutherland), *L. birdi* Armstrong, *Thysanophyllum astraeiforme* (Warren), *Sciophyllum lambarti* Harker and McLaren, *S. alaskaensis* Armstrong, and *Diphyphyllum nasorakensis* Armstrong.

In contrast to the central and eastern Brooks Range, where few lithostrotionoid corals are found above the Meramecian-Chesterian boundary, the Lisburne Hill fauna, as indicated by the microfossils, persisted in abundance into Zone 16_i (early Chesterian), then abruptly became extinct. This coral fauna is absent in beds of Zone 16_s age and younger.

Armstrong, Mamet, and Dutro (1971) reported from Zone 16_i at Cape Lewis, in the thick cyclic shallow shelf carbonate sequence, the occurrence of two new species of poorly preserved cerioid *Lithostrotionella.* Cyclic shelf carbonates of Zones 17 and 18, higher in the same section, contain only a few fragmentary solitary corals. One of the few coral taxa found in beds of Zone 17, or younger Chesterian age, is from the northeastern Brooks Range. Here, Armstrong (1972a) described *Lithostrotion (Siphonodendron) ignekensis* Armstrong in Zones 17-18 of the Alapah Limestone, from the Sadlerochit, Shublik, and Franklin Mountains.

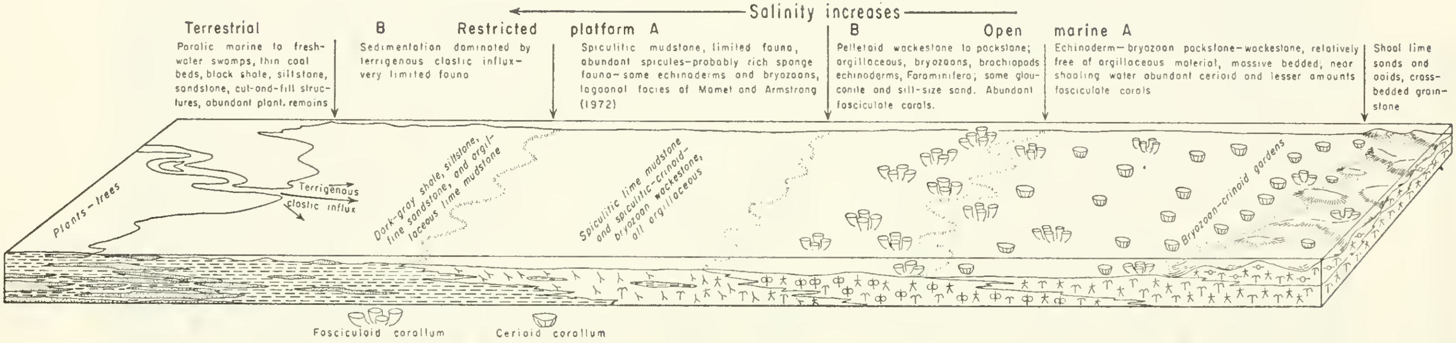
In arctic Alaska, Pennsylvanian carbonate rocks are known only from the central and eastern Brooks Range. The Wahoo Limestone of the Lisburne Group represents Morrowan (Zone 20) and Atokan (Zone 21) sediments (Text-fig. 2). Only fragments of solitary corals are known in the carbonate rocks of Morrowan age. Rugose corals are only moderately abundant in beds of Atokan age in the Wahoo Limestone. Armstrong (1972b) described two species of colonial rugose corals, *Lithostrotionella wahooensis* Armstrong and *Corwenia jagoensis* Armstrong, from beds with a foraminiferal fauna of Atokan age. Tabulate corals from the Atokan carbonate rocks are a thick-walled syringoporoid and *Michelinia* sp.

Preliminary studies of the lithostrotionoids indicate that the Lisburne Group can be divided into eight coral-assemblage zones. The zones in ascending order are: Meramecian, 4 zones: *Lithostrotion* (*S.*) *dutroi* Armstrong, *L. reiseri* Armstrong, *Lithostrotionella mclareni* (Sutherland), and *Sciophyllum lambarti* Harker and McLaren; Meramecian-Chesterian transition, 1 zone: *Lithostrotion* (*S.*) *lisburnensis* Armstrong; Chesterian, 2 zones: *Lithostrotionella* aff. *L. mclareni* (Sutherland) and *Lithostrotion* (*S.*) *ignekensis* Armstrong; Atokan, 1 zone: *Corwenia jagoensis* Armstrong.

Each assemblage zone is marked by the first appearance of the named species. The *Lithostrotion* (*S.*) *dutroi* Armstrong assemblage first occurs in Mamet's microfossil assemblage zone 11, Salem age equivalent, and is an index fossil for that part of the Lisburne Group, but the species extends upwards through the *L. reiseri* Armstrong and *Lithostrotionella mclareni* (Sutherland) coral-assemblage zones (Text-fig. 3). The base of the *L. reiseri* assemblage zone is characterized by the appearances of seven species of lithostrotionoid corals, of which *L. reiseri* is the most readily recognized and has the shortest stratigraphic range. The other six are *Diphyphyllum venosum* Armstrong, *D. klawockensis* Armstrong, *Lithostrotionella banffensis* (Warren) *s. l.*, *Sciophyllum alaskaensis* Armstrong, *Lithostrotion* (*S.*) *sinuosum* (Kelly) *s. l.*, *L.* (*S.*) *warreni* Nelson *s. l.*

The *Lithostrotionella mclareni* (Sutherland) assemblage zone of St. Louis equivalent age is also the first appearance of *Thysanophyllum astraeiforme* (Warren). The *Sciophyllum lambarti* assemblage zone is also the first appearance of *Thysanophyllum orientale* Thomson and *Lithostrotionella birdi* Armstrong. The *Lithostrotion* (*S.*) *lisburnensis* Armstrong assemblage zone which is latest Meramecian and earliest Chesterian age also contains the first occurrence of *Diphyphyllum nasorakensis* Armstrong and eight species of lithostrotionoid corals that extend from lower coral zones (Text-fig. 3). The late Meramecian-earliest Chesterian marks the maximum abundance of individual colonies and development of lithostrotionoid corals in the Lisburne Group.

Earliest Chesterian time is marked by a major extinction of lithostrotionoid corals in the Lisburne Group. A new species, *Lithostrotionella* aff. *L. mclareni,* is occasionally found in the lower and middle Chesterian strata and is an index zone marker.



Text-figure 4. — Diagrammatic drawing illustrating the transgressive facies between the terrigenous clastic rocks of the Kayak(?) Shale and Nasorak Formation and the calcareous to carbonate sedimentary rocks. The environments of abundant fasciculoid and cerioid corals are shown by symbols (after Armstrong, 1974).

L. (*S.*) *ignekensis* is an index fossil for upper Chesterian beds in the north flank of the eastern Brooks Range. It is found in association with a syringoporoid.

Corals are rare in the Morrowan beds, but Atokan beds are recognized by *Corwenia jagoensis* Armstrong assemblage zone which contains also *Lithostrotionella wahooensis* Armstrong.

PALEOECOLOGY OF LISBURNE GROUP COLONIAL CORALS

Outcrop and sedimentary structure studies combined with petrographic and diagenetic studies of the transgressive terrigenous clastic rocks of the Kayak and Kayak(?) Shales and carbonate platform rocks of the Lisburne Group have culminated in the development of facies models for the distribution of Lisburne corals.

The Kayak(?) Shale of northeastern Brooks Range and the Nasorak Formation of the sea cliffs of northwestern Alaska are Upper Mississippian cyclic transgressive, terrigenous clastic sedimentary rocks beneath the shelf carbonate rocks of the Lisburne Group. Analysis of the stratigraphic sections of the Kayak(?) Shale in the northeastern Brooks Range in sections 70A-2, 70A-4, 69A-4K, and 71A-3 and the Nasorak Formation at Cape Lewis (69A-9) shows coral distribution and facies model as shown in Text-figure 4 (from Armstrong, Mamet, and Dutro, 1971; Armstrong, 1974).

Fasciculoid corals, such as *Lithostrotion* (*Siphonodendron*) spp. and *Syringopora* spp., abundant in argillaceous-rich carbonate beds, are believed to have had a tolerance for turbid waters, whereas the cerioid corals are more abundant in the pure bioclastic wackestones and packstone.

The Lisburne Group consists of cyclic carbonate rocks deposited on a slowly sinking miogeosynclinal carbonate shelf (Text-fig. 5; Armstrong, 1970b, c, 1972b, 1974; Armstrong, Mamet, and Dutro, 1971).

Lithostrotionoid corals are found in the Lisburne Group in relatively pure well-sorted bioclastic to pelletoid wackestones and packstones which are stratigraphically adjacent to echinoderm-bryozoan-ooid grainstones. A carbonate depositional model (Text-fig. 5) for the Lisburne Group indicates maximum coral growth adjacent to the shoaling water facies on the open marine shelf and open marine platform facies (Text-fig. 5).

Corals are very abundant at some localities in the Carboniferous strata of Alaska. They form biostromal beds, but no reef-type structures or vertical accumulations are known in Lisburne outcrops.

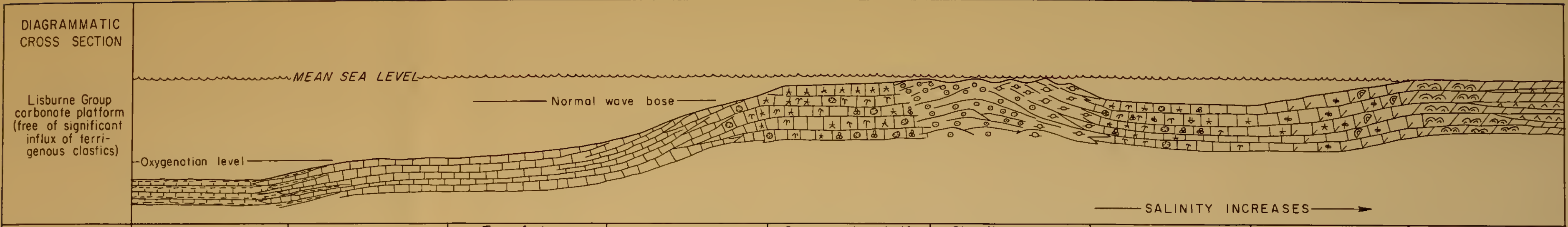
REGIONAL RELATIONSHIPS OF THE LISBURNE GROUP

CORAL FAUNAS

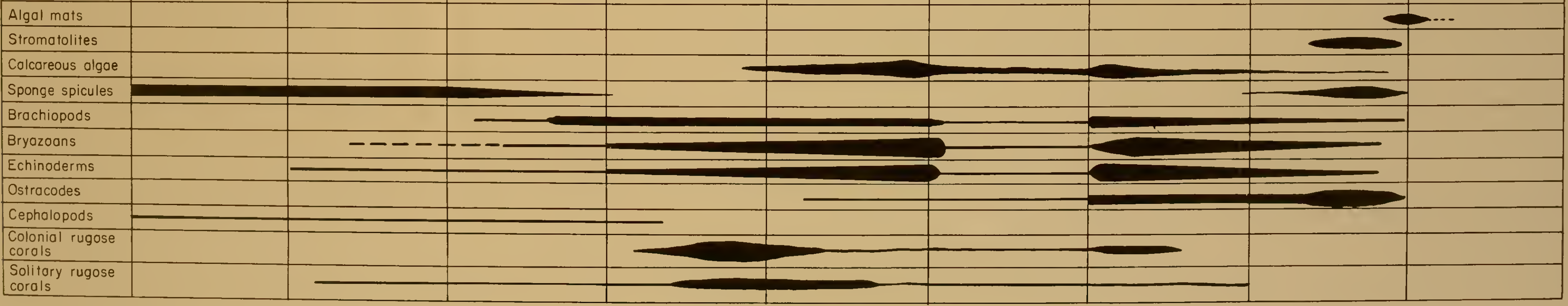
Bowsher and Dutro (1957) and Yochelson and Dutro (1960) published a megafossil zonation for the type Lisburne Group section at Shainin Lake and recognized three lithostrotionoid zones. In the Alapah Limestone they recognized a *Lithostrotion* aff. *L. asiaticum* (Yabe and Hayasaka) zone in the dark limestone member. *L.* aff. *L. asiaticum* is the same as *L.* (*S.*) *dutroi* Armstrong (1972a). This horizon at the type section marks the upper range of the species. Bowsher and Dutro's (1957) *Sciophyllum lambarti* Harker and McLaren zone in the banded limestone member is the same as the *S. lambarti* assemblage zone of this report. Their *Lithostrotionella*? sp. zone from the light-gray limestone member is an undescribed species of a cerioid lithostrotionoid with small-diameter corallites. This species is common in the uppermost Meramecian and lowermost Chesterian rocks of the Lisburne Group.

The Meramecian (Zones 12 through 15) coral fauna contains many species in common with the contemporaneous Peratrovich Formation on Prince of Wales Island, southeastern Alaska. These rocks contain the following species of corals in common (Armstrong, 1970a): *Lithostrotion* (*Siphonodendron*) *warreni* Nelson, *L.* (*S.*) *sinuosum* (Kelly), *Lithostrotionella birdi* Armstrong, *L. banffensis* (Warren), *L. pennsylvanica* (Shimer), *Thysanophyllum astraeiforme* (Warren), *Sciophyllum alaskaensis* Armstrong, and *Diphyphyllum klawockensis* Armstrong.

The Lisburne corals shown on Text-figure 3, which occur in the upper half of microfaunal Zones 13 and 14, correspond approximately to Macqueen and Bamber's (1968) macrofaunal zones 2 and 3, and those corals in Zone 15, to their macrofaunal zone 4 for the Mississippian of Alberta, Canada. Macqueen and Bamber's (1967, 1968) and Petryk, Mamet and Macqueen's (1970) papers on the Lower



Facies; facies numbers	Basin-euxinic 1	Tidal Shelf 2	Toe of slope (carbonate rocks) 3	Foreslope 4	Open marine shelf (crinoid-bryozoan gardens) 5	Shoaling water (carbonate sand banks) 6	Open platform 7A | 7B	Restricted platform 8A | 8B	Intertidal to supratidal 9
Lithology	Shales, radiolarian cherts and siltstones	Interbedded thin to medium-bedded, lime mudstones, dolomites and cherts	Interbedded limestones and dark-gray shales	Variable, depending on water energy upslope, sedimentary breccias and lime sand-lime mudstones	Bedded crinoid-bryozoan wackestones, packstones, and grainstones	Crinoid-bryozoan to ooid packstones and grainstones	Variable carbonate rocks, bryozoan-crinoid packstones-wackestones; chert common	Fine and coarse crystalline dolomites; dolomitic-crinoid-bryozoan wackestones and packstones; dolomitic pelletoid lime mudstones	Irregularly laminated dolomites and dolomitic lime mudstone, anhydrite and calcite pseudomorphs of anhydrite common-algal mats; may grade into clastic red beds
Color	Dark brown to black	Gray brown	Gray to dark gray	Gray to light gray	Light gray	Light gray	Light gray	Light gray to gray	Gray, yellow, brown, red
Bedding and sedimentary structures	Very even millimeter laminations, rhythmic bedding ripple cross-laminations, burrows, and worm trails on bedding surfaces	Thoroughly burrowed thin to medium wavy to nodular beds; bedding surfaces show diastems	Laminations may be minor, many massive beds. Lenses of graded sediments. Lithoclasts and exotic blocks	Slumps in soft sediments. Foreset bedding; exotic blocks	Massive to thick beds, some crossbedding	Medium to large-scale crossbedding; festoons common	Abundant burrows	Birdseye structure, algal mats on or near intertidal zone, stromatolites in very shallow water, graded bedding, dolomite, crossbedded sands in tidal channels	Anhydrite rhombs, bedded anhydrite, cracks, chips, dried algal mat
Terrigenous clastic rocks, admixed or interbedded	Quartz silt and shale, fine-grained siltstone; cherty	Quartz silts, siltstones and shales, well segregated beds	Some shales, silts, and fine siltstones	Some shales, silts, and fine thin-bedded siltstones	Clastic material rare	Only some quartz sand admixed	Clastic and carbonate rocks in well-segregated beds	Clastic and carbonate rocks in well-segregated beds	Windblown, land-derived admixtures, clastic rocks may be an important unit



Carboniferous of southwestern Alberta list for zones 2-4 the following species of corals in common with the Lisburne Group: *Lithostrotion* (*S.*) *warreni* Nelson, *Lithostrotionella pennsylvanica* (Shimer), *L. mclareni* (Sutherland), and *Thysanophyllum astraeiforme* (Warren). The large, solitary corals *Faberophyllum* spp. and *Ekvasophyllum* spp. are common to both areas.

Macqueen and Bamber listed from southwestern Alberta three taxa which have not been found in the Lisburne Group: *Lithostrotionella shimeri* (Crickmay), *Lithostrotion* (*S.*) *arizelum* (Crickmay) from the Meramecian, and *Lithostrotion* (*S.*) *genevievensis* Easton from the lower Chesterian.

Sando, Mamet, and Dutro's (1969, p. E7) list of lithostrotionoids from the Mississippian of the northern Cordilleran of the United States showed no species in common with the Lisburne Group.

Rugose corals from the Wahoo Limestone (Atokan) of the Lisburne Group are represented by two new species, *Corwenia jagoensis* Armstrong and *Lithostrotionella wahooensis* Armstrong. The nearest described morphologic and time-stratigraphic equivalents of the latter are *Lithostrotionella orboensis* Groot (1963) from the upper Moscovian of Spain and *Petalaxis mohikana* Fomichev (1953) from the upper Moscovian of the Donetz Basin, U.S.S.R. *Corwenia jagoensis* Armstrong shows close similarity to the late Moscovian coral *Corwenia symmetrica* (Dobrolyubova) (1958) from Spain and from the Moscow and Donetz Basins of the U.S.S.R. Taxa similar to *L. wahooensis* have not been described from the Pennsylvanian of the Cordilleran region of North America.

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ONTOGENY AND SYSTEMATICS OF TIMEISCHYTES CASTERI, N. SP.: AN ENIGMATIC DEVONIAN EDRIOASTEROID

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ABSTRACT

Timeischytes casteri, n. sp. is a member of a Late Devonian hardground community. Its ontogeny and morphology suggest relationship with several other unusual edrioasteroids which form a new suborder of isorophid edrioasteroids, the Cyathocystina.

INTRODUCTION

A new and unusual edrioasteroid, *Timeischytes casteri,* n. sp., is a numerically important member of a Late Devonian (Frasnian) hardground community of the Mason City Member, Shell Rock Formation of Iowa. Koch and Strimple (1968, p. 3) described the substrate and associated biocoenose which includes cystoids (*Adocetocystis williamsi* Strimple and Koch, *Strobilocystites calvini* White), edrioasteroids, worm tubes (*Spirorbis*), tabulate corals (*Aulopora*), scarce rugose corals (*Pachyphyllum* and *Smithiphyllum*), bryozoans (*Hernodia*), and a few small subspherical stromatoporoids. All but the stromatoporoids attached themselves to the knobby surface of a lithified, highly bored micrite. Koch and Strimple (1968, p. 5) concluded that the hardground is an erosional surface because of its irregular, rounded knobs, prominent borings filled with material from the superjacent argillaceous dolomite, conspicuous rims of pyrite impregnation, pebbles of identical limestone within the channels between knobs, and lack of evidence of an algal origin. Corrosion was probably subaerial. The encrusting organisms became established after erosion and represent a shallow subtidal or perhaps intertidal community. Other organisms, including a variety of brachiopods found in the bottoms of the channels between the knobs may represent detritus washed in from adjacent areas. One complete asteroid specimen which apparently lived in the channels has been found.

At least three species of edrioasteroids belong to this hardground community. *Hadrochthus commensalus* Bell, 1974, is known from only a few specimens. It lived attached to the theca of the cystoid *Adocetocystis williamsi.* This unique edrioasteroid-cystoid associa-

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tion suggests a commensal relationship (Bell, 1974). Members of the other two species encrusted the upper surface of the limestone knobs in incredible profusion; one knob 7 × 7 cm supports over one hundred specimens. Adults of one species, described by Thomas (1924) as *Agelacrinites hanoveri,* are commonly 20 mm in diameter; the other species, *Timeischytes casteri,* n. sp., is unusually small, with adults ranging from 4 to 7 mm in diameter. Juveniles of both species are abundant and range to less than 0.5 mm in diameter. The ontogeny of *Agelacrinites* (*sensu lato*) *hanoveri* will be presented in a separate report. (*Agelacrinites* was redefined in Bell, 1974. *Agelacrinites hanoveri* may belong to the genus *Postibulla* Bell, 1974).

Members of both encrusting species are intermixed on the knobs without apparent order and not uncommonly adjacent individuals are in contact. Where two *Timeischytes casteri* touch, the thecal margins of both are straight along the line of contact because the rest of their margins continued to expand while the contiguous parts merely thickened. A similar phenomenon occurred where two *Agelacrinites hanoveri* met. In contrast, where a specimen of *Agelacrinites hanoveri* grew into contact with a *Timeischytes casteri,* the former overgrew the latter. All stages of this phenomenon are common, ranging from specimens with only a small part of the rim overgrown to specimens entirely covered and presumably smothered. Even small *Agelacrinites hanoveri* could encroach upon larger *Timeischytes casteri* (Text-fig. 19; Pl. 3, fig. 3). The largest known *Timeischytes casteri* is partially overlapped by a large *Agelacrinites hanoveri* (Text-fig. 28; Pl. 5, figs. 3-4). Apparently *Timeischytes casteri* could not overgrow *Agelacrinites hanoveri.*

The curious ability of *Agelacrinites hanoveri* to consistently dominate by growing over adjacent *Timeischytes casteri* may be explained by the differences of their peripheral rims. The former has a polyplated flexible rim formed by five to eight circlets of plates; those of the proximal circlets are largest. The plates of each circlet are overlapped distally by plates of the next circlet; plates progressively diminish in size to the small ovoid plates of the most distal circlet. In contrast the peripheral rim of *Timeischytes casteri* (Pls. 1-5) is a massive, non-flexible structure apparently formed by six to nine large thick plates so tightly joined (either sutured or fused) that their boundaries are visible only in weathered specimens. A few small plates of an irregular and disjunct second circlet are seen in some specimens (Pl. 1, fig. 10; Pl. 3, figs. 3-4) but these are wedged between the distal margins of the proximal elements. The rim gradually thins to a diaphanous margin which appears to merge with the substrate to which it apparently was tightly cemented. The attachment of a small *Agelacrinites hanoveri* to the exterior of the massive rim of the *Timeischytes casteri* in Text-fig. 19 (Pl. 3, fig. 3) suggests the tissue investiture of the latter was exceedingly thin or perhaps nonexistent, with tissue restricted to the stroma canals.

Agelacrinites hanoveri apparently could lift the edge of its flexible and non-fused rim off the substrate upon contact with an object such as the theca of a *Timeischytes casteri* and thus overgrow it; however, it did not overgrow its own kind. In contrast, the cemented, non-flexible rim of *Timeischytes casteri* could not be raised and where it encountered a large obstruction, that section of the rim ceased extension and merely thickened. Further extension required attainment of sufficient thickness to override the object, an adaptation adequate for minor substrate irregularities but not for overriding other living edrioasteroids.

SYSTEMATIC PALEONTOLOGY

Class EDRIOASTEROIDEA Billings, 1858

Order ISOROPHIDA Bell, 1974

Suborder CYATHOCYSTINA, new subord.

Diagnosis. — Isorophida with: 1) domal or modified domal theca; 2) oral area including four or more primary oral plates, two pairs of lateral shared coverplates and, commonly, small secondary orals; 3) hydropore structure in right posterior part of oral area, formed by orals and/or ambulacral coverplates and a large hydropore oral; 4) ambulacral coverplates in a single biseries, without passageways but with intrathecal and intraambulacral extensions which firmly lock the coverplates into the theca as well as to adjacent ones; 5) uniserial floorplates without passageways; 6) large, thick and relatively few interambulacral plates; 7) valvular anal structure formed by one circlet of large triangular plates — commonly four to six; 8) peripheral rim formed by relatively few circlets of plates, in some fused to form a massive non-flexible structure or even a massive basal cup flooring as well as laterally surrounding the thecal cavity; 9) plates of the oral-ambulacral series may also become fused or lost, reducing the number of plates in all of the structures except perhaps the anal valve.

Discussion. — The suborder Cyathocystina accommodates those forms which have the unique combination of characters shown by *Timeischytes*. Higher taxa in the class Edrioasteroidea are based on morphological features that apparently relate to three different modes of respiration (Bell, 1973, 1974). *Timeischytes* (Pls. 1-4; Pl. 5, figs. 1-5) is clearly a member of the order Isorophida, for it has a domal theca, hydropore opening along the junction between plate boundaries, uniserial ambulacral floorplates without sutural passageways, and ambulacral coverplates that lock into the theca and completely hide the floorplates. The coverplates are without passageways which link the thecal cavity to the exterior of the theca. Thus *Timeischytes* is not of the suborder Lebetodiscina in which respiration was by external extensions of the hydrovascular system that extend out through coverplate passageways. Members of the Isorophina, the other suborder of Isorophida, have a valvular anal structure and respired by anal pumping. *Timeischytes* does have a valvular anal structure although it is composed of a single circlet of plates, not two or three as in the Isorophina. Moreover, *Timeischytes* has a single biseries of ambulacral coverplates, whereas the Isorophina are characterized by multiple biseries of cyclic sets of ambulacral coverplates.

In addition to *Timeischytes megapinacotus* (Pl. 5, fig. 5) and *Timeischytes casteri* (Pls. 1-4; Pl. 5, figs. 1-4), other members of this group may include:

Hadrochthus commensalus Bell, 1974, Upper Devonian, Iowa
Cyathocystis plautinae Schmidt, 1880, Middle Ordovician, Estonia
C. rhizophora Schmidt, 1880, Middle Ordovician, Estonia
C. americanus Bassler, 1936, Middle Ordovician, Tennessee (Pl. 5, figs. 6-7)
C. oklahomae Strimple and Graffham, 1955, Middle Ordovician, Oklahoma
Cyathotheca suecica Jaekel, 1927, Middle Ordovician, Sweden
C. corallum (Jaekel) 1918, Middle Ordovician, U.S.S.R.
? *Postibulla jasperensis* Harker, 1953, Lower Mississippian, Alberta, Canada

Family **CYATHOCYSTIDAE** Bather, 1899

? Characters of the suborder.

Discussion. — Bather (1899) proposed the family Cyathocystidae for *Cyathocystis plautinae.* Jaekel (1918, 1927), Bassler (1936), and Regnéll (1966) included all species of *Cyathocystis* and *Cyathotheca* in Bather's family which is here placed under the new suborder Cyathocystina with question. *Timeischytes* and *Hadrochthus* are tentatively added to the Cyathocystidae.

Most of the information on the Ordovician species is from the literature. A preliminary examination of these specimens suggests that a restudy of the Ordovician forms will separate them from the Devonian species at the family level.

Genus **TIMEISCHYTES** Ehlers and Kesling, 1958

1958. *Timeischytes* Ehlers and Kesling, Jour. Paleont., vol. 32, pp. 933-936, pl. 121, text fig. 1.

1966. *Timeischytes* Ehlers and Kesling, Regnéll, *in* Treatise Invert. Paleont., R. C. Moore (ed.), Lawrence, pt. U, Echinodermata 3, vol. 1, pp. U167, fig. 126-6.

Type species: *T. megapinacotus* Ehlers and Kesling, 1958, by original designation.

Revised diagnosis. — Theca domal; oral area with five primary oral plates, two pairs of lateral shared coverplates, secondary orals, and a large hydropore oral in the right posterior sector; oral area large in proportion to thecal diameter; hydropore apparently in the right posterior part of the oral area, along part of the anterior margin of the hydropore oral; ambulacra straight, short, broad, tapered distally to blunt ends; coverplates form a single biseries of more or less alternating plates, with intrathecal and intraambulacral extensions; floorplates uniserial; interambulacra relatively small, interambulacral plates relatively large, commonly 1 to 3 per interambulacrum; peripheral rim relatively large, with few circlets of plates.

Discussion. — *Timeischytes* was accurately described by Ehlers and Kesling in 1958. The type species of this genus was based on two small specimens, 4 mm and 4.5 mm in diameter (Pl. 5, fig. 5). The description here of the ontogeny of a second species confirms their contention that the types of *Timeischytes megapinacotus* are adults and not juveniles of some other species.

Ehlers and Kesling's systematic placement of this genus is regarded as inappropriate because they had to rely upon inadequate descriptions of other taxa.

Occurrence. — Dock Street Clay Member, Four Mile Dam Limestone, Middle Devonian — Mason City Member, Shell Rock Formation, Upper Devonian. Michigan and Iowa.

Timeischytes casteri, n. sp. Pls. 1-4; Pl. 5, figs. 1-4

Diagnosis. — Theca small, adults commonly 4 to 6 mm in diameter; hydropore oral ranges from moderate to uncommonly large; peripheral rim formed by one circlet of a few massive plates so tightly sutured (or fused) as to partially obscure their boundaries; some with a distal, incomplete, disjunct circlet of small plates.

Comparison. — *Timeischytes casteri* is similar to the type species except for the peripheral rim. In adults, this massive, nonflexible structure apparently includes up to eight or nine large geniculate plates which taper distally to a very thin edge that seems to merge with the substrate. The number of plates is uncertain because suturing (or fusion) is so tight that junctions are visible only in extensively weathered specimens. Small, subtriangular to ovoid plates may be wedged between the distal parts of the proximal ones. These form a disjunct and incomplete second circlet. The basal surface of the rim appears to have been firmly connected to the substrate. In contrast, *Timeischytes megapinacotus* (Pl. 5, fig. 5) has at least three circlets of rim plates and individual plates are distinct. The proximal circlet includes ten or eleven large geniculate plates. These are distally overlapped by smaller plates of the second circlet, usually six to eight per large proximal plate. Two to four small plates of the third and most distal circlet overlap each plate of the second circlet.

Ontogeny and morphology. — Out of several thousand specimens of *Timeischytes casteri* surveyed, 300 were photographed and studied. Line drawings of 82 specimens were made by tracing thecal plate boundaries on photographic enlargements while concurrently examining the specimens under magnification. A complete growth series is displayed by 28 of these which are included as the text figures. The photographs used as underlays for the line drawings are shown in Plates 1-5; the text-figure explanations list the plate figures with which they correspond. The smallest specimen shown, about 0.6 mm in diameter, is over twice the size of the smallest specimen found, but plate boundaries in smaller individuals were judged too tenuous to be meaningful. Even in specimens 0.6-2 mm in diameter, plate boundaries are hard to recognize. All drawings were prepared before any interpretation was made. The repetition of the pattern in other specimens gives reasonable confidence in the stages depicted here.

The extremely thin distal margin of the peripheral rim is commonly eroded. This erosion and irregularities of the substrate may make the relationship of a specimen's total diameter to its growth stage unreliable.

Plates of the oral-ambulacral series and the rim are seen first in specimens about 0.6 mm in diameter (Text-fig. 1). These include the left and right anterior primary orals (A), the central posterior oral (P_1), the hydropore oral (H), and the left and right lateral bifurcation plates (B) of ambulacral pairs I-II and IV-V respectively. The transverse oral midline extends across the specimen between the two anterior primary orals and the posterior primary oral. It reaches from the proximal tip of one bifurcation plate to the proximal tip of the other and divides the theca into anterior and posterior halves. The midlines' right and left halves define the right and left primary ambulacral radii. The anterior oral midline extends from the proximal tip of the posterior primary oral out between the two anterior primary orals and defines the anterior primary radius. Extension of this radius posteriorly allows division of the theca into right and left halves. Interambulacrals and anals are not yet present or are present but hidden beneath the rim, or not preserved. Plates of the rim are not distinct.

As thecal diameter doubles (to 1.2 mm), the initial six plates and rim increase rapidly and approximately proportionately in size (Text-figs. 2-4). Anal and interambulacral plates are seen in figures 3 and 4. The right posterior primary oral (P_2) is the next oral-ambulacral element added. The specimens suggest three or four anals are present but are partly hidden beneath the edge of the rim, as are the interambulacrals.

Text-figure 5 (1.2 mm) shows the addition of the third and final posterior primary oral (P_3), adjacent to the left margin of the first (P_1). The first ambulacral coverplate is along the anterior axis (ambulacrum III).

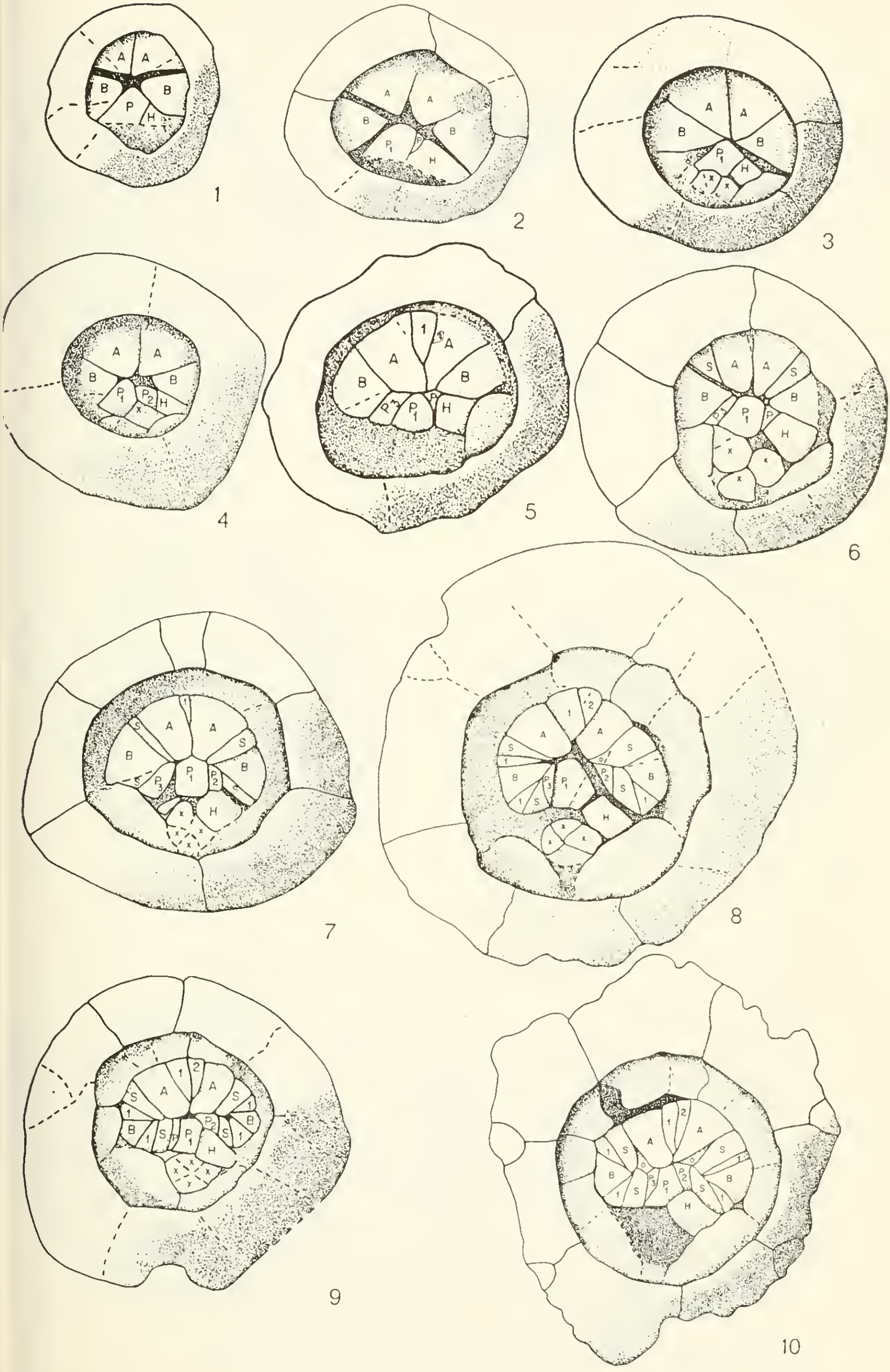
Text-figure 6 (1.2 mm) shows the intercalation of the left

EXPLANATION OF TEXT FIGURES 1-28

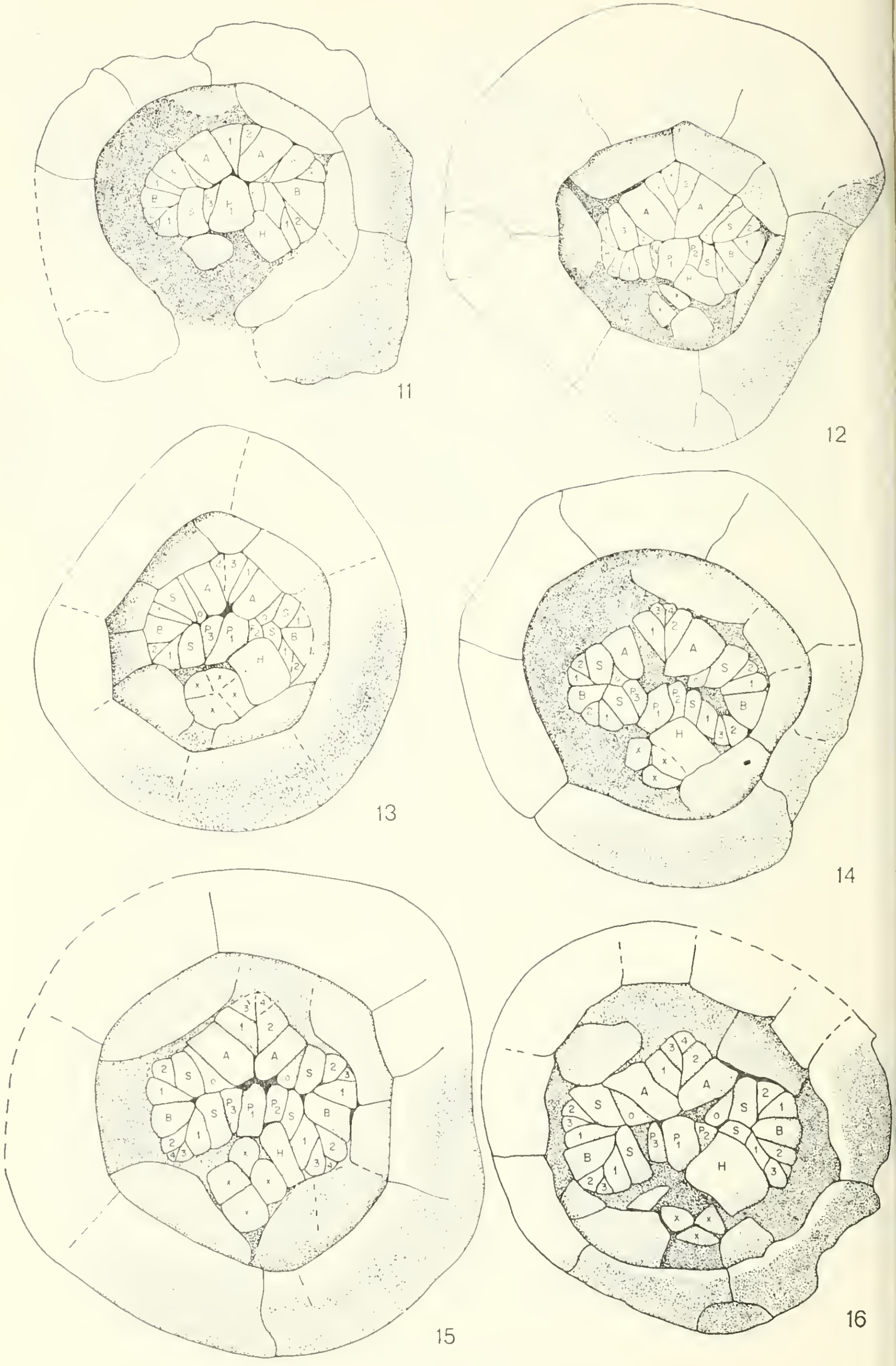
Timeischytes casteri, n. sp.

A, right and left anterior primary orals; B, right and left lateral bifurcation plates; H, hydropore oral plate; o, secondary oral plate; P_1, central posterior primary oral; P_2, right posterior primary oral; P_3, left posterior primary oral; S, right and left anterior and posterior lateral shared coverplates; X, anal plate. NYSM, New York State Museum.

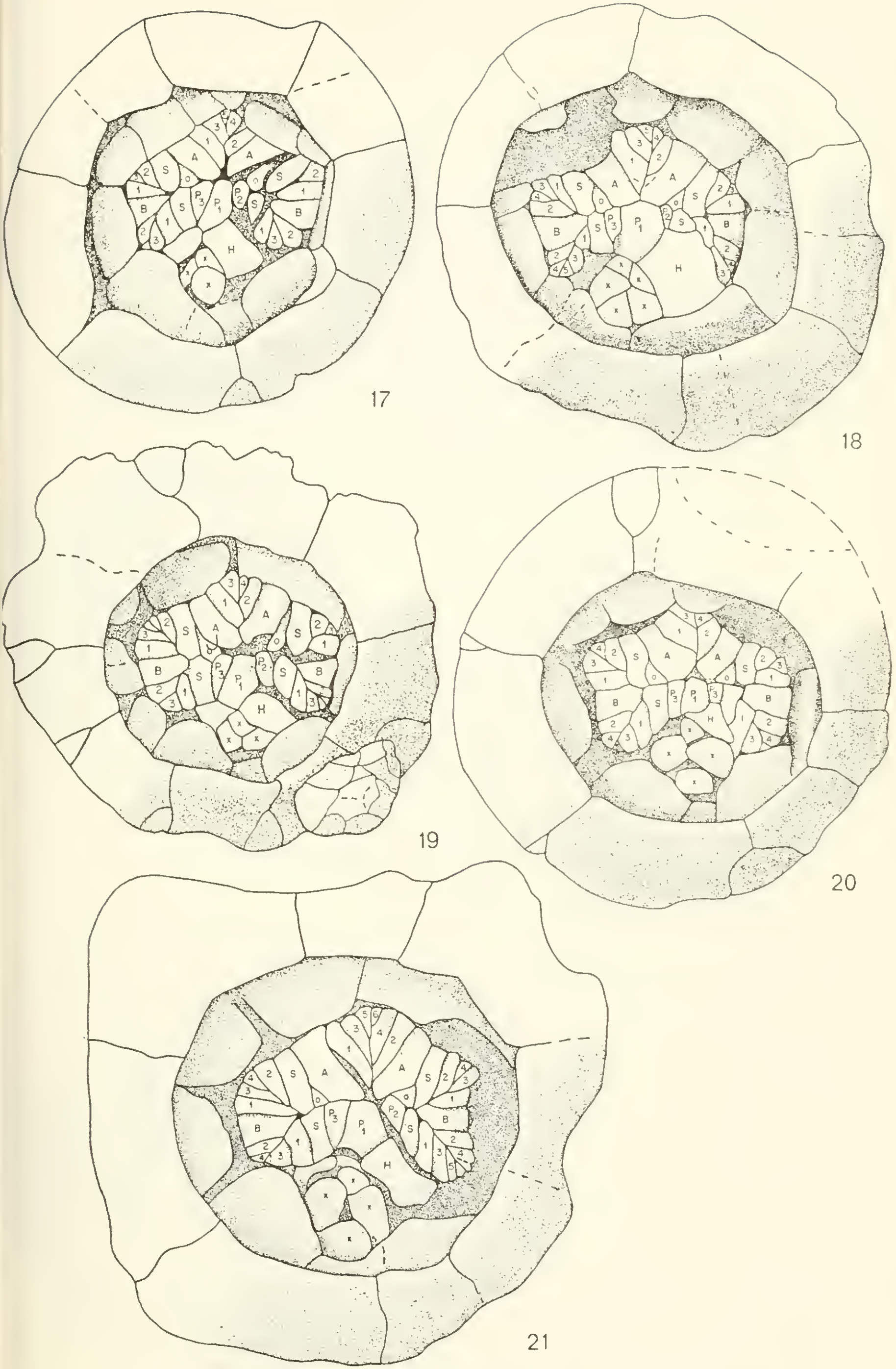
1.	Juvenile	NYSM 13263, ×40, Pl. 1, fig. 1
2.	Juvenile	NYSM 13264, ×50, Pl. 1, fig. 2
3.	Juvenile	NYSM 13265, ×40, Pl. 1, fig. 3
4.	Juvenile	NYSM 13266, ×28, Pl. 1, fig. 4
5.	Juvenile	NYSM 13267, ×35, Pl. 1, fig. 5
6.	Juvenile	NYSM 13268, ×35, Pl. 1, fig. 6
7.	Juvenile	NYSM 13269, ×35, Pl. 1, fig. 7
8.	Juvenile	NYSM 13270, ×25, Pl. 1, fig. 8
9.	Juvenile	NYSM 13271, ×25, Pl. 1, fig. 9
10.	Juvenile	NYSM 13272, ×25, Pl. 1, fig. 10
11.	Juvenile	NYSM 13273, ×25, Pl. 2, fig. 1
12.	Juvenile	NYSM 13274, ×20, Pl. 2, fig. 2
13.	Juvenile	NYSM 13275, ×20, Pl. 2, fig. 3
14.	Juvenile	NYSM 13276, ×20, Pl. 2, fig. 4
15.	Advanced Juvenile	NYSM 13277, ×25, Pl. 2, fig. 5
16.	Advanced Juvenile	NYSM 13278, ×22, Pl. 2, fig. 6
17.	Advanced Juvenile	NYSM 13279, ×20, Pl. 3, fig. 1
18.	Advanced Juvenile	NYSM 13280, ×20, Pl. 3, fig. 2
19.	Advanced Juvenile	NYSM 13281, ×20, Pl. 3, fig. 3
20.	Young Adult	NYSM 13282, ×18, Pl. 3, fig. 4
21.	Young Adult	NYSM 13283, ×22, Pl. 3, fig. 5
22.	Young Adult	NYSM 13284, ×20, Pl. 3, fig. 6
23.	Young Adult	NYSM 13285, ×25, Pl. 4, fig. 1
24.	Young Adult	NYSM 13286, ×18, Pl. 4, fig. 2
25.	Young Adult	NYSM 13287, ×17, Pl. 4, fig. 3
26.	Adult	NYSM 13288, ×17, Pl. 4, fig. 5
27.	Adult	NYSM 13289, holotype, ×10, Pl. 5, fig. 1
28.	Adult	NYSM 13290, ×11, Pl. 5, fig. 3



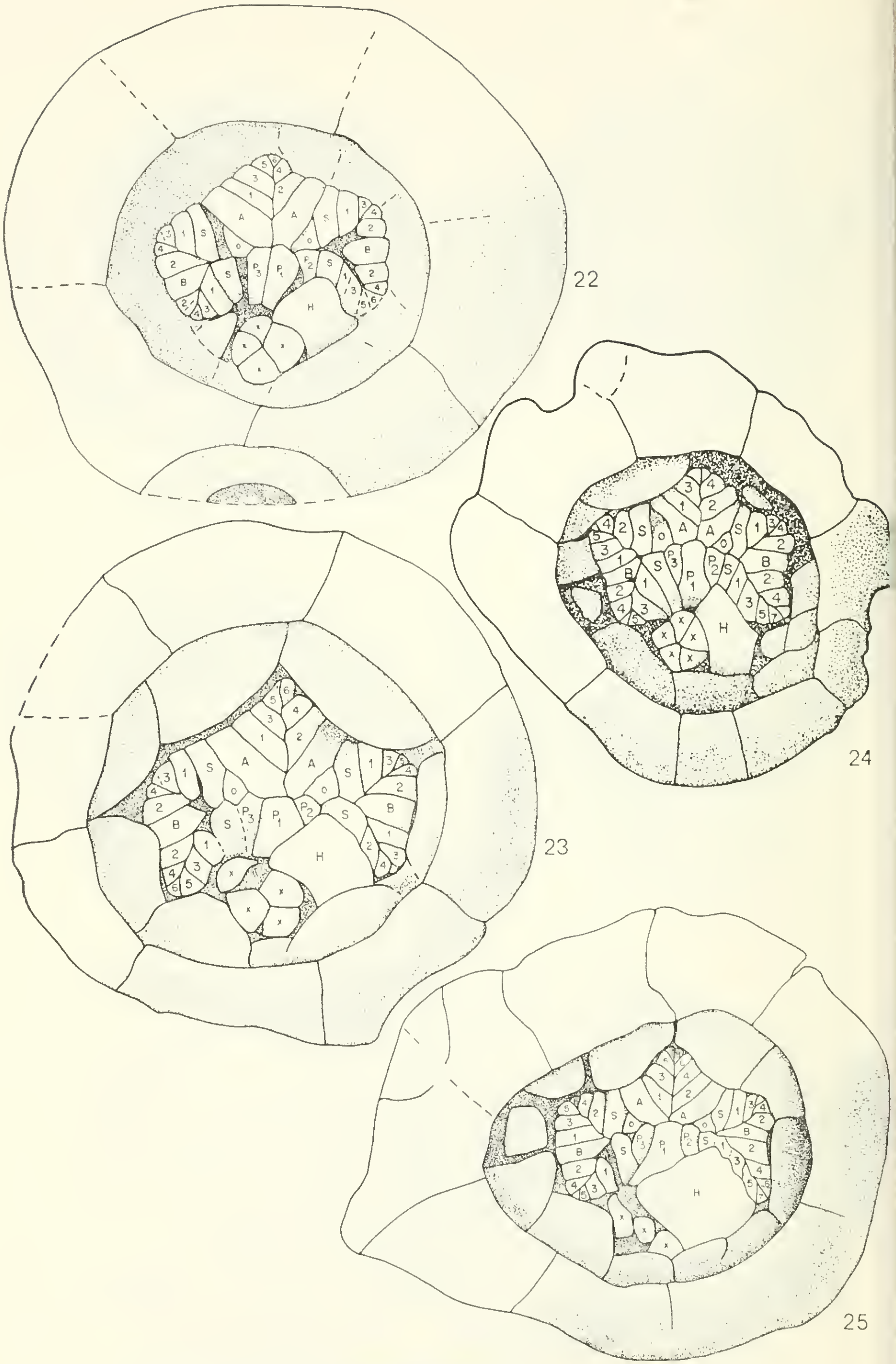
Text-figures 1-10. See explanation p. 40.



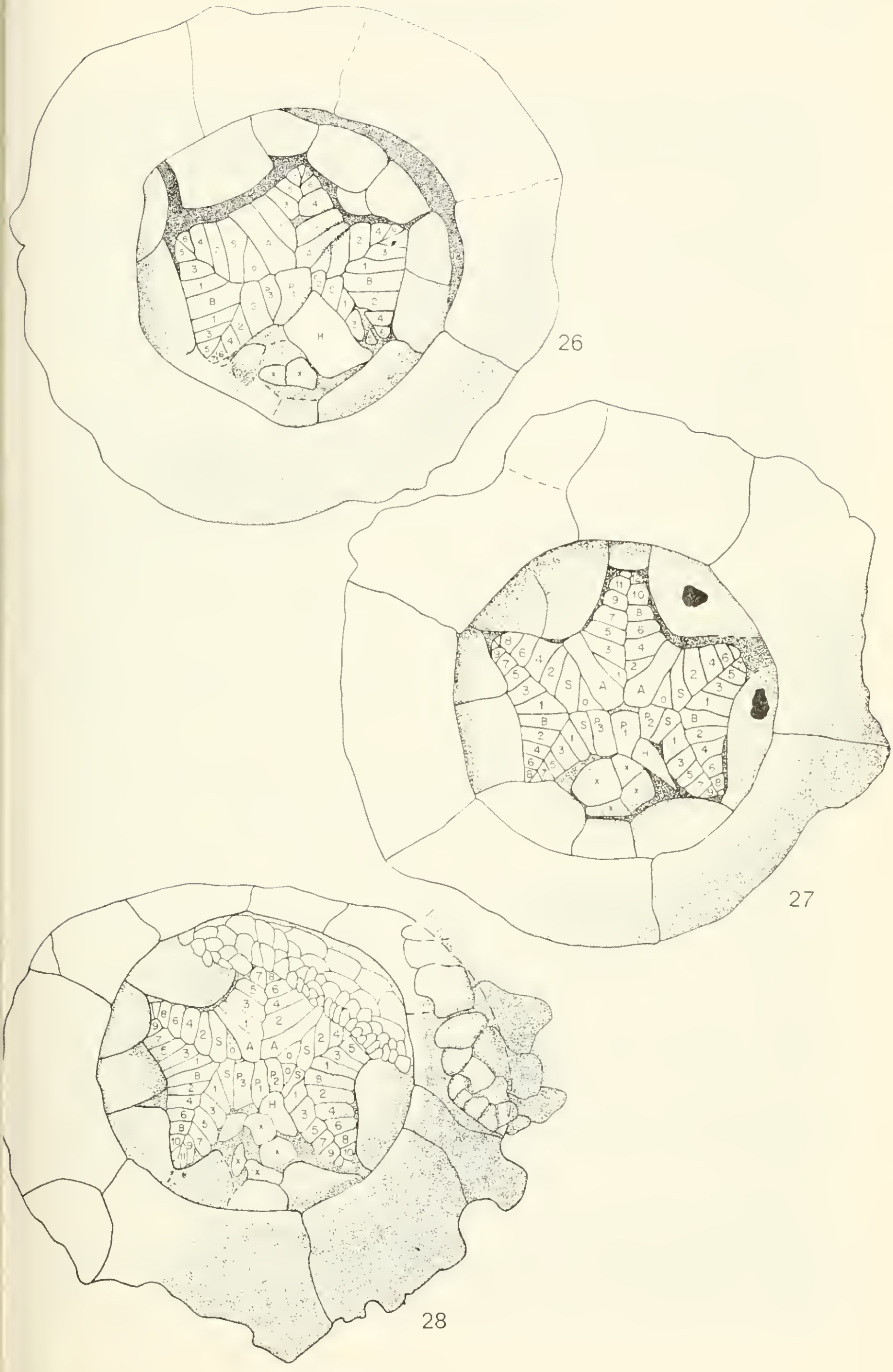
Text-figures 11-16. See explanation p. 40.



Text-figures 17-21. See explanation p. 40.



Text-figures 22-25. See explanation p. 40.



Text-figures 26-28. See explanation p. 40.

and right anterior members of the two pairs of lateral shared coverplates (S). The posterior interambulacrum includes at least two large interambulacrals and three anals (X). The rim may include six plates.

Text-figure 7 (1.3 mm) shows the intercalation of the left and right posterior members of the two lateral pairs of shared coverplates (S). The specimen suggests at least one interambulacral plate covers each interambulacrum except the posterior where there are two. The rim includes seven plates.

Text-figure 8 (2.2 mm) reveals the intercalation of a secondary oral (o) between the right anterior primary oral and right anterior shared coverplate. Ambulacra I, II and V each have their first coverplates; ambulacrum III has two, whereas IV apparently has not yet begun to develop. Four anals are present. At least one plate per interambulacrum and about eight rim plates are included. This specimen marks the initial bifurcation of the two lateral primary ambulacral radii to form four lateral ambulacra.

Text-figure 9 (1.8 mm) is similar to figure 8 except that the first coverplate of ambulacrum IV has appeared, whereas none of the secondary orals are visible.

Text-figure 10 (2.2 mm) shows the presence of both anterior secondary orals (o) which completes the basic complement of orals found in adults, although one additional secondary oral may be added between the right posterior primary oral (P_2) and the right posterior shared coverplate (S). These include: one right and one left anterior primary oral (A); a central (P_1), a right (P_2), and a left (P_3) posterior primary oral; two pairs of lateral shared coverplates (S), one right and one left, each with one member anterior and one posterior to the transverse oral midline; two secondary orals (o) along the transverse oral midline, wedged between the proximal ends of each anterior primary oral and the adjacent shared coverplate, one left, one right; and one large hydropore oral (H). All five ambulacral radii are established: I-II flanking the left bifurcation plate, IV-V flanking the right one, and III being represented by coverplates between the two anterior primary orals along the distal part of the anterior oral midline. The rim shows seven large proximal plates in this specimen and four small ones of the disjunct second circlet.

Text-figures 11-14 (2.0-2.7 mm) show that the ambulacra develop independently and at various rates. The oral-ambulacral series retains the primary three-part symmetry (one anterior and two lateral radii) throughout development to this point. Each apparently has six to eight rim plates, but boundaries are often obscure. Each interambulacrum has one or two plates, except the posterior which has three or four. The interambulacrals are commonly vague.

Text-figures 15-19 (2.7-2.9 mm) are advanced juveniles or young adults with several coverplates in each ambulacrum, although commonly IV lags behind and III leads in development. The five part symmetry of the adult is apparent in these specimens which also demonstrate the erratic size of the hydropore oral. Text-figure 19 shows a tiny *Agelacrinites hanoveri* growing on the rim of the *Timeischytes casteri.*

Text-figures 20-25 (3.2-4 mm) are young adults which show that homologous ambulacra continue to add coverplates at different rates in different individuals. This series also shows the incredibly large size of the hydropore oral in some. These and the following specimens are considered to be adults (sexually mature individuals) because they have the full complement of characters found in the species. Further increase in size results only in lengthening of the ambulacra and minor changes in allometry.

Text-figures 26-28 (4.2-7.3 mm) are adults. The ambulacra lengthen and coverplates may number 13 per ambulacrum. Ambulacra IV commonly has fewer plates than any other. Any of the other ambulacra may be the longest. A new oral plate, a right posterior secondary oral, is seen in Text-figure 28. This is the only known specimen of 2.2 mm or more in diameter with an additional oral. In figure 28, the rim of a large *Agelacrinites hanoveri* overlaps the right anterior margin. In Text-figure 27, the distal ends of the two anterior primary orals are unusually large and encroach on both the adjacent shared coverplates and the proximal coverplates of ambulacrum III.

Discussion. — *Timeischytes casteri* presents several peculiarities. Perhaps most obvious is the lack of a well-marked hydropore. By analogy, the structure is expected in the right posterior part of the oral region where a large plate homologous to hydropore plates of other edrioasteroids does occur — but no opening is apparent. In most edrioasteroids the margins of the plates bounding the pore are upturned or thickened to form a raised rim. No such rim has been seen.

The size of the hydropore plate ranges widely and some are so large that they totally dominate ambulacrum V. Where unusually large, the plate is often convex, suggesting that a large chamber may lie beneath. Sexual dimorphism may explain this feature, but it appears to be gradational and to occur in advanced juveniles as well as adults. During ontogeny this plate commonly undergoes rapid initial growth until specimens reach 3-4 mm in diameter. Thereafter it apparently is negatively allometric because it is relatively small in all known specimens over 5 mm.

Respiration is not straightforward. The anal structure is valvular and suggests anal pumping; yet the rim, which is a relatively large part of the theca, is not flexible. Flexibility seems to be limited to the junctions between the interambulacrals and the rim, and perhaps also with the ambulacral-oral series. This limited flexibility would inhibit pumping unless some sort of compensatory device allowed for volume changes that would complement the anal pumping. Perhaps the greatly enlarged hydropore plate served this function. The proportionately smaller hydropore plates of larger specimens may indicate a greater flexibility of the oral surface within the rim, thus reducing the demand for a compensation chamber. However, if an individual such as the one in figure 25 had the proportions of that in figure 28, the hydropore plate would need to be resorbed.

Etymology. — This enigmatic edrioasteroid is named in honor of Kenneth E. Caster.

Specimens. — Holotype NYSM 13289, Paratypes, NYSM 13263-13288, 13290. Near the middle of the Mason City Member, Shell Rock Formation, Upper Devonian (Frasnian). Williams Quarry, E½, NW¼, SW¼, sec. 38, T96N, R18W, Floyd County near Nora Springs, Iowa. Collectors: William H. White, Jr. and B. M. Bell, 1967.

Measurements. — The axial diameter (through the oral pole along the anterior primary radius) is given first, followed by the transverse diameter (through the oral pole along the lateral primary radii, normal to the axial diameter):

13263 — 0.63 mm × 0.59 mm; 13264 — 0.60 mm × 0.66 mm; 13265 — 0.8 mm × 0.9 mm; 13266 — 1.2 mm × 1.3 mm; 13267 — 1.0 mm × 1.2 mm; 13268 — 1.1 mm × 1.2 mm; 13269 — 1.3 mm × 1.3 mm; 13270 — 2.3 mm × 2.2 mm; 13271 — 1.8 mm × 1.8 mm; 13272 — 2.3 mm × 1.9 mm; 13273 — 1.8 mm × 2.0 mm; 13274 — 3.0 mm × 2.9 mm; 13275 — 2.8 mm × 2.5 mm; 13276 — 2.7 mm × 2.7 mm; 13277 — 2.8 mm × 2.6 mm; 13278 — 2.8 mm × 2.5 mm; 13279 — 2.9 mm × 2.7 mm; 13280 — 3.0 mm × 3.0 mm; 13281 — 2.6 mm × 2.9 mm; 13282 — 2.9 mm × 3.2 mm; 13283 — 3.3 mm × 3.1 mm; 13284 — 3.6 mm × 3.8 mm; 13285 — 2.8 mm × 2.8 mm; 13286 — 3.4 mm × 3.4 mm; 13287 — 3.7 mm × 4.4 mm; 13288 — 4.2 mm × 4.4 mm; 13289 — 6.9 mm × 7.3 mm; 13290 — 5.4 mm × 6.5 mm.

EVOLUTION

One can arrange the species of the Cyathocystina in an interesting series which is not related to stratigraphic occurrence. Forms such as *Timeischytes megapinacotus* (Pl. 5, fig. 5) and *Hadrochthus commensalus* would represent primitive members of a distinct lineage of anal pumpers with a single biseries of ambulacral coverplates (in contrast with the other anal pumpers, the Isorophina, which have multiple biseries or cyclic sets of coverplates). Other characteristics of this new group are the generally small thecal size, the single circlet of plates in the anal valve, the few and relatively large thick interambulacrals, and the peripheral rim with only three or four (or fewer) circlets of plates.

Timeischytes casteri would represent a trend toward fusion. The rim comprises a single circlet of plates, occasionally with a few small plates of a second disjunct circlet wedged between the distal lateral margins of the plates of the first. The rim plates are either fused or virtually fused by tight sutures. The rim is high relative to thecal diameter placing the food gathering area well above the substrate.

Continuation of the trend toward fusion would result in genera like *Cyathocystis* and *Cyathotheca* (Pl. 5, figs. 6-7). Species of both are characterized by a massive cup or calyx which laterally surrounds the thecal cavity and also forms a basal floor. The thecal cavity is entirely enclosed and the upper oral surface is elevated far above the substrate. Fusion may also affect the oral-ambulacral series as shown by *Cyathocystis oklahomae* in which these plates are distinct but appear to be tightly sutured laterally so that those adjacent to each interambulacrum function as a single unit, all opening together. The climax of this tendency toward fusion would be represented by *Cyathotheca suecica* which has a fused basal calyx, and only five large plates covering the oral surface. Anal plates probably form a valve over the posterior anus (Jaekel, 1927, pl. 1, figs. 1-3).

The stratigraphic occurrence of the above species is in the reverse order of that in the senario. Although *Timeischytes casteri* is slightly younger than *Timeischytes megapinacotus,* the "end products" of the sequence are Ordovician. But a trend from fused to polyplated species seems unlikely because all known Cambrian edrioasteroids are polyplated. Interpretation of the massive *Cyathotheca suecica* as a primitive form would necessitate a polyphyletic origin for edrioasteroids. It seems more plausable that there existed an evolutionary sequence progressing from forms similar to *Timeischytes megapinacotus* to those similar to *Cyathotheca suecica.* However, the trend manifested itself at least twice, once in the Ordovician and again in the Devonian. If true, one would expect to find primitives such as *Timeischytes megapinacotus* in the Early or Middle Ordovician. This primitive stock must have survived at least into the Devonian, where it is represented by *Timeischytes megapinacotus* and the ecologically specialized *Hadrochthus commensalus.* The partially fused *Timeischytes casteri* may represent an end to this Devonian trend toward fusion, or perhaps predicts the occurrence of Devonian *Cyathotheca*-like forms.

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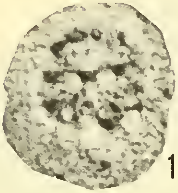
EXPLANATION OF PLATE 1

Timeischytes casteri, n. sp.

Figure

1. NYSM 13263, ×40, oral surface (Text-figure 1)
2. NYSM 13264, ×50, oral surface (Text-figure 2)
3. NYSM 13265, ×40, oral surface (Text-figure 3)
4. NYSM 13266, ×28, oral surface (Text-figure 4)
5. NYSM 13267, ×30, oral surface (Text-figure 5)
6. NYSM 13268, ×30, oral surface (Text-figure 6)
7. NYSM 13269, ×30, oral surface (Text-figure 7)
8. NYSM 13270, ×20, oral surface (Text-figure 8)
9. NYSM 13271, ×20, oral surface (Text-figure 9)
10. NYSM 13272, ×20, oral surface (Text-figure 10)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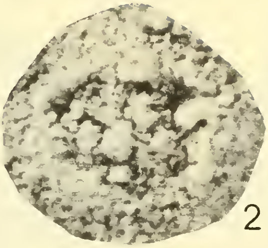
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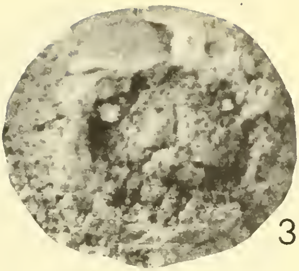
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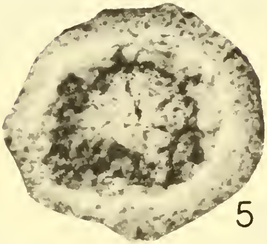
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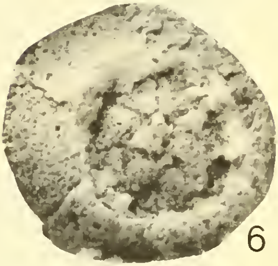
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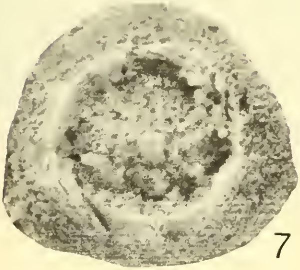
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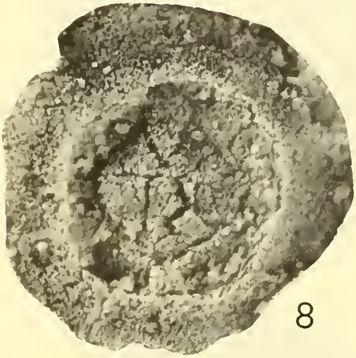
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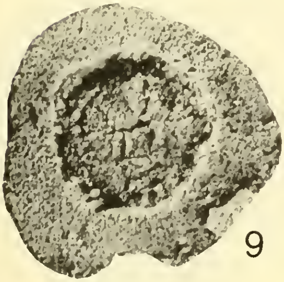
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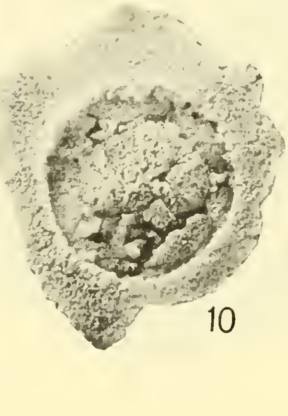
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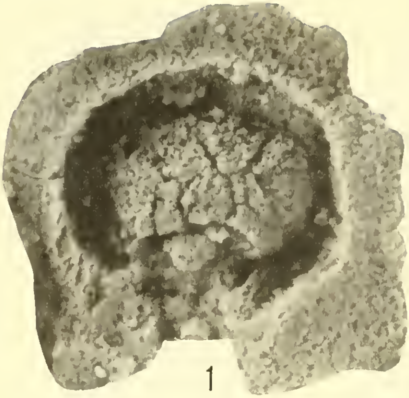
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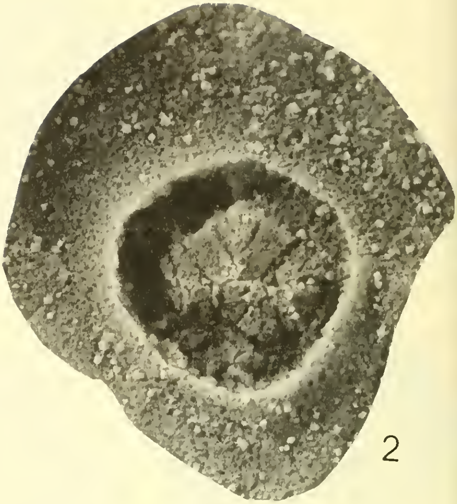
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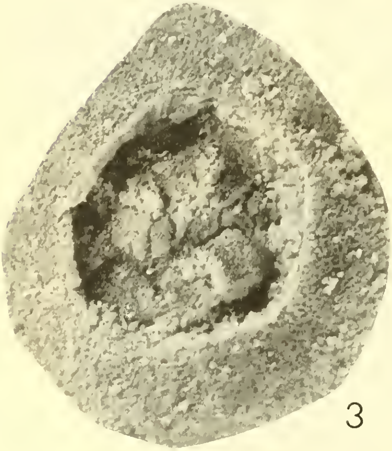
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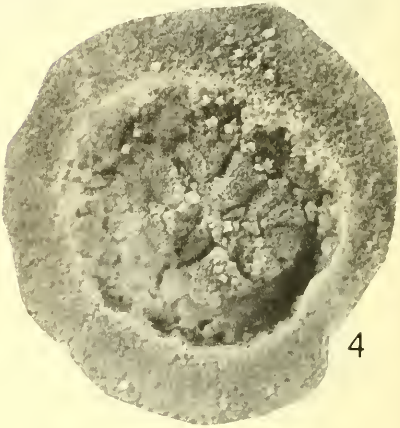
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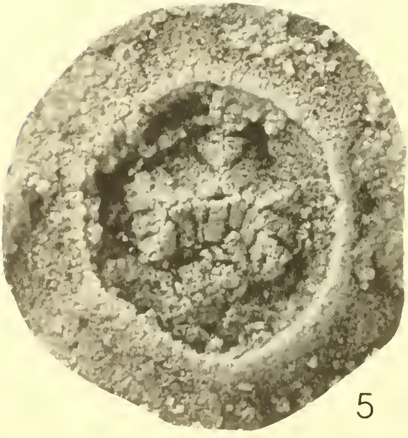
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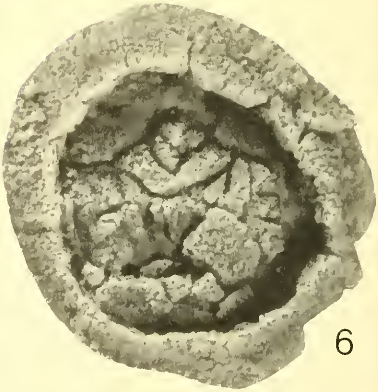
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EXPLANATION OF PLATE 2

Timeischytes casteri, n. sp.

Figure

1. NYSM 13273, ×25, oral surface (Text-figure 11)
2. NYSM 13274, ×20, oral surface (Text-figure 12)
3. NYSM 13275, ×20, oral surface (Text-figure 13)
4. NYSM 13276, ×20, oral surface (Text-figure 14)
5. NYSM 13277, ×20, oral surface (Text-figure 15)
6. NYSM 13278, ×20, oral surface (Text-figure 16)

EXPLANATION OF PLATE 3

Timeischytes casteri, n. sp.

Figure

1. NYSM 13279, ×20, oral surface (Text-figure 17)
2. NYSM 13280, ×20, oral surface (Text-figure 18)
3. NYSM 13281, ×20, oral surface (Text-figure 19)

   A juvenile *Agelacrinites hanoveri* is attached to the rim.
4. NYSM 13282, ×18, oral surface (Text-figure 20)
5. NYSM 13283, ×18, oral surface (Text-figure 21)
6. NYSM 13284, ×17, oral surface (Text-figure 22)

   Part of a small *Agelacrinites hanoveri* covers the posterior edge of the rim.


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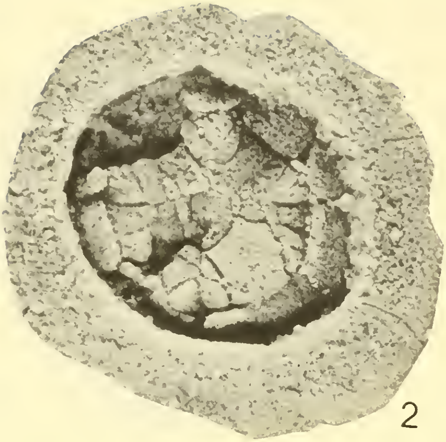
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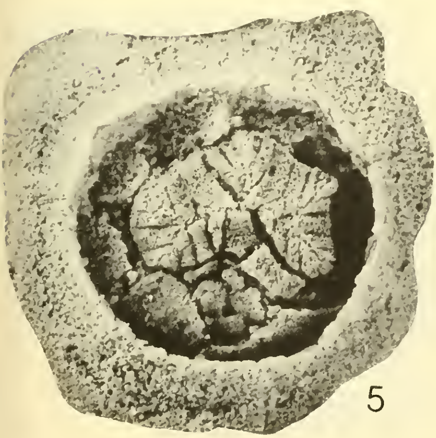
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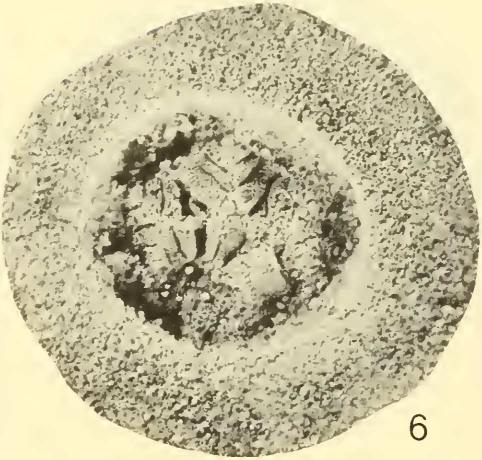
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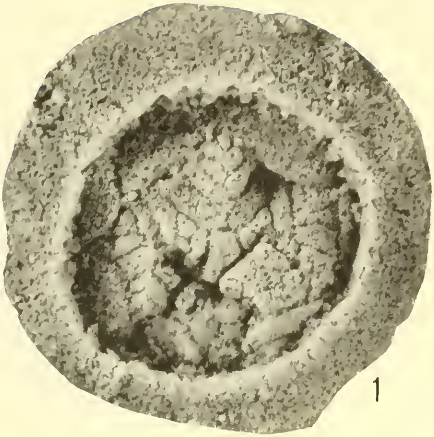
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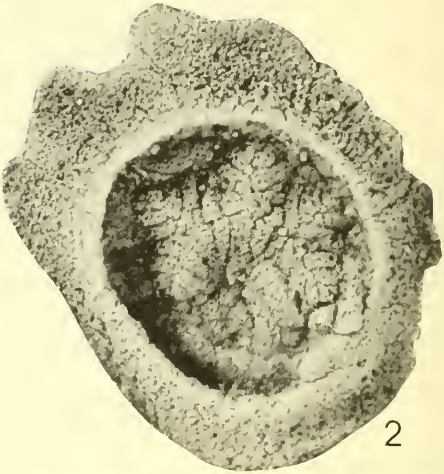
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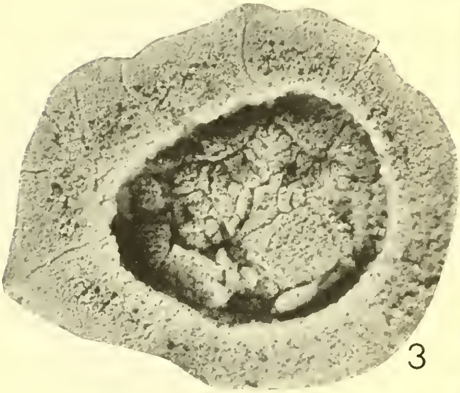
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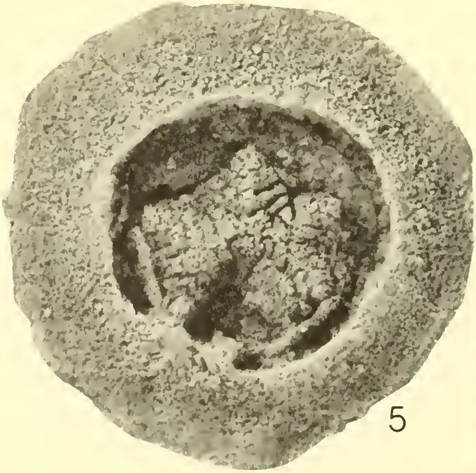
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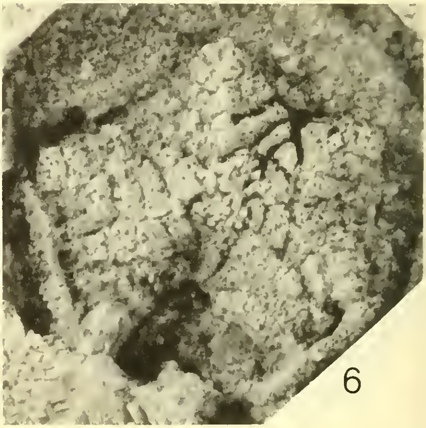
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EXPLANATION OF PLATE 4

Timeischytes casteri, n. sp.

Figure

1. NYSM 13285, ×20, oral surface (Text-figure 23)
2. NYSM 13286, ×18, oral surface (Text-figure 24)
3. NYSM 13287, ×14, oral surface (Text-figure 25)
4. NYSM 13287, ×25, oral-ambulacral area (Text-figure 25)
5. NYSM 13288, ×14, oral surface (Text-figure 26)
6. NYSM 13288, ×25, oral-ambulacral area (Text-figure 26)

EXPLANATION OF PLATE 5

1-4 **Timeischytes casteri,** n. sp.

Figure

1. NYSM 13289, ×8, oral surface (Text-figure 27)
2. NYSM 13289, ×14, oral-ambulacral area (Text-figure 27)
3. NYSM 13290, ×9, oral surface (Text-figure 28)

   Specimen partly covered by the rim of an *Agelacrinites hanoveri.*
4. NYSM 13290, ×15, oral-ambulacral area (Text-figure 28)
5. **Timeischytes megapinacotus** Ehlers and Kesling, 1958

   Paratype, Univ. Michigan Museum Paleont. #35428, Dock Street Clay, Four Mile Dam Formation, Traverse Group, Middle Devonian, Alpena, Michigan, ×15, oral surface.
6. **Cyathocystis americanus** Bassler, 1936

   Holotype, United States National Museum #91846, Ottossee Formation, Blount Group, Middle Ordovician, Knoxville, Tennessee, ×10, oral surface.
7. **Cyathocystis americanus** Bassler, 1936

   Holotype, United States National Museum #91846, Ottossee Formation, Blount Group, Middle Ordovician, Knoxville, Tennessee, ×8, lateral view.


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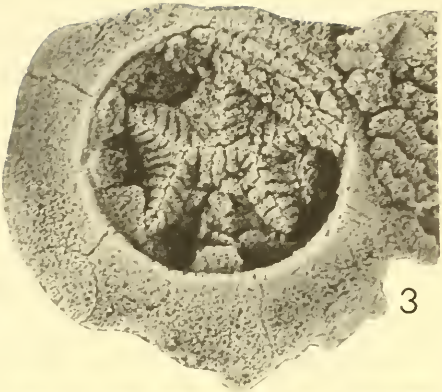
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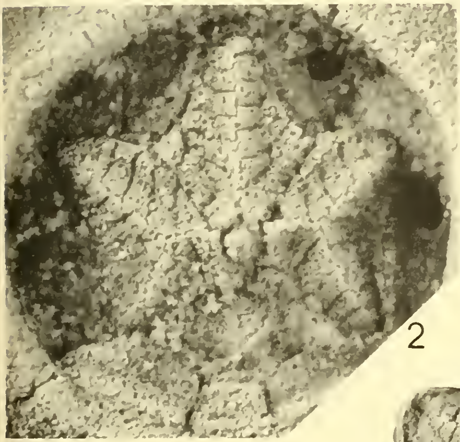
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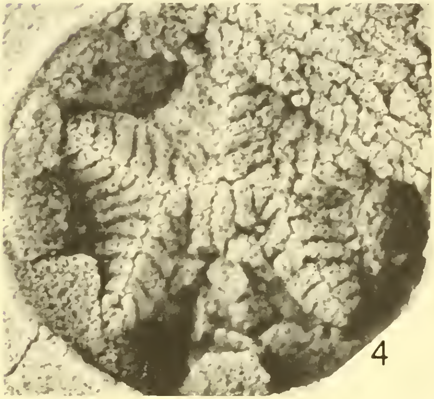
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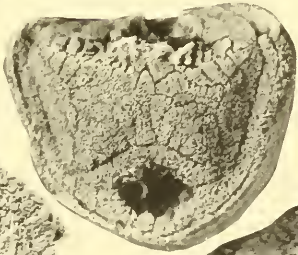
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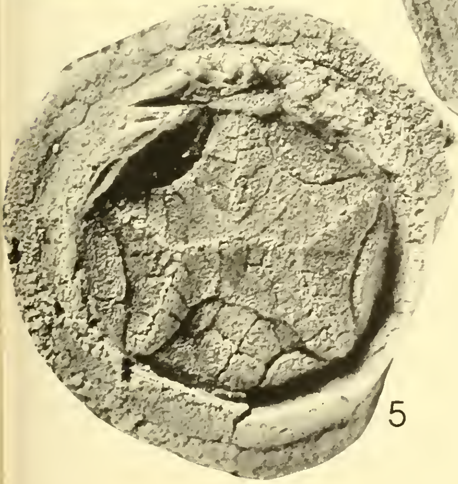
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7

PODIAL EFFICACY OF SOME ORDOVICIAN ASTEROIDS (ECHINODERMATA) FROM NORTH AMERICA

J. Wayne Branstrator
University of California
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ABSTRACT

The role of brachial hydrovascular organs in various early asteroids was determined by the degree of development of internal ampullae in each. Ordovician euasteroid forms had less efficient hydrovascular systems in terms of respiration than do modern asteroids. The modern condition of ampullae passing between consecutive ambulacral ossicles likely developed from an earlier condition of ampullar passage at the junction of ambulacral and adambulacral columns.

No evidence of dorsal transverse ambulacral musculature has been found in any Ordovician asteroid specimen from North America. However, evidences of ventral transverse ambulacral muscles and the dentition between adjacent opposite ambulacral ossicles suggest that the ambulacral groove could be opened and closed in these early forms. The musculature of the dorsal skeleton and body wall is proposed as the force antagonistic to the ventral transverse muscles.

INTRODUCTION

The water-vascular system of fossil asteroids offered little potential for fossilization, although something of its anatomy and function can be determined from analyses of those preserved skeletal elements intimately associated with the system during life. Coupled with information from modern asteroids, data from these perivascular ossicles provide much information about the paleobiology of early members of the subclass.

This report surveys the brachial water-vascular system morphologies of euasterid (Bronn, 1860) stelleroids from Upper Ordovician strata in the vicinity of Cincinnati, Ohio. Not all cited fossils were found in the Cincinnati region, but all show affinities to species which have been found there. Euasterids have opposed ambulacral columns in each arm and single or multiple dorsal madreporites. In the Cincinnati region this includes species which belong to the pustulose families Hudsonasteridae, Mesopalaeasteridae, and Promopalaeasteridae, and the paxillate families Petrasteridae and Urasterellidae.

MATERIALS AND ACKNOWLEDGMENTS

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TUBE FEET AND AMPULLAE OF MODERN ASTEROIDS

In living asteroids brachial tube feet, or podia, protrude from ambulacral grooves on the ventral arm surfaces. They are commonly disposed in two, four, or more longitudinal columns in each groove, depending upon the species, the maturity of the individual, and their location relative to the length of the arm. Depending upon the taxon, each tube foot may terminate in a simple or saggitate point or a sucking disc.

A podium issues from between each two consecutive ambulacral ossicles in the paired ambulacral columns for the length of each arm. Communication with other podia is by lateral canals which extend from each podium to the brachial radial water vessel located deep in the ambulacral groove. This radial water vessel is just external to the abutting, opposed ambulacral ossicle columns. Immediately internal to the ossicular columns each podium joins or develops into an ampulla.

To varying degrees, the histology of the brachial hydrovascular system in all types of living echinoderms has been studied. The various canals and organ walls are composed of an inner epithelium continuous throughout the entire water-vascular system, intermediate layers of connective tissue and muscle, and an external epithelium. The external epithelium of the podia is continuous with that of the covering of the remainder of the body. In ampullated echinoderms, the external epithelium of the internal ampullae is continuous with that of outer lining of the periviceral coelom.

HYDROVASCULAR FUNCTION IN ARMS OF MODERN ASTEROIDEA

Tube feet are used for locomotion, fixation, digging, and food manipulation by asteroids. They also play an important part in respiration. Farmanfarmaian (1966) noted that echinoderms commonly employ outpouchings of the water-vascular system, such as tube feet in asteroids, as respiratory surfaces and demonstrated (Farmanfarmaian, 1959) that oxygen traverses the ampullar membrane by diffusion after being transported to the ampullae from podia by means of ciliary currents in the modern echinoid *Strongylocentrotus purpuratus* (Stimpson). Although it has not been documented, similarities in histologies suggest that such is probably the case in modern asteroids as well. Meyer (1935) demonstrated that in *Asterias rubens* Linné, a European asteroid species, approximately ten percent of an animal's total oxygen uptake is accomplished through the podia in each arm. This suggests that in such animals about one half of the required oxygen is taken into the theca via the tube feet. Animals without dermal papulae or other ancillary modes of oxygen uptake probably acquire nearly all their oxygen by diffusion from the surrounding seawater into the podia.

Both hemal system and water-vascular system have been rejected by zoologists as effective circulatory systems in echinoids (Farmanfarmaian and Phillips, 1962). Oxygen and nutrients are probably circulated to internal organs by means of the ciliary currents within the periviceral coelomic fluid. That "skin gills" or papulae are extensions of the coelomic wall of many echinoderms indicates that coelomic fluid is, at least to some degree, involved in gaseous transport. Thus, in ampullated modern echinoderms oxygen absorbed by the external podia reaches the circulatory periviceral coelomic fluids by means of the internal ampullae.

The mechanisms of podial extension among modern asteroids is reasonably well understood. Nichols (1969; 1972) and others have presented accounts of podial extension and retraction by asteroids, noting that both the radial canal and ampullae supply and hold fluid for such action.

STRUCTURE OF ORDOVICIAN ASTEROID BRACHIA

Three aspects of early asteroid brachia are important to an understanding of the hydrovascular system: (1) the nature of the ampullar perforations through the ambulacral columns; (2) the ambulacral-adambulacral junction; and (3) the ability of these early asteroids to rotate their ambulacral ossicles about a common fulcrum and thereby open and close the ambulacral groove.

Uniform as modern asteroids are in possessing ampullar perforations through ambulacral columns near mid-width of each ambulacral ossicle, Ordovician members of the subclass passed their ampullae into the theca nearer the abradial termini of these ossicles. No known North American Ordovician forms show any evidence that podial perforations existed between the main bodies of the brachial ambulacral ossicles. Some, possibly, did not possess internal ampullae. Those with internal ampullae passed them from the open ventral groove into the arm through perforations bounded by four ossicles at the junction of ambulacral and adjacent adambulacral columns (arrows; Pl. 1, fig. 4; Pl. 2, fig. 3). In modern asteroids, a much stronger perivascular skeleton has developed with ossicles of the ambulacral column alternate to those of the adjacent adambulacrals. This alternate arrangement precludes the possibility of podial perforations at the ambulacral-adambulacral junction; the ampullar perforations lie between successive ambulacral ossicles. A large promopalaeasterid specimen (Pl. 1, fig. 6) shows that in some large Ordovician individuals, however, a few non-brachial, buccal podia achieved the condition of modern asteroids where ampullae are located away from the adambulacral-ambulacral junction. Crowding the mouth areas of these fossil forms, the fact that the most proximal adambulacrals were fused with the most proximal ambulacrals and the need for the ampullar reservoir probably resulted in such an ampullar condition.

Other than in the ventral buccal area described above, the junction between ambulacral and adambulacral ossicles in Ordovician asteroids appears to have allowed some slight degree of ambulacral groove closing by the sliding or rotating of adambulacrals on the abradial, ventral end of the ambulacral ossicles. Algor (1971) reported, as noted by both Spencer (1913, p. 21) and Schuchert (1915, p. 43), that adambulacrals were each articulated with a single ambulacral in early forms. Algor went on to imply, however, that adambulacrals were responsible for closing the normally shallow podial groove in a large group of early Paleozoic starfishes typified by *Petraster speciosus* (Miller and Dyer) and *Platanaster ordovicus* Spencer because he could find no evidence that these Paleozoic forms possessed antagonistic oral and aboral transverse ambulacral musculature allowing the ambulacral ossicles to rotate about a common fulcrum and thereby open and close the ambulacral groove. Several *P. speciosus* specimens, however, do show a fornix formed by the ambulacral columns of the brachia (Pl. 2, fig. 5) even though the remainder of the skeleton seems to have suffered depression during preservation. This, along with the apparent ambulacral dentition (Blake, 1973, p. 9) in some well-preserved specimens of that species (Pl. 2, fig. 6, arrow), and all other Ordovician species known from materials which present appropriate views, suggests that many early forms could erect their ambulacral columns and thus close the groove as in modern forms. Further, many early species, including *P. speciosus,* show areas on the ventral, perradial ambulacral surfaces which were likely areas of ventral transverse muscle attachment (Pl. 2, fig. 2, arrow). Antagonistic dorsal transverse muscles have left no such record of their insertion areas. Possibly the maintenance of massive dorsal ossicles (Pl. 2, fig. 1) by these early asteroids bespeaks the possibility that the skeletal-muscle system of the dorsal theca performed the flattening of the ambulacral groove accomplished by ambulacral dorsal transverse muscles in modern forms.

COMPARATIVE BRACHIAL STRUCTURE OF NORTH AMERICAN EUASTERIDS

A. HUDSONASTERIDAE

Hudsonasteridae is composed of several genera from Europe and North America. All species share the trait of extremely simple, but massive brachial skeletons composed only of ambulacral, adambulacral, inferomarginal, superomarginal, and carinal ossicle columns. Spines articulated upon spine-base pustules typify the external surfaces of all ossicles except the ambulacrals. Specimens are usually small, although some reach a primary radius (R) of four centimeters. Most show evidence that relatively large dermal papulae were emitted from between dorsal ossicles (Pl. 1, fig. 2, arrow). In most species the consecutive ambulacral ossicles appear to abut one another (Pl. 1, fig. 1). In *Macroporaster matutinus* (Hall), however, serial ambulacrals overlapped as in most other early stelleroids (Pl. 1, fig. 3). In either case, the podia were housed in depressions in the ambulacral column with the base of each podium in contact with two ambulacral ossicles. The basins were biserial on each arm, showing no tendency to become quadriserial. If internal ampullae existed, as the abradial notches in the ambulacral columns suggest, they passed through the brachial skeleton abradially.

There was little room in the interior of the hudsonasterid arm for bulbous ampullae (Branstrator, 1969). The small size of the organism may indicate that respiratory limitations existed, due to poorly developed internal ampullae, thus limiting potential body size. If the dorsal skeleton was functional in controlling the attitudes of the ambulacral columns as proposed above, this would impose limits on the amount of dorsal skeleton that could be relinquished to areas for respiratory papulae. When limits were reached, maximum size would be fixed until internal ampullae could further develop or dorsal transverse muscles could become functional.

B. MESOPALAEASTERIDAE

Schuchert (1914) erected *Mesopalaeaster* to accommodate those Paleozoic species he considered intermediate in form between his Ordovician genera *Hudsonaster* and *Promopalaeaster*. Within this new genus he included 15 species, eight of them provisionally. Of the four remaining Ordovician forms originally included, only the type species, *Palaeaster shafferi* Hall, 1868, can remain. *Palaeaster finei* Ulrich and *Mesopalaeaster proavitus* Schuchert are promopalaeasterids and *Mesopalaeaster intermedius* Schuchert is a lanthanasterid (Branstrator, in preparation).

The mesopalaeasterid plan is similar to that of the hudsonasterid in that ossicles remain massive except for the addition of small ossicles in single or multiple series between the marginal columns and between the superomarginal and carinal columns. These changes allowed more papular area and more intrabrachial space for internal organs, including ampullae, within the brachial cavities. The dorsum was not substantially weakened because ossicles joined by muscles still traversed the papular areas between primary ossicle columns (Pl. 1, fig. 5).

Because they are in better condition than the holotype, other specimens of *M. shafferi* supply critical information as to the nature of the ventral surface of the species. Holotypes of *Palaeaster spinulosus* Miller and Dyer, 1878, and *P. exculptus* Miller, 1881, belong to this species. They reveal an ambulacral condition similar to that of *Macroporaster* Raymond in which long, placoid ambulacrals overlapped a proximal oral flange of the next distal ambulacral at ossicular mid-width (Pl. 1, fig. 4). This flanging was probably a device to increase flexibility, yet maintain strong muscle connections between consecutive ambulacrals. The mesopalaeasterids developed brachia considerably longer than those of any hudsonasterid.

The perforations (Pl. 1, fig. 4, arrows) between the perivascular ossicles at columnar junctions are larger in the mesopalaeasterids than among the hudsonasterids. The increased internal brachial volume could have allowed greater development of internal ampullae permitting the mesopalaeasterids greater body size because of increased respiratory capacity. The use of ampullae as fluid reservoirs for podial extension and contraction became possible at this stage.

C. PROMOPALAEASTERIDAE

Compared to the above groups, the promopalaeasterids had wide proximal brachia and greater internal arm volume, but the same abradial ampullar perforation location (Pl. 2, fig. 3, arrow). They developed the largest and most massive bodies of all Ordovician asteroids. *Promopalaeaster magnificus* (Miller) and *P. dyeri* (Meek) are known with brachial lengths well over seven centimeters. Although only the proximal portions of the brachia are preserved, a specimen (MUGM 6809) from the Liberty Formation (Upper Ordovician) near Oxford, Ohio, had a brachial length greater than fifteen centimeters.

On the proximal parts of the arms quadriserial podial basins were defined by alternate inflections of interpodial ridges on successive ambulacral ossicles (Pl. 2, fig. 2). Clearly, canals had to be maintained between flanges of successive ambulacral ossicles for connecting vessels between perradially placed podia and the abradial skeletal perforations which led to internal ampullae. Canals also had to be maintained for lateral canals between abradially placed podia and the radial water vessel. The existence of these former canals (Pl. 2, fig. 2) is direct evidence that internal ampullae did exist in these early forms.

On the distal brachia the promopalaeasterids retained the biserial podial condition. No Ordovician asteroid is known to have developed quadriserial podia for the length of each arm. However, during the Ordovician the quadriserial condition came to occupy more of the brachial length in successively later known promopalaeasterid specimens.

The significance of the dichotomous podial condition in the promopalaeasterids is debatable. How this podial condition served the promopalaeasterid body plan can be suggested. Its efficacy was probably involved in the size achieved by individuals. Proximally the arms were capable of housing large, bulbous ampullae which assisted the dermal papulae in adequately oxygenating the perivisceral coelomic fluid. This could have compensated for the increased thecal volume and the consequent decrease in surface area for papular structures per unit area. The deep, flanged podial basins may indicate the presence of terminally suckered tube feet requiring secure connections between tube feet and skeleton to meet stresses generated by the action of these feet. The ability to hang onto a firm substrate by means of suckered podia, or to hold prey in the buccal area (necessary if promopalaeasterids had evolved the stomach everting feeding habit) was increased by the increased number of proximal podia.

D. URASTERELLIDAE

The urasterellid *Salteraster Stürtz* differs from forms described above in several basic ways. In this group the adambulacrals are the most prominant external ossicles. Only a single marginal series is discernible on each lateral arm surface. This latter series is separated from a distinct carinal series by several columns of paxillae, the columns of which increase in number with brachial size.

As in the mesopalaeasterid the ambulacral ossicles were opposite those of the adjacent column and each joined a single adambulacral

(Pl. 2, fig. 4). The ossicles, however, were much shorter and less placoid than those of the mesopalaeasterids. Each overlapped slightly the next more distal ambulacral. The group possessed large passages into the brachia for the passage of ampullae (contrary to the suggestion of Hudson, 1916, pp. 124-125), although the brachia were long and narrow and the ambulacral ossicles massive, allowing little room for the accommodation of bulbous internal ampullae.

E. PETRASTERIDAE

Richmondian (upper Upper Ordovician) rocks around Cincinnati have yielded numerous specimens of *Petraster speciosus* (Miller and Dyer). As previously mentioned, Algor examined some specimens of this species and characterized a large group of early Paleozoic asteroids from his findings. The species differs from all other forms known from the Cincinnati Area in that its brachia were extremely wide at their bases forming broad interbrachial arcs as in the modern genus *Patiria* Gray. Its adambulacrals were comparatively wide and the ventral surface was flat, with the exception of the groove formed by the ambulacral ossicles. As in the urasterellids, the dorsal ossicles seem to have functioned as paxillae, and papulae were numerous on the dorsal surface, issuing from between nearly all ossicles (Pl. 2, fig. 5, arrow).

The petrasterid thecal shape permitted considerable space in the brachia for ampullae and probably gonads and gastric caecae as in most extant asteroids. Ampullar perforations were large (Pl. 2, fig. 6).

CONCLUSIONS

These observations suggest the general podial development achieved by asteroid species found in the North American Ordovician. Whether this condition falls on the main line of asteroid evolution is yet to be determined from discovery of additional material and similar observations on contemporaneous specimens from elsewhere and later specimens more closely allied to modern forms.

Although not yet verified by later or earlier specimens, the Ordovician forms described suggest a sequence of body plans and developments leading to the modern asteroid podial condition:

(1) A small, weakly vagile stelleroid without defined brachia or internal ampullae. Adjacent ambulacral columns fused or weakly

jointed. Podia functional in locomotion and moving food to mouth. Podial respiration secondary to papular respiration; oxygen carried to viceral area and waste gases to podia in hydrovascular fluids via the radial canals.

(2) A larger, vagile, brachiated stelleroided with podial ampullae passing into brachia through perforations at ambulacral-adambulacral column junctions. Adjacent ambulacral columns fulcral to form a closed or open groove under the control of weak transverse ambulacral ventral muscles and the antagonistic action of muscles of the dorsal body wall. Podia effective in respiration, locomotion and food manipulation. Predaceous abilities limited by fragile junction between ambulacral and adambulacral ossicles.

(3) Potentially even larger, modern asteroid plan with dorsal transverse muscles taking over the role of groove opening. Ampullar perforations located perradially allowing stronger alternate arrangement of ambulacral and adambulacrals for the addition of active predation to the repertoire of opportunistic feeding strategies. A shorter route for gas exchange between podia and ampullae also achieved by perradial ampullar perforations.

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EXPLANATION OF PLATE 1

Figure

1. **Protopalaeaster narrawayi** Hudson

Ambulacrals of holotype in dorsolateral aspect and proximal to the right. Dorsal ossicles are gone from specimen. Note abutting surfaces between consecutive ambulacral ossicles. Black River Group (Middle Ordovician), near Ottawa, Ontario. ROM 18881; × 12.

2, 3. **Macroporaster matutinus** (Hall)

2. Trenton Group (Middle Ordovician), "shelly layers" at Trenton Falls, New York. Dorsal aspect. Arrow points to one of series of implied papular openings between carinal and superomarginal columns. Holotype. AMNH 119; × 5.

3. Trenton Group (Middle Ordovician), Rathbone Creek, Newport, New York. Ventral aspect of ambulacrals (bottom series) and adambulacral columns, proximal to the left. Note overlapping flanges on ambulacral ossicles. MCZ 459; × 25. (Photographs through xylol to increase contrast between specimens and matrix.)

4, 5. **Mesopalaeaster shafferi** (Hall)

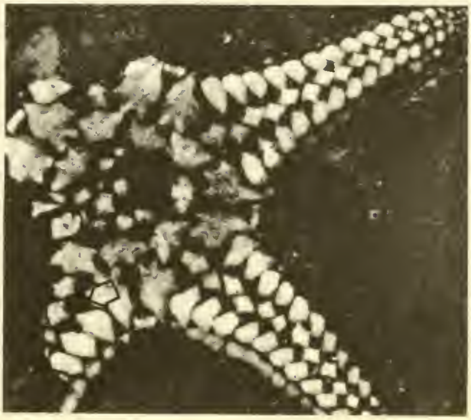
4. Richmond Group (Upper Ordovician), near Waynesville, Ohio. Ventral aspect, proximal to the right. Note ampullar perforations (arrows). Holotype of *Palaeaster exculptus* Miller. USNM 60608; × 9.

5. Maysville Group (Upper Ordovician), Cincinnati, Ohio. Dorsal aspect of arm, somewhat disrupted, proximal to bottom. Note ossicles between primary series (ossicles of respective series labeled: i, inferomarginals; s, superomarginals; c, carinals). Holotype of *Palaeaster spinulosus* Miller and Dyer. MCZ 16; × 6.

6. **Promopalaeaster** sp.

Ventral aspect of most proximal perivascular ossicles of a large promopalaeasterid. Note true interossicular perforations for buccal podia (arrow). Richmond Group (Upper Ordovician), Jefferson Co., Indiana. FMNH (Walker Coll.) 10981; × 6.

1



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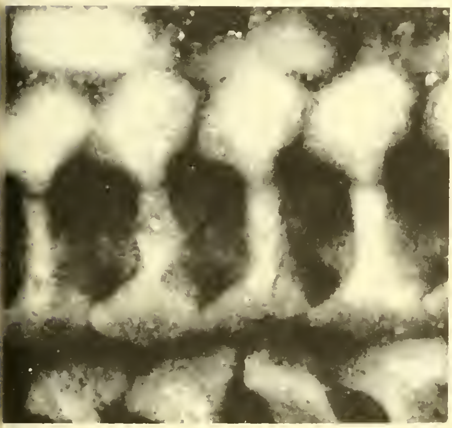

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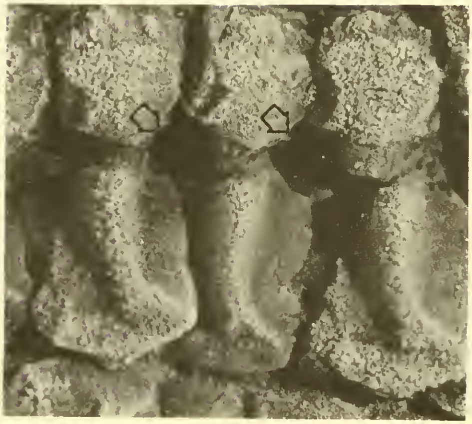

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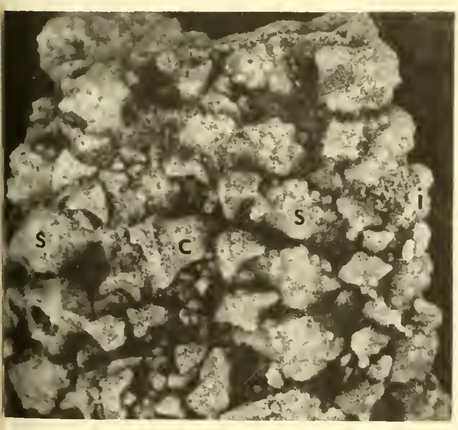

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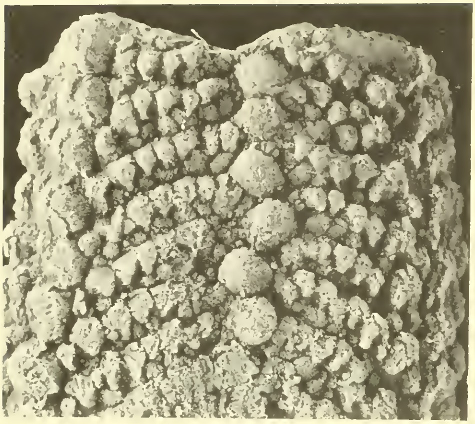

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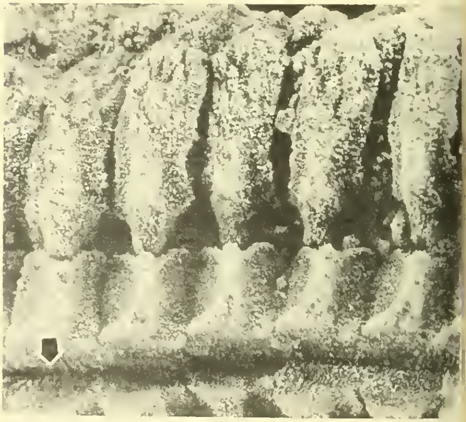

6

EXPLANATION OF PLATE 2

Figure

1, 2. **Promopalaeaster magnificus** (Miller)

1. Richmond Group (Upper Ordovician), near Waynesville, Ohio. Dorsal aspect of arm at mid-length. Note biserial diagonal series of adradial ossicles in papular area between carinals and superomarginals. Proximal is toward bottom. Holotype. USNM 40883A; × 3.

2. Ventral aspect, most proximal to left. Note alternating podial basins, ampullar perforations abradially, connecting canals for abradial podia with radial canal and for perradial podia with ampullar perforations. A ventral transverse muscle attachment area is marked with an arrow. Paratype. USNM 40883C; × 7.

3. **Promopalaeaster** sp.

Maysville Group (Upper Ordovician), Cincinnati, Ohio. Aboral aspect of ambulacral columns from mouth area. Note location of ampullar perforations abradially (arrow) and absence of clear evidence of ambulacral dorsal transverse muscles. UCM specimen; 12 ×.

4. **Salteraster pulchella** (Billings)

Trenton Group (Middle Ordovician), distorted specimen from Hull, near Ottawa, Ontario. Sigmoid adambulacrals each join a single ambulacral leaving a large ampullar perforation. Proximal to the right. GSC 1397; × 25. (Xylol photograph).

5, 6. **Petraster speciosus** (Miller and Dyer)

5. Richmond Group (Upper Ordovician) Adams Co., Ohio. Note ambulacral arch and papular pores (arrow). OSU specimen; Richard Douce, collector; × 3.

6. Clinton Co., Ohio. Note dentition (arrow), attachment area for ventral transverse muscles on perradial end of transverse ventral flange, wide adambulacrals and ampullar pores. USNM 70175; × 6.

LOWER CARBONIFEROUS BRACHIOPODS FROM AXEL HEIBERG AND MELVILLE ISLANDS, CANADIAN ARCTIC ARCHIPELAGO

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ABSTRACT

Two small Viséan brachiopod faunas collectively consisting of 15 species are described from Axel Heiberg and Melville Islands, Canadian Arctic Archipelago. They represent the first Lower Carboniferous marine invertebrates to be reported from this region. Two of the species are new, *viz. Composita casteri* and *Anthracospirifer borealis.* These faunas appear to share faunal elements of both Eurasian affinity and North American affinity but cannot be precisely correlated with previously described faunas.

INTRODUCTION

Lower Carboniferous (Dinantian) marine invertebrates have not been reported previously from the Canadian Arctic Islands. The purpose of this paper is to describe the brachiopod faunas of two small Visean collections from Melville and Axel Heiberg Islands.

In 1955, R. Thorsteinsson of the Geological Survey of Canada collected a number of brachiopods (GSC locality 26403) from a limestone "inclusion" within an evaporitic piercement dome called the South Fiord Diapir on the north side of South Fiord, Axel Heiberg Island (lat. 79° 26′ N, long. 94° 05′ W). W. W. Nassichuk of the GSC made a similar collection (GSC locality C-4126) in 1967 from a limestone block carried to the surface by a gypsiferous diapir at the northeast margin of Barrow Dome, northern Sabine Peninsula, Melville Island (lat. 76° 39′ N, long. 109° 02′ W). These collections are the basis for this paper. According to Nassichuk (personal communication, 1974) both collections must have been derived from the Otto Fiord Formation, which in its type area near Hare Fiord, Ellesmere Island, ranges in age from Late Chesteran to Early Atokan.

The manner of preservation of the specimens in these collections is variable including some specimens with original shell material; others have remnant structures preserved in replacement materials. There are also a number of molds of external and internal surfaces, often with one surface impressed on another surface of the same specimen. In general, preservation of the external morphology is reasonably good for most of the species. Articulated specimens of some species were serially sectioned, and the necessary internal details were worked out for several other species by one means or another in order to identify them properly.

I am grateful to W. W. Nassichuk of the Geological Survey of Canada for making these collections available to me for study. G. A. Cooper, of the National Museum of Natural History, and Mackenzie Gordon, Jr., of the U.S. Geological Survey, provided useful suggestions and discussions concerning some of the species. I also thank R. E. Grant of the National Museum of Natural History for permission to peruse that institution's great comparative collections of brachiopods.

AGE OF THE FAUNAS

Fifteen species of articulate brachiopods have been identified collectively, the seven most common ones that make up the bulk of the collections occurring at both localities. Seven of the eight remaining species are restricted to the Axel Heiberg locality and one to the Melville Island locality.

The fauna of the more diverse Axel Heiberg Collection (GSC locality 26403) consisting of 14 of the 15 brachiopod species described in this paper is listed below.

Overtonia sp.
Setigerites cf. *S. altonensis* (Norwood and Pratten)
†*?Eomarginifera* sp.
Productus sp.
†*Ovatia* cf. *O. minor* (Snider)
Indeterminate wellerellid
†*Composita casteri,* n. sp.
†*Cleiothyridina* sp. cf. "*Composita*" *offirmata* Bell
†*Crurithyris* cf. *C. acadica* (Bell)
†*Anthracospirifer borealis,* n. sp.
"*Brachythyris*" cf. *B. dichotomus* Litvinovich
Phricodothyris, n. sp.
Martinia sp.
†*Beecheria formosa* (Hall)

The Melville Island collection (GSC locality C-4126) is less diverse and contains representatives of the seven species marked above with a dagger (†) plus one other species described as *Hustedia,* n. sp.

The species marked with a dagger make up the bulk of both collections, excluding the *?Eomarginifera* sp.

Because of its greater diversity it is possible to estimate a Viséan age for the Axel Heiberg collection with some assurance. The genera *Overtonia* Thomas, 1914, and *Setigerites* Girty, 1939, are not known from strata younger than the Viséan, whereas the genera

Productus J. Sowerby, 1814, and *Martinia* M'Coy, 1844, are not known from strata older than the Viséan, nor is the subfamily Marginiferinae which includes the species identified here as *?Eomarginifera* sp. Additional species that point to a Viséan age for the Axel Heiberg fauna are *Ovatia* cf. *O. minor* (Snider), which is compared to a species of Viséan age in Arkansas, and *Beecheria formosa* (Hall), a species restricted to Viséan formations in the North American mid-continent. *Crurithyris* cf. *C. acadica* (Bell) and *Cleiothyridina* sp. cf. *"Composita" offirmata* Bell are comparable to the species of those names from the Windsor Group of Nova Scotia. Lastly, the unusual species described as *"Brachythyris"* cf. *B. dichotomus* Litvinovich is compared to a Viséan species from the Soviet Union.

The age of the Melville Island fauna is much less certain. Melville Island and Axel Heiberg Island are not geographically proximate at the present time. Notwithstanding the several hundred miles that separate them, the two brachiopod faunas are similar in faunal composition, distribution of the numerically abundant species, and mode of preservation. I consider it likely that these collections were recovered from stratigraphic units of essentially the same age. But lacking the more definitive age indicators of the Axel Heiberg collection there remains the possibility that the Melville fauna is facies controlled. Consequently, I consider a Viséan age assignment to be probable or tentative, not conclusive. In either case I have little doubt that the two collections represent similar fossil communities and depositional environments.

SIMILARITIES WITH OTHER FAUNAS

Lee (1909) described a Viséan arctic fauna from Novaya Zemlya. His study included a number of brachiopod species, none of which is definitely identical with the species described here, although his *Productus cherneyensis* may be identical with the *Overtonia* sp. from Axel Heiberg Island. His *Squamularia* sp. *a* may be closely related to the Canadian form described as *Phricodothyris*, n. sp.. Other similarities are less significant.

The brachiopod fauna of the Windsor Group of Nova Scotia as described by Bell (1929) shows some similarities with these arctic faunas. As pointed out above *Crurithyris acadica* (Bell) and *"Com-*

posita" *offirmata* Bell may have arctic representatives. Also, the Windsor species *Beecheria davidsoni* Hall and Clarke, is closely similar to *Beecheria formosa* (Hall). In general, the Windsor fauna is a hodgepodge of Eurasian forms and North American forms.

It is interesting to note the dissimilarity between these arctic Viséan faunas and those reported by Waterhouse (1971, pp. 110-116) from the northern Yukon Territory. The cosmopolitan genera *Martinia, Crurithyris,* and *Ovatia* are found in common but the stratigraphically diagnostic genera appear to constitute distinctly different assemblages.

It seems likely that the arctic faunas described here also represent a melding of Eurasian faunas and North American faunas. *Eomarginifera* and *Productus sensu strictu* have not been reported from North America, whereas several of the other species, including the *Ovatia, Setigerites, Anthracospirifer,* and *Beecheria* appear to be most closely related to North American taxa.

SYSTEMATIC PALEONTOLOGY

Order STROPHOMENIDA Öpik

Suborder PRODUCTIDINA Waagen

Superfamily **PRODUCTACEA** Gray

Family **OVERTONIIDAE** Muir-Wood and Cooper

Subfamily **OVERTONIINAE** Muir-Wood and Cooper

Genus **OVERTONIA** Thomas

Overtonia sp. Pl. 1, figs. 6, 7

Discussion. — A single natural impression of a brachial valve exterior from GSC locality 26403, Axel Heiberg Island, is assigned to *Overtonia* on the basis of its shape and ornamentation. This medium-sized specimen is about 19.6 mm wide and about 15.1 mm long. It has a wide hingeline with well-developed ears delineated by a distinct ventrally directed flexure of the shell. The visceral disc is moderately concave with no indication of a trail. The ornament consists of numerous distinctive pits and, although decorticated, the surface appears to have been lamellose and weakly rugose. There are moderately numerous small erect spine bases clearly arranged in single concentric bands on each of the lamellae. An impression of the pedicle valve beak suggests that it was pointed, narrow, and slightly overhanging the hingeline. These characters leave little doubt that the specimen belongs in the subfamily Overtoniinae.

The lack of costation, presence of numerous large pits, and single rows of erect spine bases on each lamella preclude the assignment of this species to most genera of the Overtoniinae. The pits and spines of the brachial valve of the genus *Krotovia* Frederiks are quincuntially arranged and dissimilar to the ornament of the specimen considered here. *Fimbrinia* Cooper has recumbent spine bases on the brachial valve and smaller ears than those of *Overtonia. Scoloconcha* Gordon lacks pits on the brachial valve.

The arctic species differs from the type species of *Overtonia, O. fimbriata* (J. de C. Sowerby), in its more concave visceral disc and larger pits on the brachial valve.

Lee's illustrations (1909, pl. 2, figs. 37, 37a) of the types of *Overtonia cherneyensis* (Lee, 1909) from the Viséan of Novaya Zemlya show a pedicle valve similar in width to that of the Axel Heiberg specimen. If the large thick tubercles on the pedicle valve of *O. cherneyensis* reflect similarly large pits on the brachial valve, then the Canadian species might well be identical to the one from Novaya Zemlya.

Genus **SETIGERITES** Girty

Setigerites cf. S. altonensis (Norwood and Pratten) Pl. 1, figs. 4, 5

1855. *Productus altonensis* Norwood and Pratten, Acad. Nat. Sci. Philadelphia, Jour., ser. 2, vol. 3, p. 7, pl. 1, figs. 1a-c.

Discussion. — A single pedicle valve from GSC locality 26403, Axel Heiberg Island, agrees in most ascertainable details with *Setigerites altonensis,* originally described from the Salem Limestone of the upper Mississippi Valley region of Illinois and Missouri. Unfortunately, neither of the ears is complete in this specimen and the presence of a brush of spines cannot be determined, the only remaining detail necessary for an exact identification. *Setigerites altonensis* has been reported from several formations of Meremecian age (Viséan) in North America. Sarycheva (1963, pp. 185-186, pl. 25, figs. 2-6) reported it from the Viséan of the Kuznetsk Basin of the Soviet Union.

Family **MARGINIFERIDAE** Stehli
Subfamily **MARGINIFERINAE** Stehli
Genus **EOMARGINIFERA** Muir-Wood

? **Eomarginifera** sp. Pl. 1, figs. 2, 3, 21, 22

Discussion. — A small marginiferid specimen from the Axel Heiberg collection (GSC locality 26403; Pl. 1, figs. 2, 3) is tentatively assigned to *Eomarginifera,* although the specimen differs in several important respects from the more typical species of the genus. Another specimen from the Melville Island collection (GSC locality C-4126; Pl. 1, figs. 21, 22), a natural mold of a brachial valve exterior, is assigned here also but with less justification.

The Axel Heiberg specimen is unequivocally assigned to the Marginiferinae on the basis of its form, ornament, and internal characters. It consists of a nearly complete pedicle valve with the impression of the brachial valve interior on the other surface. It is about 11.7 mm wide and part of the trail is missing. The pedicle valve is strongly inflated and has a relatively narrow umbonal region for the genus. The ventral surface is very weakly capillate or finely costellate and appears to be abraded so that most of the fine ornament is missing. The visceral disc is sparsely rugose and little evidence of ribbing is preserved. There are eight symmetrically arranged large spine bases: two in a row on each flank just anterior to the ears; two on the venter at the anterior edge of the visceral disc; and two at the antero-medial margin of the preserved portion of the trail. A few more smaller spine bases are scattered over the visceral disc and trail. Ears are not preserved and, if present, must have been small. The impression of the brachial valve interior is not well preserved, but there is a small sessile cardinal process (bilobed?) and very pronounced raised elongate-trigonal adductor scars. The visceral disc is more concave than that of the brachial valve from Melville Island. There appears to be a very thin low breviseptum and there are indications of lateral ridges extending to the cardinal margins. A weak low anterior ridge is present at the front of the visceral disc and several rows of fine endospines are found here and on the trail.

The impression of a brachial valve exterior from Melville Island is about 11.3 mm wide and well geniculated with a short trail. Its visceral disc is moderately concave and the ears are small, well delineated by a flexure of the shell, and reflecting the presence of lateral ridges that extend to the cardinal margins diverging slightly from the hingeline. The visceral disc is weakly rugose and the whole surface is weakly capillate with about 19 or 20 capillae per 5 mm on a small portion of pedicle valve still attached to the dorsal trail.

The narrow inflated profile and weakly geniculate pedicle valve visceral disc are not characteristic of the Marginiferidae but the symmetrically aranged spines leave little doubt about the relationships of at least the Axel Heiberg specimen. The specimens are too poorly preserved to allow definite conclusions about their morphology, and as a result, generic assignment.

Eomarginifera has not been reported from North America. In Eurasia it appears in the Viséan and ranges into the Namurian.

Family **PRODUCTIDAE** Gray

Genus **PRODUCTUS** J. Sowerby

Productus sp. Pl. 1, fig. 1

Discussion. — A single specimen from GSC locality 26403, Axel Heiberg Island, is assigned to the genus *Productus* Sowerby on the basis of its size, ornament, large visceral disc, and diaphragm in the brachial valve. This specimen is preserved in a manner characteristic of the genus and there can be little doubt as to its generic identity. The lack of a long folded trail suggests that the specimen is probably not *P. productus* (Martin), but it is not possible on the basis of this single specimen to suggest the species to which it might belong.

The genus *Productus s.s.* is common in Viséan strata of Eurasia and according to Muir-Wood and Cooper (1960, p. 240) ranges into the Namurian and Westphalian.

Family **LINOPRODUCTIDAE** Stehli

Subfamily **LINOPRODUCTINAE** Stehli

Genus **OVATIA** Muir-Wood & Cooper

Ovatia cf. O. minor (Snider) Pl. 1, figs. 8-20, 23-32

1915. *Productus ovatus* var. *minor* Snider, Oklahoma Geol. Sur., Bull. 24, p. 79, pl. 3, figs. 19-21.

Description of the arctic specimens. — Shell small for genus, longer than wide, greatest width attained anterior to the hingeline; lateral profile strongly convex; outline of visceral area of both valves subcircular to subovate; fold and sulcus not produced in either valve; ears of both valves small, subangular; body cavity small.

Pedicle valve strongly inflated, most convex in umbonal region; venter evenly rounded, flanks curving sharply and evenly to lateral margins; very small ears delineated by abrupt flexure; beak small, narrow, slightly overhanging hingeline; ornament consist irregularly spaced rugae in visceral region, several stronger rugae at ears, and about 15 or 16 rounded capillae per 5 mm in larger specimens (measured about 10 mm from beak) which increase by intercalation; row of spines at hingeline and at least one row extending around ears of rugae; long medially-directed clasping spines preserved in one juvenile specimen.

Pedicle valve interior with moderately impressed chordate muscle field; ears delineated anteriorly by narrow ridges region to near lateral margins.

Brachial valve with moderately to strongly concave visceral disc with slight geniculation developed in some specimens; visceral disc weakly rugose; spines not observed; ears small, well delineated from visceral disc but rarely preserved; capillae as in opposite valve except many increase by bifurcation as well as by intercalation.

Brachial valve interior with sessile bilobed cardinal process very thin median septum extending about half way across visceral disc; lateral ridges not observed, possibly much reduced; adductor scars not observed.

Comparisons. — Snider's description of *Ovatia minor* as a "variety" of *Ovatia ovata* (Hall) is scanty and his illustrations of the types minimal. The species has not been re-illustrated and a more complete description is needed for accurate comparison with similar species.

Easton (1962, p. 51) stated that *O. minor* (Snider) has about 21 capillae in 5 mm, presumably on the anterior venter. My own estimates taken from Snider's illustrations of the types would indicate that there are only about 14 or 15 capillae in 5 mm on Snider's largest specimen (fig. 19). Easton did not state if he obtained his figures from the types or from other specimens.

Ovatia semicubiculatus (Bell), from the Windsor Group of Nova Scotia (Viséan), *O. duodenarius* (Easton), from the Big Snowy Group of Montana (Namurian), and *Ovatia pumilus* Sutherland and Harlow, from the La Pasada Formation (Westphalian) of New Mexico, are small species of *Ovatia* similar to *O. minor* (Snider). *Ovatia semicubiculatus* can be distinguished by its larger ears and broader ventral umbo. *O. duodenarius* can be differentiated by its slightly coarser ornament of about 12 capillae in 5 mm, scattered prominent nodular spine bases on the pedicle valve, smaller size, and its usually less inflated profile. *O. pumilus* can be distinguished by its finer ribbing and broader umbonal region.

Occurrence and abundance.—This species is well represented in the collections from both Axel Heiberg and Melville Islands. The specimens in the two collections are indistinguishable in all respects and there is no doubt that they represent the same species. The GSC locality 26403 collection consists of 18 specimens and the GSC locality C-4126 collection consists of 23 specimens.

Order RHYNCHONELLIDA Kuhn

Superfamily **RHYNCHONELLACEA** Gray

Family **WELLERELLIDAE** Likharev

Indeterminate Wellerellid Pl. 4, figs. 33-35

Discussion.—Two specimens of a small rhynchonellid from GSC locality 26403, Axel Heiberg Island, are generically indeterminate but are assigned to the family Wellerellidae for the following reasons. These small specimens have smooth shells, rhynchonelliform outline and profile, and well-developed fold-sulcus. The largest specimen, illustrated on Plate 4 was serially sectioned. Although it is severely recrystallized, dental plates are clearly preserved, the cardinalia are indistinct but there is no indication of a septalium or dorsal septum, and the crura appear to be simple and bladelike. In profile neither specimen is inflated. If the preceding interpretation of the poorly preserved cardinalia is correct then it is unlikely that these specimens should be assigned to the family Pugnacidae Rzhonsnitskaya, the members of which possess a septalium, albeit a reduced one, and are usually inflated in profile. The arctic specimens are small, possibly juveniles, which might explain the complete lack of anterior ribbing. On the other hand a mature specimen lacking anterior ribbing, and possessing the internal characters described above would be difficult to assign to any previously described genus.

Order SPIRIFERIDA Waagen

Suborder RETZIIDINA Boucot, Johnson, and Staton

Superfamily **RETZIACEA** Waagen

Family **RETZIIDAE** Waagen

Genus **HUSTEDIA** Hall and Clarke

Hustedia, n. sp. Pl. 3, figs. 36, 37, 42

Discussion. — Two retziid specimens from GSC locality C-4126, Melville Island, are assigned to *Hustedia* on the basis of external morphology. Both specimens are nearly complete although one of them is badly crushed and not suitable for illustration or serial sectioning. These specimens are similar in their small size, subcircular outline, and ornamentation, both having ten costae on the pedicle valve and nine on the brachial valve. The cardinal extremities are distinctly compressed.

This arctic *Hustedia* is similar in outline and ornament to some juveniles of *Hustedia acuticosta* Newell from the Late Pennsylvanian of the mid-continent. However, adults of the latter are substantially larger and usually have more numerous costae.

Some specimens of *Hustedia brentwoodensis* Mather from the Morrowan Series of Oklahoma and Arkansas have only ten costae on the pedicle valve but this species is laterally compressed and subtrigonal in outline.

Hustedia remota (Eichwald) from the Upper Carboniferous and Lower Permian of the Soviet Union, as figured by Chernyshev (1902, pp. 107-109, pl. 47, figs. 8-11) is similar to *Hustedia,* n. sp. in outline and number of costae but is larger and lacks distinctly compressed lateral extremities.

Hustedia, n. sp. is externally most closely similar to *Hustedia indica* Waagen from the Permian of Pakistan. It can be distinguished from the latter by its smaller size, narrower umbonal region, and better compressed lateral extremities.

Suborder ATHYRIDIDINA Boucot, Johnson, and Staton

Superfamily **ATHYRIDACEA** M'Coy

Family **ATHYRIDIDAE** M'Coy

Subfamily **ATHYRIDINAE** M'Coy

Genus **COMPOSITA** Brown

Composita casteri, n. sp. Pl. 2, figs. 1-12; text-fig. 1

Description. — Shell medium to small for genus, about equally biconvex, length and width nearly equal or slightly wider than long; outline subcircular in all growth stages; lateral profile lenticular; maximum width at about midlength; fold and sulcus weakly developed in most specimens; anterior margin slightly emarginate in some specimens, evenly curved in others; anterior commissure usually weakly uniplicate, almost rectimarginate in some specimens; ornament simple, consisting of irregularly spaced growth varices.

Pedicle valve most convex in umbonal region, curving evenly to antero-lateral margins; cardinals margins compressed; sulcus narrow, shallow, weakly to moderately developed in anterior two-thirds of valve; beak small, erect; foramen small, round; delthyrium occluded by dorsal umbo.

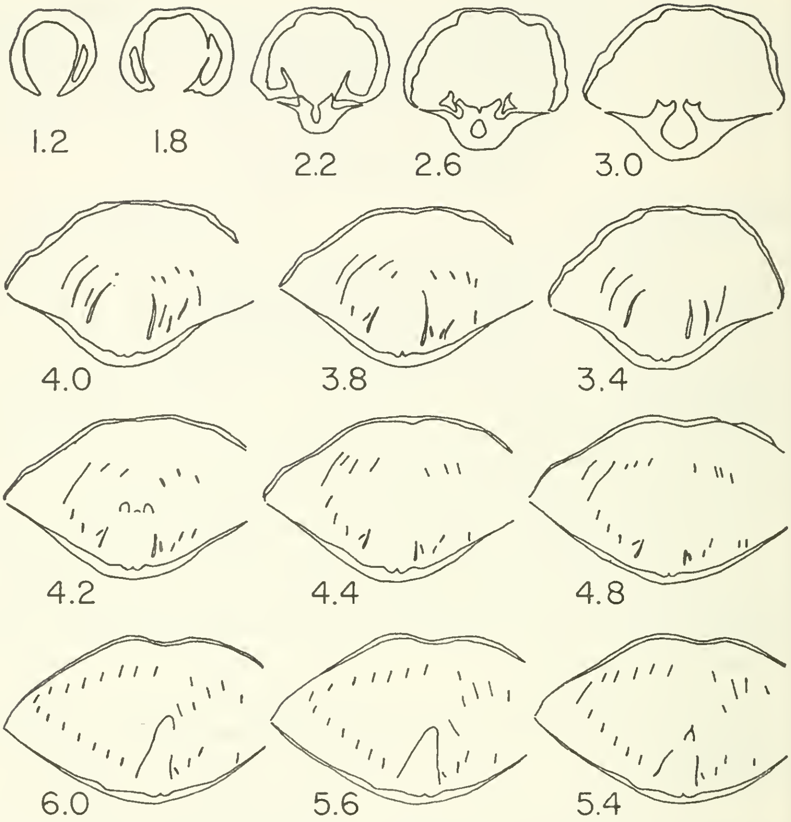
Pedicle valve interior with short medially concave, slightly divergent dental plates; ventral muscle field moderately impressed; teeth small.

Brachial valve most convex in umbonal region, curving evenly to antero-lateral margins; cardinal margins compressed; fold poorly produced in most specimens, often virtually indistinguishable from flanks.

Brachial valve interior with apically perforate, medially cleft, subquadrate, cardinal plate; postero-lateral edges of cardinal plate produced into ventrally curved flanges forming medial sides of sockets; brachidium athyridid; spiralia composed of about eight whorls; adductor field weakly impressed.

Holotype. — GSC 34085, Pl. 2, figs. 1-4.

Measurements of types. — Holotype GSC 34085 : length, 12.5 mm, width, 13.2 mm, thickness, 6.8 mm; paratype GSC 34086 : length, 11.9 mm, width, 11.7 mm, thickness, 7.1 mm; paratype GSC 34087 : length, 9.6 mm, width, 9.3 mm, thickness, 6.1 mm.



Text-figure 1.—Transverse serial sections, × 3, of *Composita casteri*, n. sp., from GSC locality C-4126, Melville Island (GSC 34118). Numbers below figures refer to distance in mm of each section from the pedicle valve beak.

Distinguishing characters. — This species is characterized by its moderate to small size, subcircular outline, weakly developed fold-sulcus, and compressed cardinal margins.

Comparisons. — Species of the genus *Composita* with compressed cardinal margins are not common. *Composita pikensis* Carter from the Burlington Limestone (Tournaisian) of Missouri and *Composita immatura* (Girty) from the Madison Limestone of the western states and the Gilmore City Limestone of Iowa are similar to *C. casteri* in this respect, and also have poorly developed fold-sulcus as well. *C. pikensis* differs from *C. casteri* in its elongate outline, virtual lack of a fold-sulcus, smaller size, and internal details. *C. immatura* differs from *C. casteri* in its elongate outline, larger size, and indistinct fold-sulcus.

Immature specimens of *Composita ovata* Mather, 1916, a widely identified North American species from Late Mississippian and Pennsylvanian horizons, may be difficult to distinguish from *C. casteri* because they commonly have a subcircular outline with compressed cardinal margins and a weakly developed fold-sulcus. However, mature specimens of *C. ovata* lose the compressed cardinal margins, develop broad ventral umbones, and are usually much larger than *C. casteri.*

Some specimens of *Composita windsorensis* Bell, 1929, from the Windsor Group (Viséan) of Nova Scotia, are similar to *C. casteri,* n. sp.. *C. windsorensis* apparently can vary greatly in outline, size, and development of the fold-sulcus. A dorsal sinus or medial groove is present in some specimens and others are elongate. *Composita casteri* does not have a dorsal sinus and is very rarely elongate. These two species may be closely related.

Occurrence and abundance. — This species is found in the collections from both Axel Heiberg Island and Melville Island. The GSC locality C-4126 collection consists of 30 specimens and the three types are from this locality. The GSC locality 26403 collection is small with only five specimens, all of which are smaller on the average than those of C-4126.

Genus **CLEIOTHYRIDINA** Buckman

Cleiothyridina sp. cf. **"Composita" offirmata** Bell Pl. 2, figs. 13-27

1929. *Composita offirmata* Bell, Geol. Sur. Canada, Mem. 155, pp. 136-137, pl. 20, figs. 24-24d.

Discussion. — This small transversely subovate to subcircular species of *Cleiothyridina* is well represented in the two arctic collections. Specimens from both collections agree in size, the weak shallow sometimes indistinct ventral sulcus, the lack of a dorsal fold, and in most other external details. Two of the twelve adult specimens from GSC locality 26403 are subcircular in outline, the other ten being transversely subovate. All six of the larger shells from GSC locality C-4126 are transversely subovate in outline. The only other notable difference between these collections is the greater thickness of several specimens from locality 26403 than is usual for those from locality C-4126. It is unlikely that these small differences would justify separate specific distinction for the two collections.

The outermost shell layers are usually absent from most of the specimens from these collections, producing illusory smooth surfaces marked only by indistinct growth varices. One or two specimens from each collection show very faint ribbing, an impression of the lamellar spines commonly found on the inner shell layers of this genus (Pl. 2, figs. 22-23). The characteristic spinose lamellar ornament of the genus *Cleiothyridina* is preserved on several small specimens from locality C-4126.

Composita offirmata Bell, from the Lower Windsor Group of Nova Scotia, is a small transversely subovate athyridid similar in size, outline, and most external details to many of these arctic specimens. The Nova Scotia species was apparently based on a single specimen, making accurate comparison difficult. The Nova Scotia holotype differs from the arctic specimens in its slightly more distinct ventral sulcus and more inflated umbones. One can see from Bell's illustrations that his specimen is spalled, and there is a possibility that *Composita offirmata* Bell is a *Cleiothyridina.*

Cleiothyridina cestriensis (Snider, 1915) from the Upper Mississippian of Oklahoma is similar in size and outline to the arctic species but can be differentiated by its smaller beak, broader cardinal margins, lack of a ventral sulcus, and thinner profile. *Cleiothyridina elegans* Girty, 1910, from the Fayetteville Shale of Arkansas is possibly a senior synonym of *C. cestriensis* but, unfortunately, Girty's types have never been illustrated.

Cleiothyridina sublamellosa var. *atrypoides* Girty, 1910, also from the Fayetteville Shale, is another species that may be similar to the arctic species, but again, Girty's types have not been illustrated and comparison with it is difficult. Girty's description (1910, p. 223) suggests that *C. atrypoides* could be distinguished from the arctic form by the presence of a dorsal fold and a distinct consistent ventral sulcus.

Suborder SPIRIFERIDINA Waagen

Superfamily **CYRTIACEA** Frederiks

Family **AMBOCOELIIDAE** George

Genus **CRURITHYRIS** George

Crurithyris cf. C. acadica (Bell) Pl. 2, figs. 28-42

1929. *Ambocoelia acadica* Bell, Geol. Sur. Canada, Mem. 155, pp. 141-142, pl. 22, figs. 3-4b.

Discussion. — A medium-size transverse species of the genus *Crurithyris* George is well represented in the collections from both Axel Heiberg Island and Melville Island. There are no consistent external differences between the specimens of the two localities. This arctic species is characterized by its transverse outline, broad shoulders, the lack of a ventral sulcus or groove, and a moderately incurved ventral beak. It is similar in external aspect with the Windsor Group species described by Bell as *Ambocoelia acadica,* except for the latter's smaller size.

Crurithyris cf. *C. acadica* can be readily distinguished from Mississippian species of this genus by its medium size and lack of ventral sulcus. *Crurithyris planoconvexa* (Shumard), the common Pennsylvanian species, is characteristically subcircular to subovate in outline, with a more strongly incurved ventral beak, and is usually smaller.

Superfamily **SPIRIFERACEA** King

Family **SPIRIFERIDAE** King

Subfamily **PROSPIRINAE** Carter

Genus **ANTHRACOSPIRIFER** Lane

Anthracospirifer borealis, n. sp. Pl. 3, figs. 1-32; text-fig. 2

Description. — Shell smaller than average for genus, unequally biconvex, pedicle valve thicker and slightly more inflated than brachial valve; outline transversely subovate in all growth stages;

greatest width attained near or posterior to mid-length; cardinal extremities usually rounded, rarely subangular; fold and sulcus narrow and moderately produced; anterior commissure uniplicate; macro-ornament consists of simple or bifurcate rounded costae and irregularly spaced growth varices; median sulcal costa simple posteriorly, simple or, more rarely, bifurcated anteriorly; other sulcal costae bifurcate from medial edges of sulcus-bounding costae; micro-ornament consisting of faint capillae and fine growth lines.

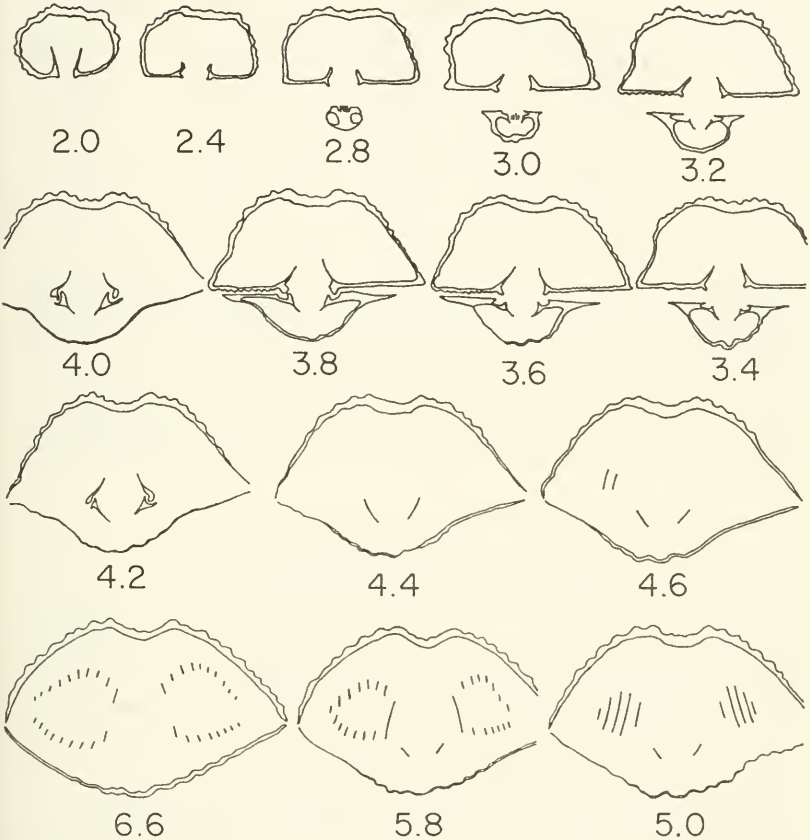
Pedicle valve most convex umbonally in lateral profile; beak small and incurved; flanks evenly convex, sloping evenly and gradually to lateral margins; umbo of medium breadth and extending posterior to opposite valve; interarea of moderate height, curved, sharply defined, apsacline, vertically grooved in weathered specimens, not truncated at lateral extremities; delthyrium apparently open, triangular, apical angle about 60 degrees or less; hingeline denticulate; shallow rounded sulcus originating in beak as a groove, widening evenly to anterior margin, forming sulcal angle of about 21 to 27 degrees; lateral slopes with about 8 to 11 rounded costae in large specimens, one or two of which may be formed by bifurcation from primary costate; first lateral costa on each side of sulcus commonly bifurcating from sulcus-bounding costa anterior to beak region; sulcus with three, four, or more rarely, five sulcal costae.

Interior of pedicle valve with short slightly divergent dental adminicula; teeth small, slender, bladelike.

Brachial valve most convex umbonally, less inflated than pedicle valve; beak inconspicuous; dorsal interarea very low, anacline; fold low and inconspicuous in umbonal region, being delineated mainly by deeply impressed fold-bounding grooves, and rising gradually above flanks anteriorly to form moderately prominent fold; ornament similar and complementary to that of pedicle valve.

Brachial valve interior with sessile striate cardinal process supported by small short medial callus; socket ridges fused with crural bases; spiralia composed of numerous shorls.

Holotype. — GSC 34103, Pl. 3, figs. 13-16.



Text-figure 2.—Transverse serial sections, × 2, of *Anthracospirifer borealis*, n. sp., from GSC locality C-4126, Melville Island (GSC 34119). Numbers below figures refer to the distance in mm of each section from the pedicle valve beak.

Table 1. — Measurements in millimeters of *Anthracospirifer borealis*, n. sp.

GSC#	GSC locality	Length	Width	Thickness
34098	C-4126	16.1	18.7	11.2
34102	26403	16.0	±19.5	10.4
34099	C-4126	12.4	16.1	7.6
34103	26403	11.6	15.4	8.0
34100	C-4126	10.4	12.6	6.9
34104	26403	9.6	12.2	5.8
34105	26403	8.2	±10.0	5.2
34101	C-4126	6.8	7.7	4.9

Distinguishing characters. — This species is characterized by its rounded ears, transversely subovate outline, narrow moderately developed fold-sulcus with three, four, or five sulcal costae, 8 to 11 rounded lateral costae, one or two of which may bifurcate, a medial sulcal costa that may bifurcate, first lateral costae that commonly bifurcate from the sulcus-bounding costae anterior to the umbonal region, and small size.

Comparisons. — *Anthracospirifer borealis* is similar to *A. birdspringensis* Lane, 1963, *A. welleri* (Branson and Greger), and *A. opimus* (Hall). *Anthracospirifer birdspringensis* is larger, more transverse, with more numerous costae. *A. welleri* is similar in size but is usually more elongate and has a simple medial sulcal costa and simple lateral costae. *A. opimus* is usually more elongate than *A. borealis* and has fewer lateral costae. Also, *A. opimus* has a simple medial sulcal costa and the lateral costae bifurcate rarely.

Occurrence and abundance. — *A. borealis* is common in the collections from both islands. The GSC locality C-4126 collection, including types, consists of 40 specimens, most of which are complete or nearly complete. The GSC locality 26403 collection comprises 11 specimens including types.

Family **BRACHYTHYRIDIDAE** Frederiks

Genus **BRACHYTHYRIS** M'Coy

"Brachythyris", n. sp. **cf. B. dichotomus** Litvinovich

1969. *Brachythyris dichotomus* Litvinovich, Ministerstvo Geol. Kazakh. SSR. "NEDRA", pp. 269-270, pl. 64, figs. 3, 4.

Discussion. — A single poorly preserved fragmentary specimen of an unusual brachythyridid was collected at GSC locality 26403, Axel Heiberg Island. This large specimen is not suitable for illustration but preserves enough morphologic details to demonstrate its similarities to another enigmatic brachythyridid, *viz., B. dichotomus* Litvinovich, from the Viséan of central Kazakhstan. *"Brachythyris" dichotomus* possesses unusual ornamentation for this family of spiriferaceans. Whereas almost all genera placed in this family by Carter (1974) have simple lateral ribbing, only the genus *Lithothyris* Roberts, from the Upper Devonian of northwestern Australia, and the two Viséan occurrences of Kazakhstan and the Canadian Arctic have lateral costae that bifurcate, albeit only rarely at that. Both *Litothyris* Roberts and *"Brachythyris" dichotomus,* including the arctic specimen at hand, have a distinctly costate fold-sulcus, a character shared by the genus *Skelidorygma* Carter. The latter genus, however, lacks bifurcating lateral costae.

The Axel Heiberg specimen has coarser costae and is larger than the specimens illustrated by Litvinovich and no doubt represents an undescribed species.

Superfamily **RETICULARIACEA** Waagen

Family **ELYTHIDAE** Frederiks

Genus **PHRICODOTHYRIS** George

Phricodothyris, n. sp. Pl. 3, figs. 33-35

Discussion. — There are two specimens of an undescribed species of the genus *Phricodothyris* in the GSC locality 26403 collection. Both specimens were closely similar in external morphology, and one was serially sectioned in order to confirm the generic identification.

This arctic species can be readily differentiated from the common North American Pennsylvanian form, *P. perplexa* (McChesney), by its smaller size and narrower more elongate umbonal region in the pedicle valve, with resultant greater length-width ratio.

Phricodothyris rostrata (Kutorga) from the Stephanian and Lower Permian of the Urals and central Asia resembles this arctic form in having an elongate or rostrate umbonal region, but it is also larger and more elongate in outline.

Phricodothyris pyriformis Pavlova from the Lower Permian of the central Urals is similar to *Phricodothyris,* n. sp. in outline but has a broader ventral umbo and is substantially larger.

Some specimens of *Phricodothyris* aff. *lineata* (Martin) from the Lower Namurian of Kazakhstan, as figured by Litvinovich (1969, pl. 68, figs. 5, 12), are similar to the arctic species described here. Both of Litvinovich's specimens are larger with slightly broader umbonal regions than the arctic species.

Family **MARTINIIDAE** Waagen

Genus **MARTINIA** M'Coy

Martinia sp. Pl. 3, figs. 38-41

Discussion. — Two small specimens from GSC locality 26403 are assigned to the genus *Martinia* M'Coy. One of these specimens is preserved as an internal mold and there is no evidence of dental adminicula or tabellae. The two specimens are characterized by their small size, nearly equidimentional subcircular outline, and an obscure sulcus in the anterior third of the pedicle valve.

"Martinia" sp. A of Easton (1962, pp. 72-73, pl. 10, figs. 1-3) from the Heath Formation of Montana is similar to this species in outline and the weak development of the ventral sulcus.

Order TEREBRATULIDA Waagen

Suborder TEREBRATULIDINA Waagen

Superfamily **DIELASMATACEA** Schuchert

Family **HETERELASMINIDAE** Likharev

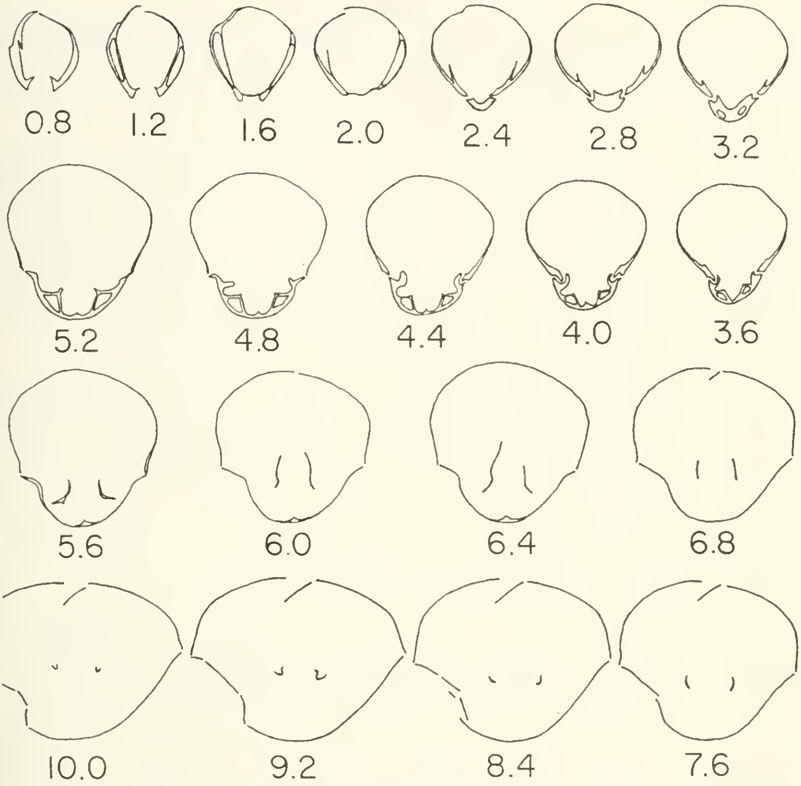
Genus **BEECHERIA** Hall and Clarke

Beecheria formosa (Hall) Pl. 4, figs. 1-32; text-fig. 3

1856. *Terebratula formosa* Hall, Albany Inst., Trans., vol. 4, p. 6.

Discussion. — The most abundant species in both of these arctic collections is a medium-sized to large species of the genus *Beecheria* Hall and Clarke. The Melville Island collection (GSC loc. C-4126) consists of over 90 specimens including juveniles. The Axel Heiberg collection (GSC loc. 26403) consists of about 40 specimens total and also includes several juveniles.

The specimens in these collections are highly variable in size, relative thickness, outline, and degree of inflation of the dorsal umbo, particularly the specimens from Melville Island. However, a gradation exists in each collection between the various extremes and I am forced to conclude that there is only one species represented here. Several specimens from each collection were serially sectioned and the interiors, although all assignable to the genus *Beecheria,* are also highly variable in internal details with no apparent correlation between internal morphology and external variability.



Text-figure 3.—Transverse serial sections, × 2, of *Beecheria formosa* (Hall) from GSC locality C-4126, Melville Island (GSC 34120). Numbers below the figures refer to the distance in mm of each section from the pedicle valve beak.

The only major difference between the two collections pertains to maximum size. The largest specimens from GSC locality 26403 are slightly smaller and less inflated than those of locality C-4126, but the former collection is much the smaller of the two.

Beecheria formosa (Hall) is a widely identified species in formations of Meramecian (Viséan) age in North America. Beznosova (1963, pp. 339-340) also reported it from the Kuzentsk Basin of the Soviet Union. Hall's small types are from the Salem Limestone of Indiana and are apparently juveniles. Whitfield (1882, p. 55) has pointed out the great variability in form and size of this species, a characteristic taken into account in the present identification.

In a few of the larger specimens from GSC locality C-4126 the anterior third or so of the pedicle valve venter is flattened, or even more rarely, slightly sulcate. Only two of the 40 specimens from locality 26403 have an anteriorly flattened venter (one of them is illustrated on plate 4, figs. 13-16). A weakly uniplicate anterior commissure is characteristic of the specimens from both collections, including those lacking a sulcate or flattened venter, as it is for the Salem Limestone materials upon which the species is based.

Individual specimens in both arctic collections are similar to various types and illustrated specimens of *Beecheria arkansanum* (Weller) from the Fayetteville Shale of Arkansas, *Beecheria subspatulum* (Weller) from the Morrow Group of Arkansas, *Beecheria illinoisensis* (Weller) from the Paint Creek Fm. of Illinois and Kentucky, and *Dielasma compressa* Snider from the Moorefield and Fayetteville Formations of Oklahoma. However, most specimens of these species have distinctive and consistent external morphology and are readily differentiated from most specimens of *Beecheria formosa.*

Beecheria davidsoni Hall and Clarke from the Windsor Group of Nova Scotia, is externally closely similar to *B. formosa* (Hall), and like it is highly variable in form, according to Bell (1929, p. 144). The largest specimens of *B. davidsoni* measured by Bell are substantially smaller than the largest specimens from either arctic collection. Bell (p. 146) differentiated *B. davidsoni* from *B. formosa* on their slightly dissimilar interiors. The interiors of the arctic specimens vary so much that it seems possible that the differences noted by Bell are not systematically significant.

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EXPLANATION OF PLATE 1

Figure

1. **Productus** sp.

Natural mold of brachial valve visceral disc exterior and that portion of the pedicle valve trails anterior to the diaphragm, GSC 34070, from GSC locality 26403, Axel Heiberg Island; × 1.

2, 3, 21, 22. **?Eomarginifera** sp.

2, 3. Ventral and anterior views of GSC 34071, Axel Heiberg Island, GSC locality 26403. 21, 22. Ventral and anterior views of natural mold of brachial valve exterior of GSC 34072, from GSC locality C-4126, Melville Island; × 2.

4, 5. **Setigerites cf. S. altonensis** (Norwood and Pratten, 1855)

Ventral and lateral views of pedicle valve, GSC 34073, from GSC locality 26403, Axel Heiberg Island; × 1.

6, 7. **Overtonia** sp.

6. Natural mold of brachial valve exterior, GSC 34074, from GSC locality 26403, Axel Heiberg Island. 7. Latex cast of the same specimen; × 1.5.

8-20, 23-32. **Ovatia cf. O. minor** (Snider, 1915)

8, 9. Ventral and anterior views of a pedicle valve, GSC 34075, from GSC locality 26403. 10-12. Ventral, anterior, and lateral views of a pedicle valve, GSC 34076, from locality 26403. 13, 14. Ventral and anterior views of a natural mold of a brachial valve exterior, GSC 34077 from locality 26403. 15, 16. Ventral and anterior views of a natural mold of a brachial valve exterior, GSC 34078, from locality C-4126. 17, 18. Ventral and anterior views of a pedicle valve, GSC 34079, from locality 26403. 19, 20. Ventral and anterior views of natural mold of a pedicle valve exterior, GSC 34080, from locality 26403. 23, 24. Ventral and dorsal views of a nearly complete specimen, GSC 34081, from locality C-4126. 25-27. Ventral, anterior, and lateral views of a pedicle valve, GSC 34082, from locality 26403. 28, 29. Ventral and anterior views of a pedicle valve, GSC 34083, from locality C-4126. 30-32. Ventral, anterior, and lateral views of a pedicle valve, GSC 34084, from locality C-4126; × 2.


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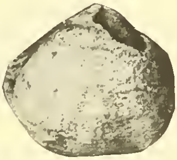
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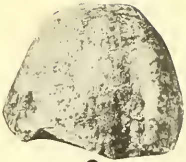
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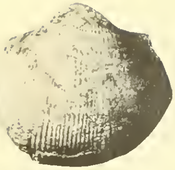
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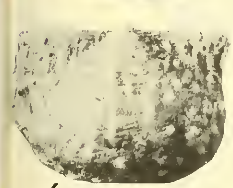
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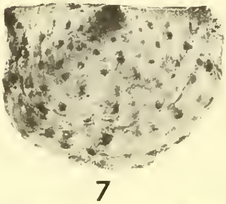
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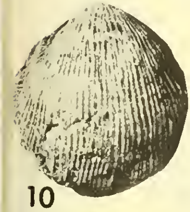
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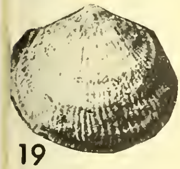
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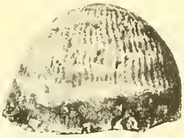
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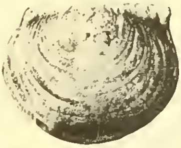
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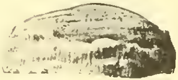
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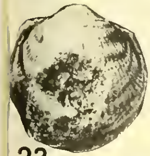
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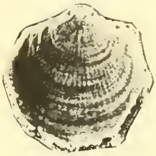
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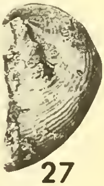
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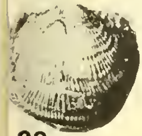
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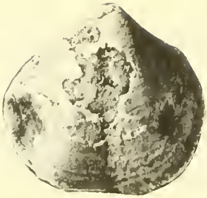
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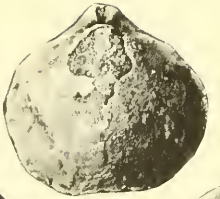
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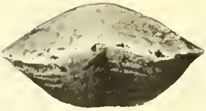
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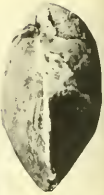
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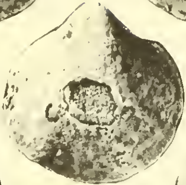
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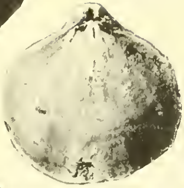
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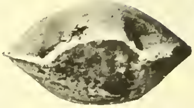
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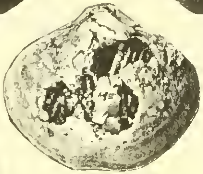
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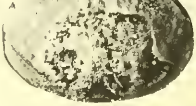
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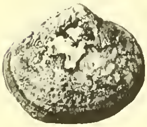
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EXPLANATION OF PLATE 2

Figure

1-12. **Composita casteri,** n. sp.

Ventral, dorsal, anterior, and lateral views of three specimens (GSC 34085, 34086, and 34087, respectively) from GSC locality C-4126, Melville Island; × 2.

13-27. **Cleiothyridina** sp. cf. **"Composita" offirmata** Bell, 1929

Ventral, dorsal, and lateral views of five specimens, GSC 34088 through 34092, respectively. 13-15, 19-21, from Axel Heiberg Island, GSC locality 26403; 16-18, 22-24, 25-27, from Melville Island, GSC locality C-4126; × 1.5.

28-42. **Crurithyris** cf. **C. acadica Bell,** 1929

28-30, 31-33, 37-39, 40-42. Ventral, dorsal, and lateral views of four specimens (GSC 34093 through 34096, respectively) from Axel Heiberg Island, GSC locality 26403. 34-36. Ventral, dorsal, and lateral views of a specimen, GSC 34097, from Melville Island, GSC locality C-4126; × 2.

EXPLANATION OF PLATE 3

Figure

1-32. **Anthracospirifer borealis,** n. sp.

1-4, 9-12, 17-20, 29-32. Ventral, dorsal, lateral, and anterior views of four specimens (GSC 34098 through 34101, respectively) from Melville Island, GSC locality C-4126. 5-8, 13-16, 21-24, 25-28. Ventral, dorsal, lateral, and anterior views of four specimens (GSC 34102 through 34105, respectively) from Axel Heiberg Island, GSC locality 26403; × 1.5.

33-35. **Phricodothyris,** n. sp.

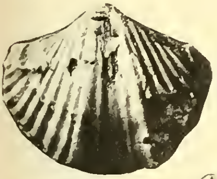
Ventral, dorsal, and lateral views of a complete specimen, GSC 34106, from Axel Heiberg Island, GSC locality 26403; × 2.

36, 37, 42. **Hustedia,** n. sp.

Ventral, dorsal, and lateral views of a complete specimen, GSC 34107, from Melville Island, GSC locaity C-4126; × 2.

38-41. **Martinia** sp.

Ventral, dorsal, anterior, and lateral views of a complete specimen, GSC 34108, from Axel Heiberg Island, GSC locality 26403; × 1.5.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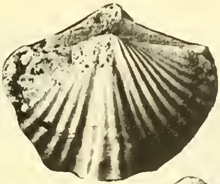
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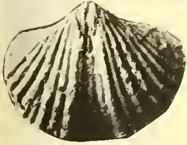
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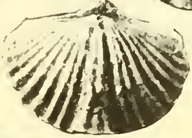
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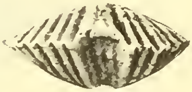
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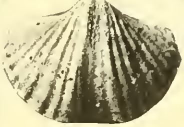
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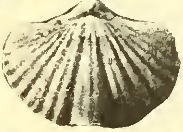
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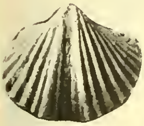
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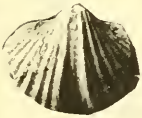
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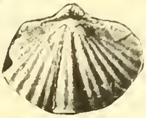
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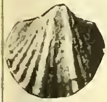
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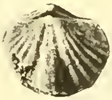
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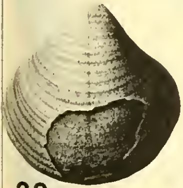
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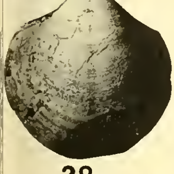
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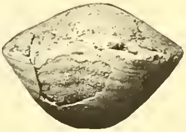
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PLATE 4


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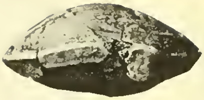
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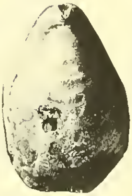
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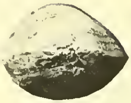
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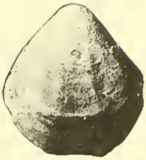
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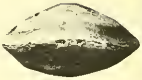
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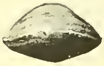
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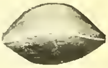
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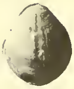
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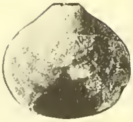
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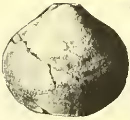
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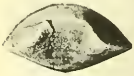
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EXPLANATION OF PLATE 4

Figure

1-32. **Beecheria formosa** (Hall, 1856)

1-4, 9-12, 21-24, 25-28. Ventral, dorsal, anterior, and lateral views of four specimens (GSC 34109 through 34112, respectively) from Melville Island, GSC locality C-4126. 5-8, 13-16, 17-20, 29-32. Ventral, dorsal, anterior, and lateral views of four specimens (GSC 34113 through 34116, respectively) from Alex Heiberg Island, GSC locality 26403; × 1.

33-35. Indeterminate wellerellid.

Ventral, dorsal, and anterior views of a nearly complete specimen, GSC 34117, from Axel Heiberg Island, GSC locality 26403; × 2.

MIDDLE DEVONIAN BONE BEDS AND THE COLUMBUS-DELAWARE (ONONDAGAN-HAMILTONIAN) CONTACT IN CENTRAL OHIO

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ABSTRACT

The Columbus-Delaware (Onondagan-Hamiltonian) contact in central Ohio is drawn at the base of the lower part (bone bed 7 of present terminology) of the lower bone bed of Westgate and Fischer (1933) which constitutes the basal part of Stauffer's (1909) I Zone of the Delaware Formation as revised herein; the contact is one of paracontinuity (Conkin and Conkin, 1973a), involving as it does slight but significant physical and faunal discontinuities.

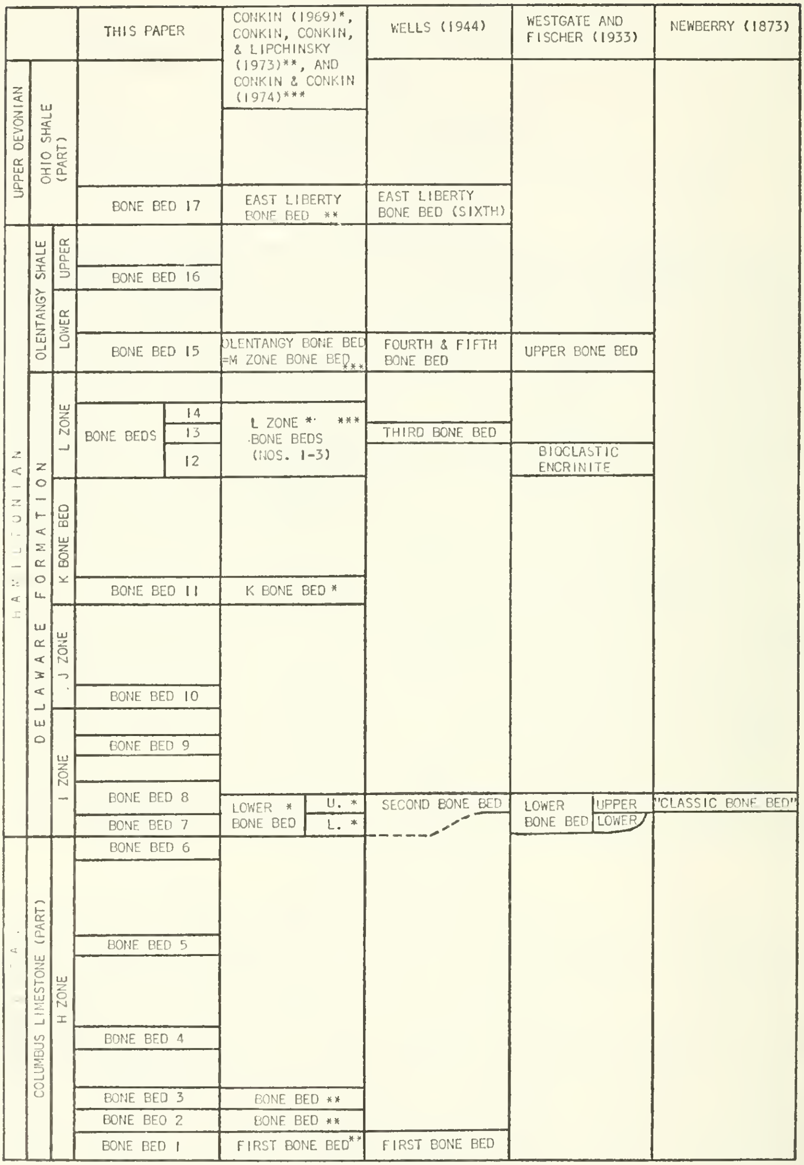
We presently recognize 17 bone beds in the Devonian of Ohio, 16 of which are in the Middle Devonian (below the Ohio Shale); of these 16 bone beds, six are in the Onondagan Columbus Limestone (all in Stauffer's 1909 H Zone) and eight are in the Hamiltonian Delaware Formation (I to L Zones). Stauffer's (1909) M Zone of the Delaware Formation does not exist, for the L Zone (Conkin and Conkin, 1974) includes both the L and M Zones of Stauffer (1909). The two bone beds recognized by Tillman (1970) in the upper Hamiltonian Olentangy Shale are bone beds 15 and 16 of present terminology. The East Liberty Bone Bed of the Bellefontaine area of Logan County, at the base of the Upper Devonian Ohio Shale, is bone bed 17.

Erroneous past placement of the Columbus-Delaware contact just above Newberry's (1873) classic bone bed (that is, at the base of the "Tioga? Bentonite?") causes certain Hamiltonian guide fossils to be allocated to the Onondagan Columbus Limestone; that is, bone bed 7 and the classic bone bed portion of bone bed 8 (the lower and upper parts respectively of Westgate and Fischer's 1933 lower bone bed) bear restricted lower Hamiltonian fossils, especially *"Martinia" maia* (Billings) and *"Delthyris consobrina"* (d'Orbigny) a form of *Brevispirifer, B.* cf. *B. lucasensis* (Stauffer)).

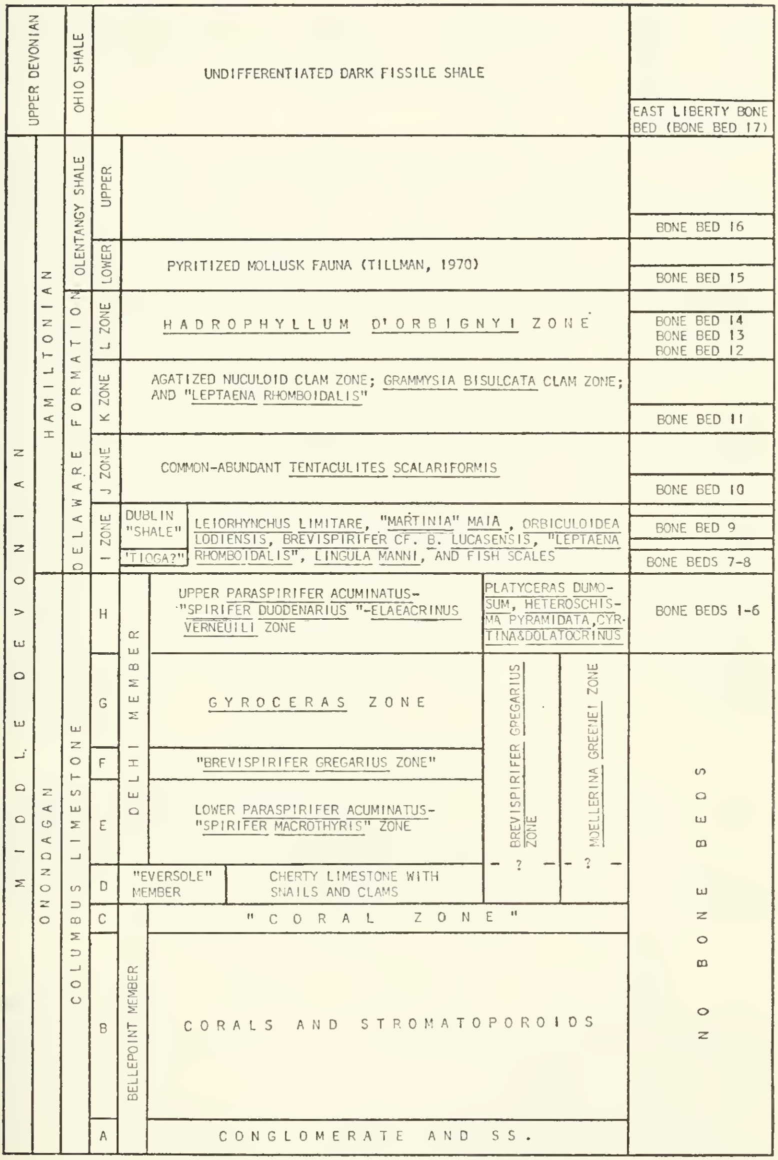
The I Zone (Westgate and Fischer's 1933 lower bone bed and the Dublin "Shale" of Franklin and southern Delaware counties, and its dominantly limestone northern facies) of the Delaware Formation may correlate with the lowest Hamiltonian Dundee Limestone of Michigan and northwestern Ohio.

INTRODUCTION

Bone beds can be used as keys for differentiation and correlation of stratigraphic intervals within the Middle Devonian of Ohio (and indeed, of the whole east-central United States). Including the bone beds previously recorded in the Middle Devonian limestones in central Ohio (Newberry, 1873; Westgate and Fischer, 1933; Wells, 1944; Conkin, 1969; Conkin, Conkin, and Lipchinsky, 1973; and Conkin and Conkin, 1974), we now recognize six bone beds in the Columbus Limestone (all in Stauffer's 1909 H Zone) and eight bone beds in the Delaware Formation (I-L Zones). There are, thus, 14 bone beds in the Columbus-Delaware sequences. Two bone beds recognized by Tillman (1970) in the upper Hamiltonian Olentangy Shale, make 16 bone beds altogether in the Middle Devonian below the Ohio Shale in central Ohio (Text-figs. 1, 2). A seventeenth bone



Text-figure 1. Relationships between the 17 Devonian bone beds presently recognized in central Ohio and the bone beds previously reported (all bone beds here shown in their correct stratigraphic positions regardless of original placement).



Text-figure 2. Composite generalized Devonian stratigraphy as displayed variously in Franklin, Delaware, and Logan counties in central Ohio (stratigraphic intervals not drawn to scale).

bed (Text-figs. 1, 2), the East Liberty Bone Bed (Wells, 1944), occurs at the base of the Upper Devonian Ohio Shale in the Bellefontaine area (Text-fig. 3) of Ohio (Conkin, Conkin, and Lipchinsky, 1973).

Paracontinuities (Conkin and Conkin, 1973a, pp. 12, 13) are often associated in the Middle Devonian with bone beds. Paracontinuities are disconformities which exhibit a slight, though significant, faunal discontinuity and slight, though clearly discernable, channeling of the underlying rocks. The rocks which overlie paracontinuities have a basal detrital unit, such as a bone bed. Bone beds combined with paracontinuities are straitigraphically significant and have proven useful in delimiting stratigraphic units (of regional extent) which otherwise have defied precise definition. We place the Columbus-Delaware (Onondagan-Hamiltonian) contact at a position which is marked by the paracontinuity at the base of bone bed 7 (the lower part of Westgate and Fischer's 1933 lower bone bed) situated at the base of the I Zone of the Delaware Formation (Pl. 1, figs. 1, 3, 7, 9; Text-figs. 1, 2). Further, the stratigraphic units within the H Zone of the upper part of the Columbus Limestone (Text-figs. 1, 2, 4) and the I, J, K, and L Zones of the Delaware Formation (Text-figs. 1, 2, 5-9) are delimited precisely for the first time, primarily on the bases of paracontinuities and associated bone beds.

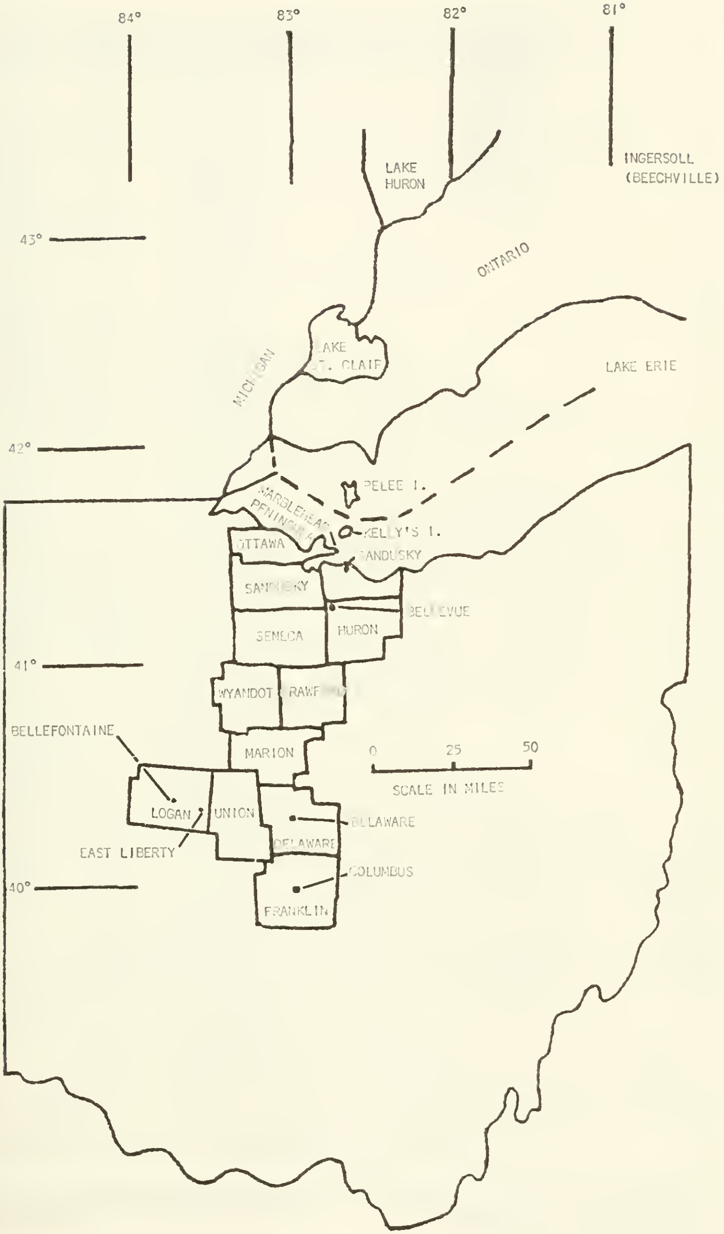
PAST WORK ON THE BONE BEDS AND THE COLUMBUS-DELAWARE CONTACT IN CENTRAL OHIO

Pertinent past information concerning the bone beds and the Columbus-Delaware contact in central Ohio (Text-fig. 3), along with our comments and explanations where necessary, follows.

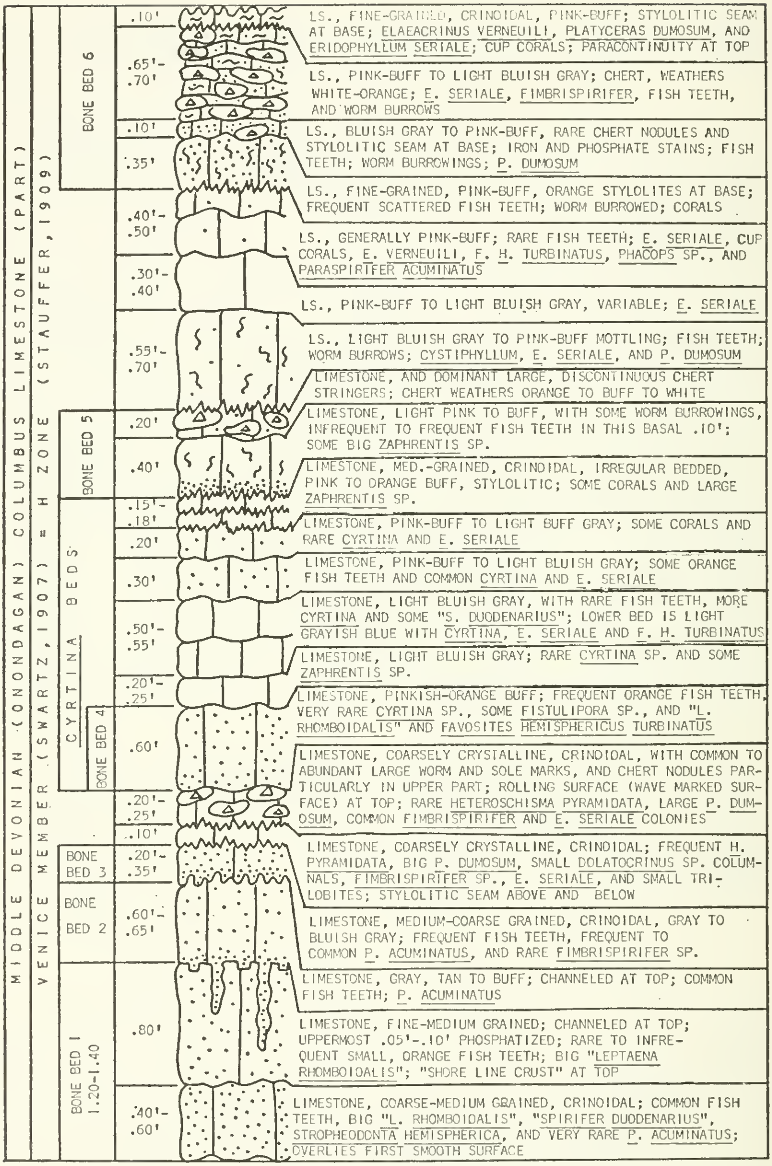
WORK OF NEWBERRY, WINCHELL, AND ORTON

Newberry (1873) divided the "Corniferous" of Ohio into an upper blue portion, the Sandusky Limestone, and a lower dominantly gray portion, the Columbus Limestone, which contained bluish beds in its upper part. The Columbus Limestone, at Columbus (Text-fig. 3) was considered by Newberry to have at its top "the bone bed" which has become known as "the classic Middle Devonian bone bed" (Text-fig. 1).

Winchell (1874) proposed the name Delaware Limestone for



Text-figure 3. Location of counties in Ohio referred to in this paper.



LS., FINE-GRAINED, CRINOIDAL, PINK-BUFF; STYLOLITIC SEAM AT BASE; ELAEACRINUS VERNEUILI, PLATYCERAS DUMOSUM, AND ERIDOPHYLLUM SERIALE; CUP CORALS; PARACONTINUITY AT TOP

LS., PINK-BUFF TO LIGHT BLUISH GRAY; CHERT, WEATHERS WHITE-ORANGE; E. SERIALE, FIMBRISPIRIFER, FISH TEETH, AND WORM BURROWS

LS., BLUISH GRAY TO PINK-BUFF, RARE CHERT NODULES AND STYLOLITIC SEAM AT BASE; IRON AND PHOSPHATE STAINS; FISH TEETH; WORM BURROWINGS; P. DUMOSUM

LS., FINE-GRAINED, PINK-BUFF, ORANGE STYLOLITES AT BASE; FREQUENT SCATTERED FISH TEETH; WORM BURROWED; CORALS

LS., GENERALLY PINK-BUFF; RARE FISH TEETH; E. SERIALE, CUP CORALS, E. VERNEUILI, F. H. TURBINATUS, PHACOPS SP., AND PARASPIRIFER ACUMINATUS

LS., PINK-BUFF TO LIGHT BLUISH GRAY, VARIABLE; E. SERIALE

LS., LIGHT BLUISH GRAY TO PINK-BUFF MOTTLING; FISH TEETH; WORM BURROWS; CYSTIPHYLLUM, E. SERIALE, AND P. DUMOSUM

LIMESTONE, AND DOMINANT LARGE, DISCONTINUOUS CHERT STRINGERS; CHERT WEATHERS ORANGE TO BUFF TO WHITE

LIMESTONE, LIGHT PINK TO BUFF, WITH SOME WORM BURROWINGS, INFREQUENT TO FREQUENT FISH TEETH IN THIS BASAL .10'; SOME BIG ZAPHRENTIS SP.

LIMESTONE, MED.-GRAINED, CRINOIDAL, IRREGULAR BEDDED, PINK TO ORANGE BUFF, STYLOLITIC; SOME CORALS AND LARGE ZAPHRENTIS SP.

LIMESTONE, PINK-BUFF TO LIGHT BUFF GRAY; SOME CORALS AND RARE CYRTINA AND E. SERIALE

LIMESTONE, PINK-BUFF TO LIGHT BLUISH GRAY; SOME ORANGE FISH TEETH AND COMMON CYRTINA AND E. SERIALE

LIMESTONE, LIGHT BLUISH GRAY, WITH RARE FISH TEETH, MORE CYRTINA AND SOME "S. DUODENARIUS"; LOWER BED IS LIGHT GRAYISH BLUE WITH CYRTINA, E. SERIALE AND F. H. TURBINATUS

LIMESTONE, LIGHT BLUISH GRAY; RARE CYRTINA SP. AND SOME ZAPHRENTIS SP.

LIMESTONE, PINKISH-ORANGE BUFF; FREQUENT ORANGE FISH TEETH, VERY RARE CYRTINA SP., SOME FISTULIPORA SP., AND "L. RHOMBOIDALIS" AND FAVOSITES HEMISPHERICUS TURBINATUS

LIMESTONE, COARSELY CRYSTALLINE, CRINOIDAL, WITH COMMON TO ABUNDANT LARGE WORM AND SOLE MARKS, AND CHERT NODULES PARTICULARLY IN UPPER PART; ROLLING SURFACE (WAVE MARKED SURFACE) AT TOP; RARE HETEROSCHISMA PYRAMIDATA, LARGE P. DUMOSUM, COMMON FIMBRISPIRIFER AND E. SERIALE COLONIES

LIMESTONE, COARSELY CRYSTALLINE, CRINOIDAL; FREQUENT H. PYRAMIDATA, BIG P. DUMOSUM, SMALL DOLATOCRINUS SP. COLUMNALS, FIMBRISPIRIFER SP., E. SERIALE, AND SMALL TRILOBITES; STYLOLITIC SEAM ABOVE AND BELOW

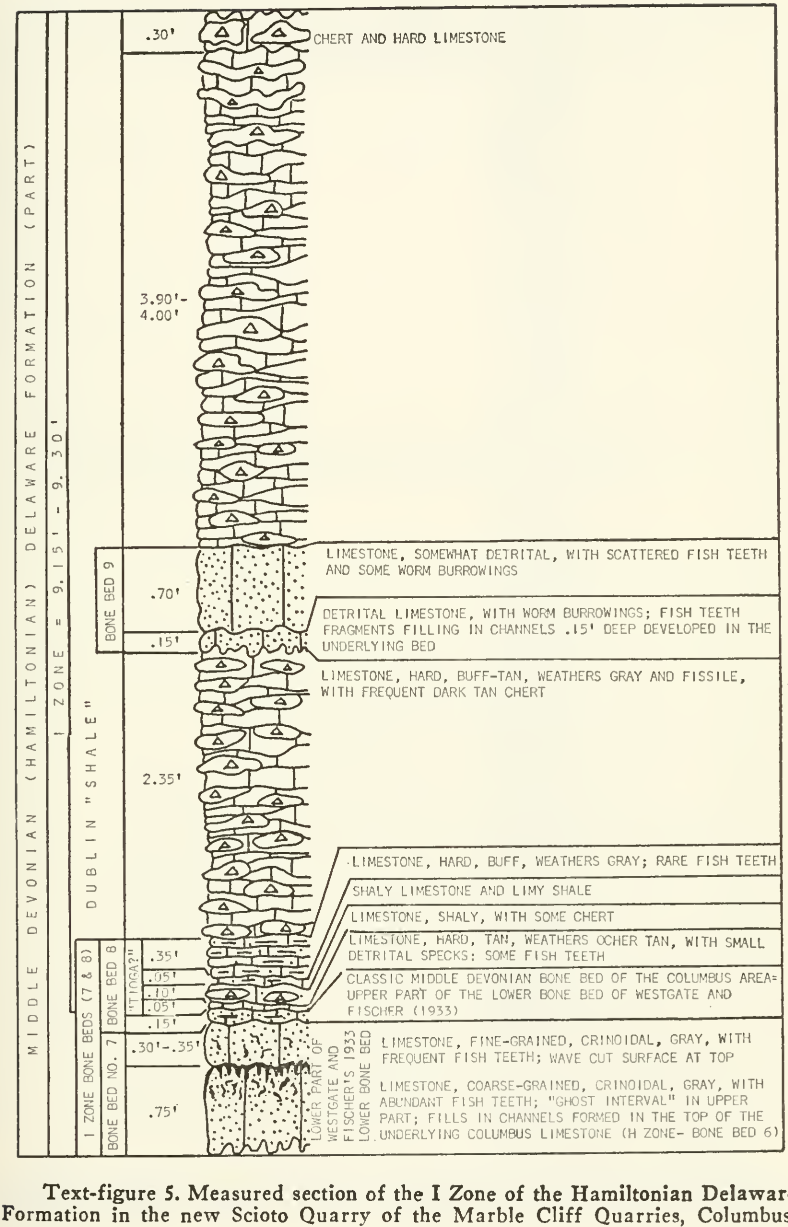
LIMESTONE, MEDIUM-COARSE GRAINED, CRINOIDAL, GRAY TO BLUISH GRAY; FREQUENT FISH TEETH, FREQUENT TO COMMON P. ACUMINATUS, AND RARE FIMBRISPIRIFER SP.

LIMESTONE, GRAY, TAN TO BUFF; CHANNELED AT TOP; COMMON FISH TEETH; P. ACUMINATUS

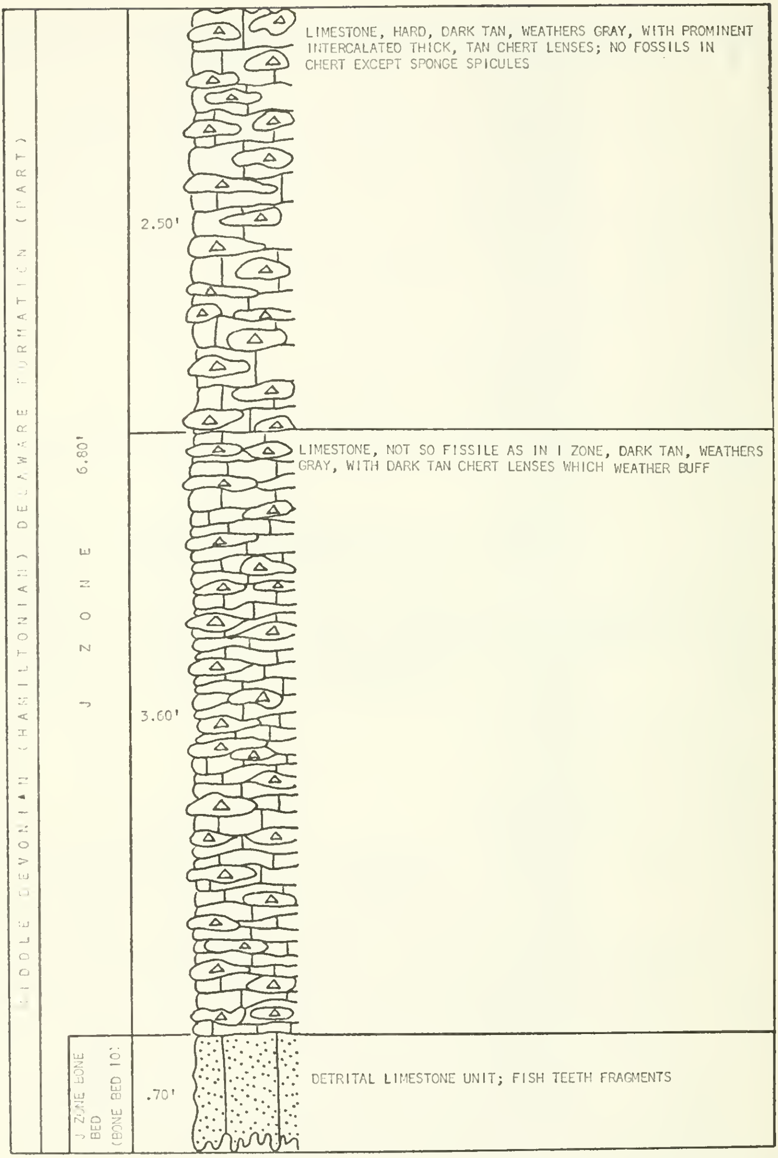
LIMESTONE, FINE-MEDIUM GRAINED; CHANNELED AT TOP; UPPERMOST .05'-.10' PHOSPHATIZED; RARE TO INFREQUENT SMALL, ORANGE FISH TEETH; BIG "LEPTAENA RHOMBOIDALIS"; "SHORE LINE CRUST" AT TOP

LIMESTONE, COARSE-MEDIUM GRAINED, CRINOIDAL; COMMON FISH TEETH, BIG "L. RHOMBOIDALIS", "SPIRIFER DUODENARIUS", STROPHEODONTA HEMISPHERICA, AND VERY RARE P. ACUMINATUS; OVERLIES FIRST SMOOTH SURFACE

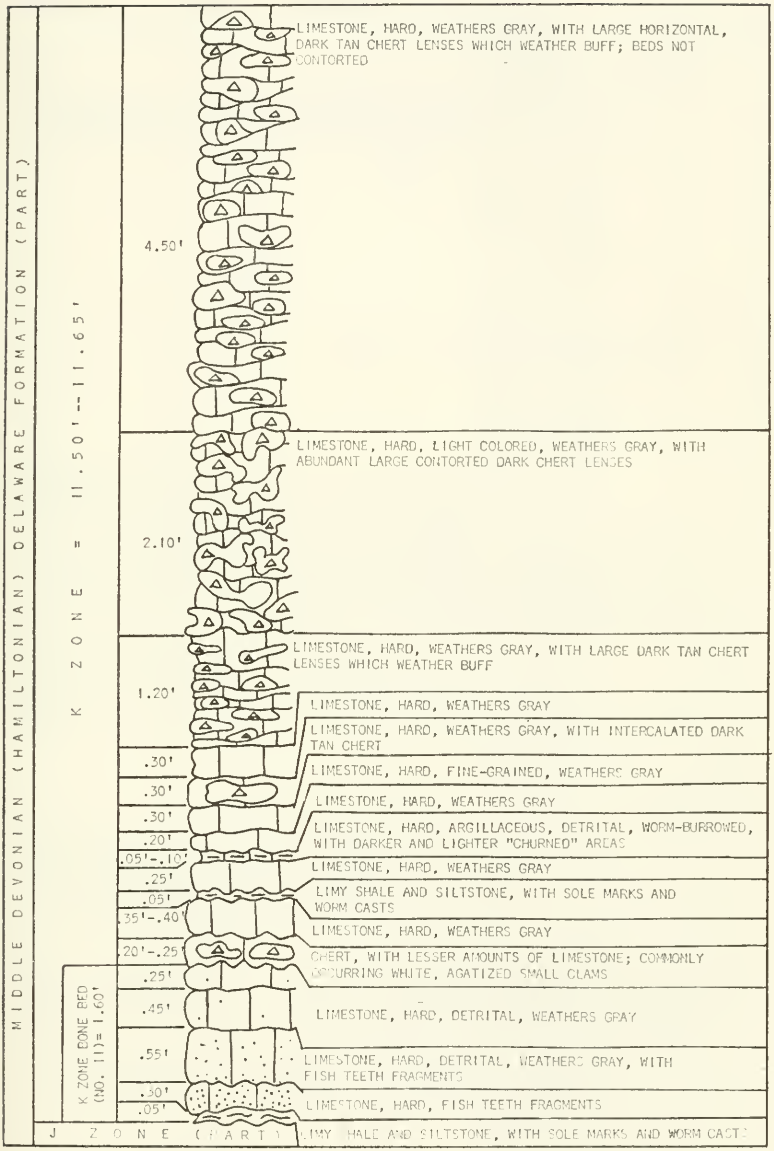
Text-figure 4. Measured section of the H Zone (Venice Member) of the Onondagan Columbus Limestone in the new Scioto Quarry of the Marble Cliff Quarries, Columbus, Ohio.



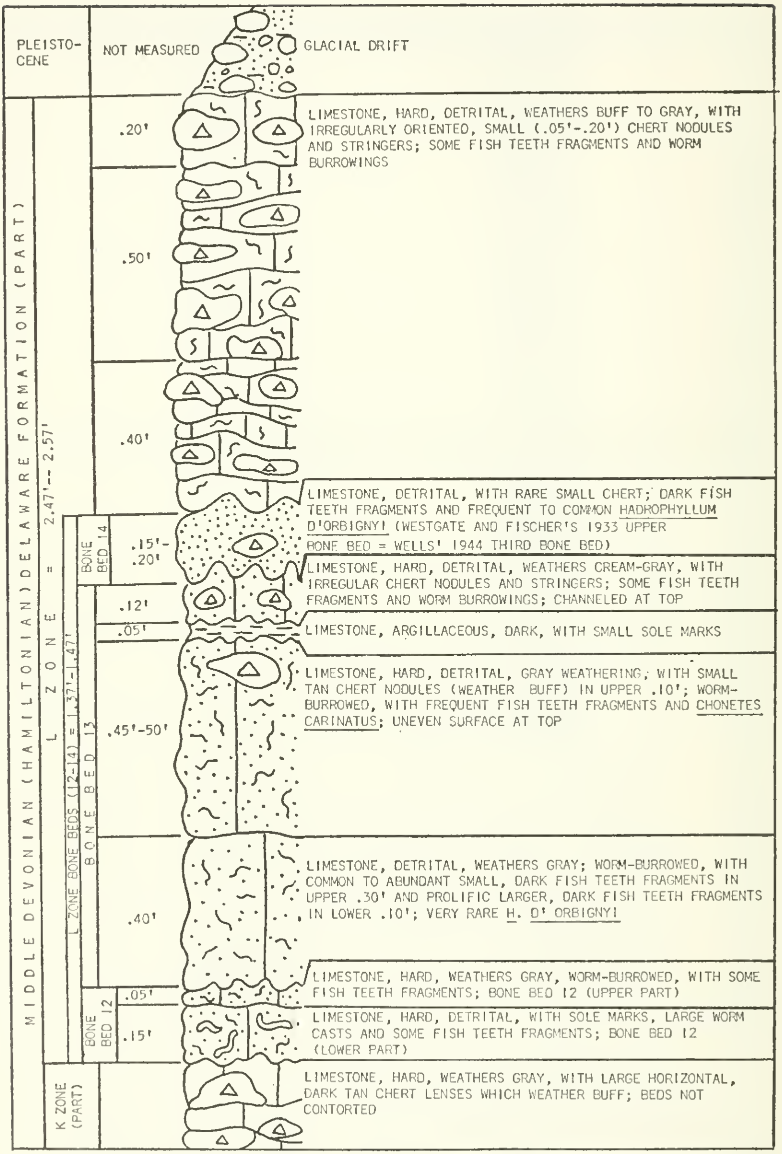
Text-figure 5. Measured section of the I Zone of the Hamiltonian Delaware Formation in the new Scioto Quarry of the Marble Cliff Quarries, Columbus, Ohio.



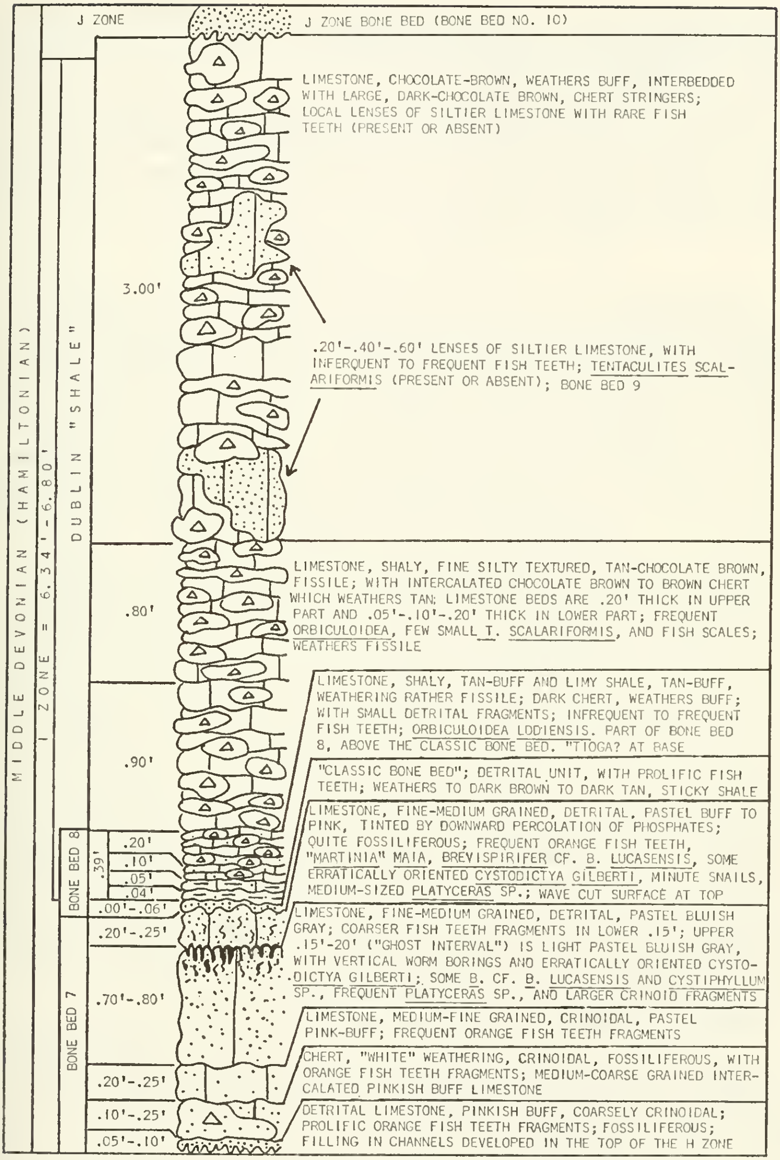
Text-figure 6. Measured section of the J Zone of the Hamiltonian Delaware Formation in the new Scioto Quarry of the Marble Cliff Quarries, Columbus, Ohio.



Text-figure 7. Measured section of the K Zone of the Hamiltonian Delaware Formation in the new Scioto Quarry of the Marble Cliff Quarries, Columbus, Ohio.



Text-figure 8. Measured section of the lower portion of the L Zone of the Hamiltonian Delaware Formation as represented in the new Scioto Quarry of the Marble Cliff Quarries, Columbus, Ohio.



Text-figure 9. Measured section of the I Zone of the Hamiltonian Delaware Formation in the north wall of the Scioto Quarry of the Marble Cliff Quarries, Columbus, Ohio.

the blue limestones of the Middle Devonian exposed at Delaware, Ohio (Text-fig. 3); Winchell correlated the Delaware with Newberry's Sandusky Limestone.

Orton (1878) considered the classic bone bed (two to four inches thick) in the Columbus area, to mark the boundary between the Columbus Limestone and the Delaware Formation, but he did not refer it to either formation.

WORK OF SWARTZ

Swartz (1907) came rather close to making correct correlation of major Middle Devonian stratigraphic units in central Ohio (the Columbus-Delaware area) and northern Ohio (the Bellevue-Sandusky-Marblehead Peninsula-Kelley's Island areas; Text-fig. 3). Swartz demonstrated the equivalency of a lower gray limestone interval in the Sandusky Limestone and the upper part of the Columbus Limestone and proposed the name Venice Member for these beds which he designated also as the Upper *Paraspirifer acuminatus*-"*Spirifer duodenarius*" horizon (Text-fig. 10). Swartz further divided the Columbus (Text-fig. 10) into a middle part, the Marblehead Member (designated as the Lower *P. acuminatus-Spirifer macrothyris* horizon) and a lower part, the Bellepoint Member, which, in essence, includes Stauffer's (1909) Zones A to C (Text-fig. 10) of the Columbus (or the interval from the top of the "Coral Zone" down to the base of the Columbus). The Bellepoint Member recently has been correlated with the Detroit River Member of the Columbus (Conkin and Conkin, 1973b, p. 33). Swartz (1907, p. 64) suppressed Newberry's (1873) Sandusky Limestone on the grounds that it is not a genetic unit but is part Delaware and part Columbus. Unfortunately, Swartz (1907, pp. 59, 60, 62), following Newberry (1873), allocated the classic Middle Devonian bone bed to the top of the Columbus Limestone.

A significant contribution of Swartz (1907, p. 60) was recognition of the two separate *Paraspirifer acuminatus* intervals in the Columbus Limestone (Text-fig. 10). We (Conkin and Conkin, 1969, pp. 73-75) recorded *P. acuminatus* in the lower 0.1 foot of the *Brevispirifer gregarius* Zone (= Conkin and Conkin's 1972 Lower *P. acuminatus* Subzone of the *P. acuminatus* Zone) at the Falls of the Ohio, Jefferson County, Kentucky, and Clark County, Indiana. Further, we recognized an Upper *P. acuminatus*-"*Spirifer duo-*

denarius" Subzone of the *P. acuminatus* Zone in the Jeffersonville Limestone at the Falls of the Ohio (Conkin and Conkin, 1972 and 1973b) which is the correlative of the upper part of Swartz's 1907 Venice Member (Text-fig. 10). We, in essence, believe that the three members of the Columbus Limestone recognized by Swartz (1907) can be extended from northern to central Ohio (Text-fig. 3), and to the northwestern Kentucky and southern Indiana area (Conkin and Conkin, 1973b, p. 33), as indicated in Text-figure 10.

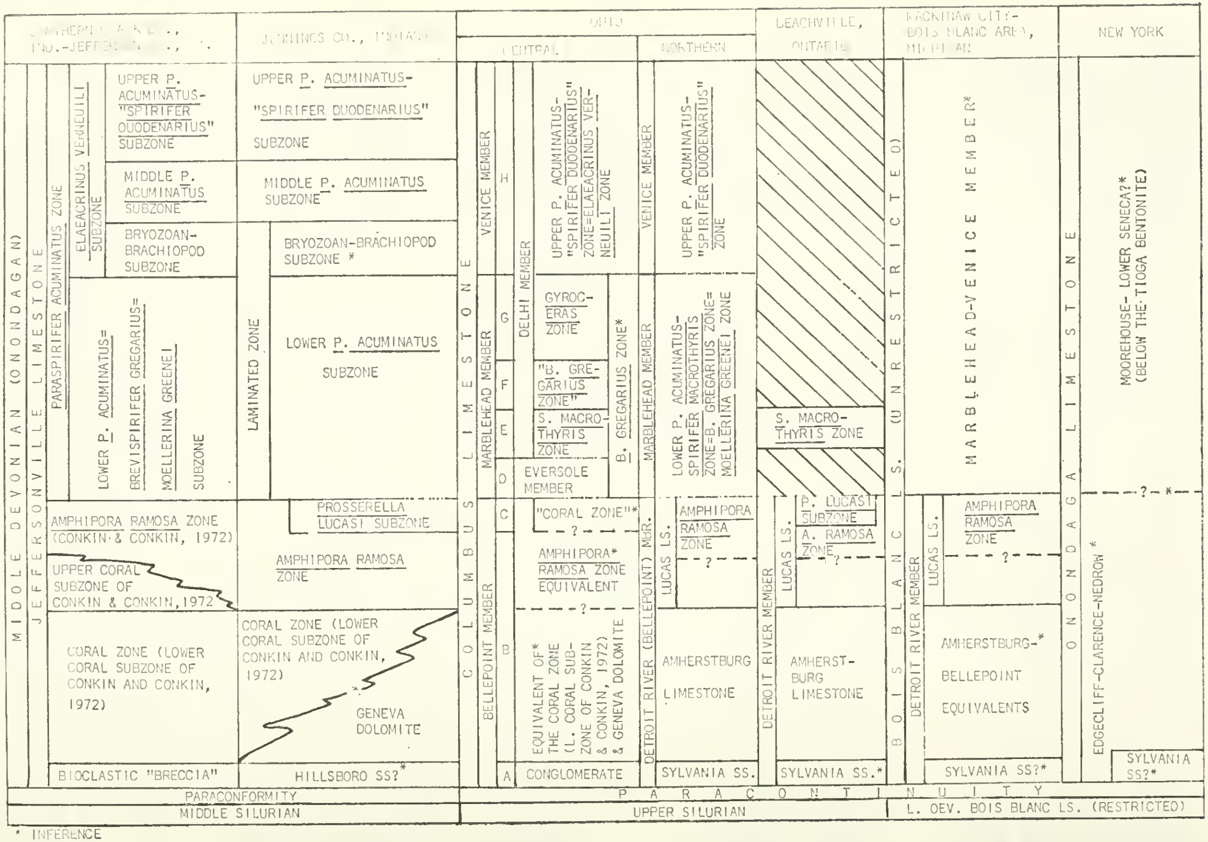
WORK OF STAUFFER

Stauffer (1909) divided the Columbus Limestone (Text-fig. 10) into eight zones (A-H) and the Delaware (Text-fig. 1) into five zones (I-M), and, as did Newberry (1873) and Swartz (1907), relegated the classic Middle Devonian bone bed (Text-fig. 1) to the top of the H Zone (Upper *Paraspirifer acuminatus*-"*Spirifer duodenarius*" Zone = Swartz's 1907 Venice Member).

WORK OF WESTGATE AND FISCHER

Westgate and Fischer (1933, pp. 1162, 1163) recognized two bone beds (upper and lower) in the Middle Devonian limestones of central Ohio (Text-figs. 1, 3). They considered their upper bone bed to be situated near the top of the Hamiltonian Delaware Formation. Stauffer (1909) had assigned the uppermost beds of the Delaware Formation, approximately ten feet of limestone overlying the *Hadrophyllum d'orbignyi* interval, to his M Zone (only the basal, *H. d'orbignyi*-bearing beds were considered to be the L Zone). Wells (1944, p. 276) later incorrectly referred Westgate and Fischer's upper bone bed to Stauffer's M Zone. In reality, the L Zone is much thicker (10 to 11 feet) than previously thought (0.3 to 1.3 feet) by Stauffer (1909), Westgate (1926), Westgate and Fischer (1933), and Wells (1944), for it actually includes both the L and M Zones of Stauffer (1909) and subsequent workers (except Conkin and Conkin, 1974).

We have determined that Westgate and Fischer's (1933) upper bone bed (Text-figs. 1, 2) lies at the base of the lower part of the Olentangy Shale (bone bed 15 of present terminology). In the west quarry (the only place where Westgate and Fischer saw their upper bone bed) of the Blue Limestone Park Quarries, in Delaware (Text-fig. 3), pre-Olentangy channels (several feet in depth) cut into the



Text-figure 10. Suggested correlation of Onondagan stratigraphic units in northwestern Kentucky, southern Indiana, central and northern Ohio, southern Ontario, northern Michigan, and New York (modified after Conkon and Conkin, 1973, fig. 1).

L Zone; in fact, at one place, the thin, coarsely crystalline, crinoidal lower Olentangy bone bed (Westgate and Fischer's upper bone bed) lies in the bottom of an eight foot deep channel cut into the L Zone. If one digs through the Pleistocene cover, Olentangy-like shale can be detected (above the upper bone bed) filling this channel which is cut into the L Zone. A few feet to the west of this channel, some 11 feet of the L Zone are exposed, creating the illusion that Westgate and Fischer's upper bone bed lies with the L Zone (the bulk of the L Zone was interpreted as the M Zone prior to Conkin and Conkin's 1974 work). The stratigraphic top of the L Zone is not exposed anywhere in this quarry because of glacial cover; however, this 11 foot exposure probably represents the approximate maximum thickness of the L Zone.

Although they did not describe it as a bone bed, Westgate and Fischer (1933, p. 1170) recognized that a coarse-grained, crinoidal "sandstone" (bioclastic encrinite), "bearing negligible amounts of fish material", situated at the base of the L Zone, was similar lithologically to their upper and lower bone beds; this bioclastic encrinite (Text-fig. 1) is indeed a bone bed and bears rare *Hadrophyllum d'orbignyi* Edwards and Haime. The L Zone really contains three separate, closely spaced, bone beds (Conkin and Conkin, 1974) extending over a basal interval in the L Zone of approximately 3.5 feet in the Delaware area and 1.5 feet in the Columbus area; Westgate and Fischer's bioclastic encrinite (Text-fig. 1) is the lowest (bone bed 12 of present terminology) of these three bone beds (12-14), as seen in Text figures 1, 2, and 8. *H. d'orbignyi* occurs frequently or commonly in bone bed 14 of the L Zone at Columbus and is abundant to prolific in occurrence in bone bed 13 at Delaware and on Bartholomew Run, Delaware County.

While the lower bone bed of Westgate and Fischer (1933, p. 1166) comprised only the classic Middle Devonian bone bed in most places, at the Williams Quarry of the Marble Cliff Quarries the lower bone bed is double and includes the classic bone bed as the upper part, and, as its lower part, includes a thicker (9-14 inches) crinoidal limestone (with commonly occurring bones, though somewhat less common than in the classic bone bed). Westgate and Fischer (1933, p. 1166) demonstrated the two-fold division of their lower bone bed in the Williams Quarry by noting the existence of a disconformity below each part. By means of the physical evidence of the lower disconformity (paracontinuity) and recognition of restricted Hamiltonian species throughout both parts of their lower bone bed, they correctly placed their lower bone bed at the base of the I Zone of the Hamiltonian Delaware Formation. In actuality, the lower part (bone bed 7 of present terminology) of Westgate and Fischer's lower bone bed occurs at the base of the I Zone everywhere in the quarries in central Ohio, even though Westgate and Fischer recognized the lower part only in the Williams Quarry (Westgate and Fischer, 1933, text-fig. 1).

WORK OF WELLS

Wells (1944) recognized six Devonian bone beds (Text-fig. 1) in Ohio and numbered them more or less in their ascending stratigraphic order. The first bone bed (bone bed I of present terminology) lies at the base of the H Zone, approximately 9.5 feet below the "Tioga? Bentonite?" in the Columbus area.

Wells' second bone bed included in places (1944, fig. 12b) both the upper and lower parts of the lower bone bed of Westgate and Fischer (1933); in other places (1944, fig. 12a), however, Wells' second bone bed comprised only the upper part of Westgate and Fischer's lower bone bed, the classic bone bed. Wells placed the base of his second bone bed at the base of the classic bone bed where the classic bone bed was prominently developed; in other places, where the bone bed is in two parts, Wells was unable to discern a lower contact and considered the contact to be gradational. In essence, the contact was extended downward to some indefinite position within (but probably to the base of) bone bed 7 of present terminology. Wells (1944), following Newberry (1873), Swartz (1907), and Stauffer (1909), considered his entire second bone bed to belong to the uppermost beds of the H Zone of the Columbus Limestone.

Wells' (1944) third bone bed (bone bed 13 of present terminology) is situated near (but not at) the base of the L Zone (Text-fig. 1); Wells' third bone bed, then, is not precisely in the stratigraphic position of Westgate and Fischer's (1933) bioclastic encrinite (bone bed 12 of present terminology). Wells (1944) recognized a fourth bone bed (Westgate and Fischer's 1933 upper bone bed, as already noted) and a fifth bone bed, and erroneously placed both bone beds at the top of the non-existent M Zone (Conkin and Conkin, 1974); in reality, Wells' fourth and fifth bone beds (Text-figs. 1, 2) are one and the same, bone bed 15 of present terminology, situated at the base of the lower Olentangy Shale. Wells' (1944) sixth bone bed (bone bed 17 of present terminology), the East Liberty Bone Bed (Text-figs. 1, 2), was recognized in the Bellefontaine Outlier of Logan County (Text-fig. 3), some 45 miles northwest of Columbus. The East Liberty Bone Bed was misplaced stratigraphically by Wells (1944, p. 282), for it belongs to the base of (and is conformable with) the Ohio Shale (Text-figs. 1, 2) in the Bellefontaine area and does not belong to the underlying limestone (actually undifferentiated Hamiltonian rather than Columbus as Wells believed). The undifferentiated Hamiltonian (some 30 feet in thickness, itself disconformably underlain by the Columbus Limestone) in the Bellefontaine area is disconformably overlain by the Ohio Shale (Conkin, Conkin, and Lipchinsky, 1973, pp. 21, 22).

Wells (1947) assigned the bulk of the I Zone (consisting dominantly of dark, fissile weathering, argillaceous limestone), immediately above his second bone bed (Westgate and Fischer's 1933 lower bone bed), in Franklin County and extreme southern Delaware County, to his Dublin Shale (Pl. 1, figs. 6-8; Text-figs. 2, 5, 9). The Dublin "Shale" is a locally restricted lithofacies which grades laterally into the dominantly limestone lithofacies of the I Zone to the north of southern Delaware County. The few inches of soft, limy, brown shale with intercalated chert stringers (Pl. 1, figs. 6-9; Text-figs. 5, 9) at the base of the Dublin Shale (above the lower bone bed of Westgate and Fischer) have been correlated tenuously with the Tioga Bentonite of New York by Janssens (1970, p. 6).

The fauna of the Dublin consist of the inarticulate brachiopods, *Lingula manni* Hall and *Orbiculoidea lodiensis* Vanuxem, the articulate brachiopod, *Leiorhynchus limitare* (Vanuxem), conodonts, fish teeth and scales, and the problematical fossil, *Tasmanites*. Limestone lenses within the Dublin in Franklin County and southern Delaware County (and the limestone facies of the I Zone to the north (Text-fig. 3) in Delaware and Marion counties) bear "*Martinia*" *maia* and "*Delthyris consobrina*" (actually a form of *Brevispirifer, B.* cf. *B. lucasensis*). *B. lucasensis* itself is definitive of the lowest Hamiltonian Dundee Limestone of northwestern Ohio and southeastern Michigan. A bone bed (directly overlying a paracontinuity) occurs in the detrital basal portion of the Dundee (Conkin, Conkin, and Lowrie, 1972, p. 314); it is probable, then, that the I Zone of the Delaware Formation is a correlative of the lowest Hamiltonian Dundee Limestone.

WORK OF THE CONKINS AND LIPCHINSKY

Conkin (1969, p. 7) recognized bone beds at the bases of the I, K, and L Zones of the Hamiltonian Delaware Formation of central Ohio; in this same paper, Westgate and Fischer's (1933) upper bone bed was placed erroneously at the base of the M Zone. Subsequently, it has become evident to us that Westgate and Fischer's upper bone bed (bone bed 15 of present terminology) belongs to the base of the Olentangy Shale; this mistake by Conkin (1969) was a result of following the opinions of all previous workers and failing to recognize the nonexistence of Stauffer's 1909 M Zone. The relationships of Westgate and Fischer's upper bone bed, the L Zone, the nonexistent M Zone of the Delaware Formation, and the Olentangy Shale have been made clear by Conkin and Conkin (1974).

Conkin (1969, p. 7) placed, on physical and faunal evidence, the base of the Delaware Formation consistently at the base of the wide spread lower part (bone bed 7 of present terminology) of Westgate and Fischer's 1933 lower bone bed (Text-fig. 1). In addition, Conkin and Conkin (1974) recognized the multiplicity of bone beds (bone beds 12-14 of present terminology) in the basal portion of the L Zone (Text-fig. 1). Finally, Conkin, Conkin, and Lipchinsky (1973, p. 19) reported (but did not assign numbers to) two new bone beds (bone beds 2 and 3 of present terminology) in the H Zone of the Columbus Limestone at Columbus (Text-fig. 1). There was never any question as to the presence and position of Wells' (1944) first bone bed (Text-figs. 1, 4), forming, as it does, approximately the basal 1.5 feet of the H Zone (the interval between Stauffer's 1909 two "smooth surfaces").

PRESENT WORK ON THE COLUMBUS-DELAWARE CONTACT IN CENTRAL OHIO

THE PARACONTINUITY AND ASSOCIATED BONE BEDS

In the Marble Cliff Quarries in general, but particularly in the

Trabue and Williams Quarries of that group of quarries, along the Scioto River at Columbus (Text-fig. 3), the lower bone bed of Westgate and Fischer (1933) is generally a maximum of one to 1.8 feet thick and consists of two parts (Pl. 1, figs. 6, 7, 9; Text-figs. 5, 9): the upper thin (two to three inches thick), shaly, classic Middle Devonian bone bed (the lower portion of bone bed 8 of present terminology) and a lower, thicker, bioclastic, crinoidal limestone (bone bed 7 of present terminology). Bone bed 7 lies disconformably (succeeding a paracontinuity) in channels (Pl. 1, figs. 1, 3, 7, 9; Text-figs. 5, 9) developed in the top (bone bed 6 of present terminology) of the H Zone (Upper *Paraspirifer acuminatus*-"*Spirifer duodenarius*" Zone = the Venice Member) of the Columbus Limestone. The upper part (classic bone bed) of the lower bone bed is directly overlain by a thin cherty, shaly limestone, and limy shale, with fish teeth (including the "Tioga? Bentonite?" interval at its base) (Pl. 1, figs. 6-9; Text-figs. 5, 9), which we include in bone bed 8 along with the classic bone bed. Bone bed 8 rests on a slightly uneven wave cut surface (Pl. 1, figs. 2, 3, 6-9; Text-figs. 5, 9) at the top of bone bed 7. The classic bone bed is poorly developed in places in the Marble Cliff quarries, but it is wide spread, even though it may be only an extremely thin veneer of fish teeth fragments (and quartz sand) in a thin, sticky shale which lies in slight channels on the wave cut surface (Text-fig. 9) of bone bed 7.

The upper portion of bone bed 7 is mottled with a faint, lavender-tan to buff color, and is underlain by a gray, more or less vertically marked interval a few inches thick which bears some worm burrows and abundant, rather erratically disposed, bryozoans (almost exclusively *Cystodictya gilberti* Meek). This mottled and worm-burrowed rock is herein termed the "ghost interval" (Pl. 1, figs. 2, 3, 5-9; Text-figs. 5, 9).

Past upward misplacement (from a few tenths of a foot to as much as 1.8 feet) of the Columbus-Delaware contact into the I Zone of the Hamiltonian Delaware Formation has resulted from the failure to recognize the two parts of Westgate and Fischer's 1933 lower bone bed, the important, prominent, and wide spread disconformity (paracontinuity) below the lower part of the lower bone bed, and the presence of restricted Hamiltonian species in both parts of Westgate and Fischer's lower bone bed. The correct placement of the Columbus Limestone-Delaware Formation (Onondagan-Hamiltonian) boundary has been further delayed by an inordinate emphasis on the locally well-developed classic bone bed and on the belief that the overlying "Tioga? Bentonite?" necessarily should mark the position of the boundary.

PALEONTOLOGIC EVIDENCE

The stratigraphic ranges of many of the Columbus and Delaware macrofossils (even some of the most highly esteemed "guide fossils") are poorly known partly as a result of this past misplacement of the Columbus-Delaware contact at a position immediately above the classic bone bed (at the base of the "Tioga? Bentonite?"), which causes the extremely fossiliferous Hamiltonian lower bone bed of Westgate and Fischer (1933) to be included with the equally fossiliferous (but faunally distinct) Onondagan H Zone of the Columbus; a few outstanding examples may be cited.

Hadrophyllum d'orbignyi was recorded by Stewart (1955, p. 168) in the H Zone of the Columbus; however, *H. d'orbignyi* is strictly Hamiltonian in all its substantiated occurrences. *H. d'orbignyi* may occur in bone bed 7 (the basal Hamiltonian unit in central Ohio), but we have encountered it only in the three bone beds (12-14) of the L Zone, three specimens from the K Zone (bone bed 11), and two specimens from the J Zone (bone bed 10).

The characteristic and restricted Hamiltonian brachiopods, *"Martinia" maia* and *"Delthyris consobrina"* (*Brevisperifer* cf. *B. lucasensis*) occur in bone beds 7 and 8 of the I Zone of the Delaware, but not below them. Both *"Martinia" maia* and *Brevispirifer* cf. *B. lucasensis* occur in the remainder of the I Zone and in the J and K Zones, especially to the north in Delaware County; further, *"Martinia" maia* is restricted to the Hamiltonian "Delaware" Formation in southern Ontario. Thus, *"M." maia* and *Brevispirifer* cf. *B. lucasensis,* by themsevles, indicate placement of the Columbus-Delaware contact immediately below the lower part (bone bed 7 of present terminology) of the lower bone bed of Westgate and Fischer (1933).

In the past, *Paraspirifer acuminatus* (Conrad) has been used to mark the H Zone of the Onondagan Columbus Limestone in the Columbus area (Text-fig. 3) and the Upper *P. acuminatus-"Spirifer* *duodenarius*" Zone (the Venice Member) of the Columbus Limestone in northern Ohio (Text-fig. 3); however, *P. acuminatus* ranges in Ohio, from the Lower *P. acuminatus-Spirifer macrothyris* Zone (the base of Marblehead Member) of the Columbus Limestone (Text-figs. 2, 10) into the basal I Zone of the Delaware Formation. Specifically, *P. acuminatus* (Pl. 1, fig. 4) is present in the lower part of the I Zone above bone bed 8 in the National Lime and Stone Company's Quarry, near Delaware; it occurs sparsely in the Marblehead Member (D-G Zones) of the Onondagan Columbus Limestone, in association with *Spirifer macrothyris* (in the Lower *P. acuminatus-S. macrothyris* Zone). *S. macrothyris* itself is most abundantly represented in Stauffer's (1909) E Zone (Text-figs. 2, 10). In northwestern Kentucky and southern Indiana (Text-fig. 10), *P. acuminatus* ranges from the base of the lower *P. acuminatus* Subzone (= the *Brevispirifer gregarius* Subzone = Conkin, Sawa, and Kern's 1970 *Moellerina greenei* Subzone) of the *P. acuminatus* Zone to the top of the Upper *P. acuminatus-"Spirifer duodenarius*" Subzone of the *P. acuminatus* Zone of the Onondagan Jeffersonville Limestone (Conkin and Conkin, 1972); *P. acuminatus* is not known to range into the Hamiltonian in southern Indiana and Kentucky.

Even in the North American standard Devonian section (Text-fig. 10), in New York, it is clear that *Paraspirifer acuminatus* cannot be used to mark the top of the Onondagan, for it ranges certainly from the Moorehouse Member of the Onondaga Limestone into the lower Hamiltonian Seneca Limestone (above the Tioga Bentonite); thus, the upper range of *P. acuminatus* is essentially the same in Ohio as it is in New York.

ACKNOWLEDGMENTS

We wish to thank Joseph M. Harper of the Marble Cliff Quarries, Columbus, Ohio, and Robert F. Annesser of the National Lime and Stone Company, Findlay, Ohio, for allowing us to study their quarries.

LIST OF LOCALITIES

FRANKLIN COUNTY

- Northwest Columbus Quadrangle
  - Norwich Township
    - Marble Cliff Quarries Area
      - Scioto Quarry, the northernmost quarry of the Marble Cliff

Quarries, just east of Dublin Road and south of Griggs Dam, on the west side of the Scioto River, Columbus, Ohio.

New Scioto Quarry, just across (west of) Dublin Road from the Scioto Quarry, between the Scioto Quarry and the Pennsylvania Railroad tracks, Columbus, Ohio.

Williams Quarry, immediately north of Trabue Road, between Dublin Road and the west bank of the Scioto River, Columbus, Ohio.

Franklin Township

Trabue Quarry, immediately south of Trabue Road, between the Pennsylvania Railroad tracks and the west bank of the Scioto River, Columbus, Ohio.

DELAWARE COUNTY

Delaware Quadrangle

Scioto Township

National Lime and Stone Company Quarry (old Klondike Quarry) just southwest of Delaware, Ohio, near the airport.

Blue Limestone Park Quarries

Old quarry (west quarry), just west of the Chesapeake and Ohio Railway tracks where the tracks cross Delaware Run, north of William Street, Delaware, Ohio.

Powell Quadrangle

Liberty Township

Bartholomew Run, a western tributary of the Olentangy River, .6 mile west of Ohio Highway 315 and .4 mile south of Ohio Highway 750, north of Dublin, Ohio.

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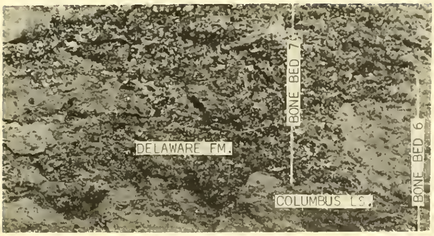
EXPLANATION OF PLATE 1

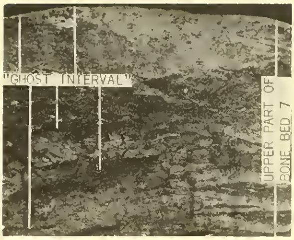
Stratigraphic relationships along the contact of the Onondagan Columbus Limestone and the Hamiltonian Delaware Formation as shown in the north wall of the Scioto Quarry (figs. 1-3; 5-9), Marble Cliff Quarries, Columbus, Ohio; *Paraspirifer acuminatus* (Conrad) from the Delaware Formation in the National Lime and Stone Company Quarry (fig. 4) at Delaware, Ohio.

Figure

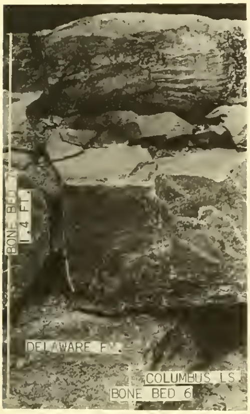
1. Close view of the slightly channeled surface of paracontinuity (seen in figures 3, 7, 9) at the top of the H Zone of the Columbus Limestone; the channels are filled with fish teeth-bearing, crinoidal limestone of bone bed 7. The Columbus-Delaware boundary is a grain per grain contact. Part of the Columbus Limestone seems to be partially surrounded by Delaware sediments due to the two-dimensional view of the three-dimensional filled channels. Bone bed 7 is 1.05-1.1 feet thick.
2. Close view of the "ghost interval" (shown in figures 3, 5-9) developed in the upper part of bone bed 7. "Ghost interval" is 0.15-0.2 feet thick.
3. Bone bed 7, overlying the channeled surface of paracontinuity at the top of the H Zone; the "ghost interval" is present in the uppermost part of bone bed 7; a wave cut surface is seen at the top of bone bed 7. Bone bed 7 is 1.05-1.1 feet thick.
4. Fragmentary specimen of *Paraspirifer acuminatus* (Conrad) from the Delaware Formation (just above bone bed 8) at the National Lime and Stone Company's Quarry; × 0.6.
5. "Ghost interval" in the upper part of bone bed 7, showing the lower part of the faint, lavender-tan to buff mottled upper portion with worm burrows and bryozoans below. "Ghost interval" is 0.15-0.21 feet thick.
6. Upper part of bone bed 7, the wave cut surface on the top of bone bed 7, and the lowest beds of the Dublin Shale (including bone bed 8 and the "Tioga? Bentonite?"). Bone bed 8 is 0.7 feet thick.
7. Section ranging from near the top of bone bed 5 of the Columbus Limestone to the uppermost beds of the J Zone of the Delaware Formation.
8. Close view of part of section in figure 7. The wave cut upper surface of bone bed 7 is overlain directly by bone bed 8 (with the "Tioga? Bentonite?" at its base), followed by the cherty, argillaceous limestone of the I Zone, and the lower part of the J Zone (with the J Zone bone bed = bone bed 10 at its base). Bone bed 8 is 0.7 feet thick.
9. Close view of part of the section in figures 7 and 8, showing the contact of the uppermost Columbus Limestone (bone bed 6 of the H Zone) below with the lowermost Delaware Formation (Westgate and Fischer's 1933 lower bone bed of the I Zone) above. The "ghost interval", at the top of bone bed 7, is succeeded directly by a wave cut surface. Bone bed 8 overlying bone bed 7 is followed by cherty, argillaceous limestone of the I Zone. Bone bed 8 is 0.7 feet thick.


BONE BED 7
DELAWARE FM.
COLUMBUS LS.
BONE BED 6

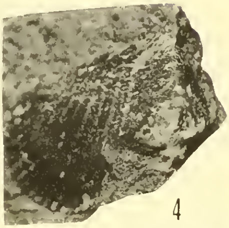
1


"GHOST INTERVAL"
UPPER PART OF BONE BED 7

2


BONE BED 1.4 FT.
DELAWARE FM.
COLUMBUS LS.
BONE BED 6

3



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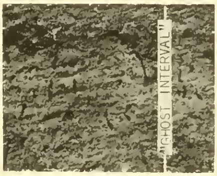
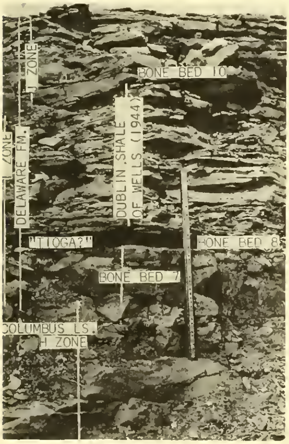

"GHOST INTERVAL"

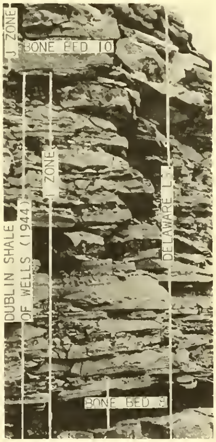
5


DUBLIN SHALE
"TIOGA?"
BONE BED 8
WAVE CUT SURFACE
BONE BED 7

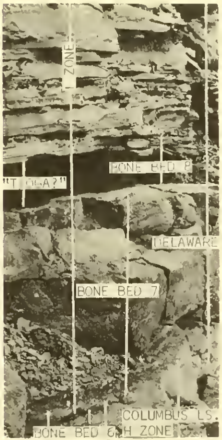
6


J ZONE
BONE BED 10
I ZONE
DELAWARE FM.
DUBLIN SHALE OF WELLS (1944)
"TIOGA?"
BONE BED 8
BONE BED 7
COLUMBUS LS.
H ZONE

7


J ZONE
BONE BED 10
I ZONE
DUBLIN SHALE OF WELLS (1944)
DELAWARE LS.
BONE BED 8

8


I ZONE
BONE BED 8
"TIOGA?"
DELAWARE
BONE BED 7
COLUMBUS LS.
BONE BED 6
H ZONE

9

NEW BIFOLIATE TUBULAR BRYOZOAN GENERA FROM THE SIMPSON GROUP (MIDDLE ORDOVICIAN), ARBUCKLE MOUNTAINS, OKLAHOMA

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ABSTRACT

The Simpson Group (Middle Ordovician) of the Arbuckle Mountains, Oklahoma, contains an abundant and well-preserved bryozoan fauna consisting mainly of trepostomes and bifoliate cryptostomes. These are most abundant in limestone beds of the group. Three new bifoliate cryptostome genera (*Amalgamoporus, Cystostictoporus,* and *Cricadictyum*) and their type species are described and illustrated. Three types of interspaces between zooecia are recognized: (1) tabulate, (2) distally cystose, and (3) laterally cystose.

INTRODUCTION

The Simpson Group (Middle Ordovician) of the Arbuckle Mountains, Oklahoma, includes the following formations in ascending order: Joins Formation, Oil Creek Formation, McLish Formation, Tulip Creek Formation, and Bromide Formation. The older two formations are considered Whiterockian in age; the younger three formations are considered Marmorian-Wildernessian in age. Each of the formations from the Oil Creek Formation through the Bromide Formation, has a basal sandstone in the area studied which generally does not contain Bryozoa. The Simpson Group contains one of the oldest known abundant and well-preserved bryozoan faunas in the world.

The oldest bryozoans to make their appearance in rocks of the Simpson Group are the trepostomes which first appear near the base of the limestone beds of the Oil Creek Formation. The first bifoliate cryptostomes appear near the base of the limestone beds of the McLish Formation and form a substantial element of the fauna in the McLish, Tulip Creek, and Bromide formations.

Brachiopods of the Simpson Group were described by Cooper (1956). The ostracodes were described by Harris (1957). Except for a short paper by Loeblich (1942) on a part of the Bromide fauna, the Simpson bryozoans have not previously been described. Three new genera, *Amalgamoporus, Cystostictoporus,* and *Cricodictyum* are proposed and their type species are described and illustrated.

Three distinct types of interspaces between zooecia are recognized: (1) tabulate interspaces which have flat or gently curved tabulae that are continuous across the interspace, (2) distally cystose interspaces characterized by convex cystiphragms that overlap each other in a direction distal to zooecial growth, and (3) laterally cystose interspaces which contain cystiphragms overlapping each other lateral to the zooecial growth direction.

All specimens studied are from the south flank of the Arbuckle Mountains, Oklahoma (Farmer, 1968). All studied material is on deposit at the U.S. National Museum (USNM), Washington, D.C.

LOCALITIES

West Spring Creek: SW¼ sec. 31, TIS, R1W, three miles east of Pooleville, Murray County, Oklahoma. USNM locality numbers 2126 (McLish Formation) and 2146 (Tulip Creek Formation). Field exposures along south side of east tributary of West Spring Creek, south of fault. Locality reached through Woodford and Joins Ranch.

U.S. Highway 77: SE¼ sec. 24, T2S, R1E, and SW¼ sec. 19, T2S, R2E. USNM locality number 2114 (McLish Formation). Field exposures on either side of U.S. Highway 77 and east of Tulip Creek, three miles north of Springer, Carter County, Oklahoma.

West Branch of Sycamore Creek. SW¼ sec. 22, T3S, R4E, Johnston County, Oklahoma. USNM locality number 2129 (McLish Formation). Field exposures along west side of west branch of Sycamore Creek.

ACKNOWLEDGMENTS

This work is an outgrowth of a doctoral dissertation prepared at the University of Cincinnati and the Smithsonian Institution under the direction of K. E. Caster and R. S. Boardman. Olgerts L. Karklins of the U.S. Geological Survey and R. S. Boardman reviewed the manuscript. Each has provided many helpful suggestions. The specimens were collected by R. S. Boardman and the writer while the latter was employed as a Museum Specialist at the Smithsonian Institution. The photography was completed at Madison College, Harrisonburg, Virginia.

SYSTEMATIC PALEONTOLOGY

Phylum BRYOZOA Ehrenberg

Superclass TUBULOBRYOZOA Cuffey

Order CRYPTOSTOMIDA Vine

Suborder PTILODICTYOIDEA Astrova

Family **RHINIDICTYIDAE** Ulrich

Genus **AMALGAMOPORUS,** n. gen.

Type species: *Amalgamoporus kecius,* n. sp.

Diagnosis. — Zoaria dichotomously branching, without external ornamentation; zooecial boundaries may be distinct, jagged, or represented by a boundary zone; zooecial wall appears amalgamate in tangential view with dark mural lacunae; median plane with obscure median tubuli.

Definitian. — Zoaria dichotomously branching and without surface ornamentation. Zoarial edges rounded, solid, without zooecia. Median tubuli not observed at zoarial edges.

Zooecia arranged in longitudinal and diagonal ranges at zoarial surface. Distally cystose interspaces may develop between zooecia.

Zooecial walls longitudinally laminate adjacent to zooecial cavities and connected by zone of transverse wall laminae. This results in an amalgamate zooecial wall as seen in tangential view. Endozone and exozone not distinct; exozone arises by gradual thickening of walls.

Median plane contains obscure median tubuli.

Remarks. — *Amalgamoporus* is similar to *Stictopora* in that the zooecial boundary may be a distinct, jagged, dark line. It is similar to *Escharopora* in the amalgamate appearance of the zooecial wall in tangential section. It differs from all genera in having a boundary zone with mural lacunae and in having obscure median tubuli. The name refers to the amalgamate appearance of the zooecial walls in tangential section.

Amalgamoporus kecius, n. sp. Pl. 1, figs. 1-2; Pl. 2, fig. 1

Description. — Zoarial branching occurs at irregular intervals and angles. Nature of basal attachment not observed. Branch width ranges from 1.45 mm to 3.0 mm. Branch thickness ranges from 0.5 mm to 1.43 mm. Zoarial surfaces smooth. Zoarial edges solid, without zooecia, rounded. Pustules abundant in zooecial walls. Zooecia intersect zoarial surface obliquely at angles varying from 40° to 80°.

Zooecia oval at zoarial surface. They are slightly sigmoidal and gently curved from their point of budding to the zoarial surface. Angle of divergence of zooecia from the median plane in the endozone ranges from 40° to 65°. Angle made by exozone and median plane ranges from 38° to 62°. Diaphragms number from one to three, most zooecia having only one diaphragm emplaced early in the exozone. Zooecia that contain two or three diaphragms show first diaphragm emplaced early in exozone and subsequent ones emplaced near zoarial surface. Diaphragms may be planar or sigmoidal.

Zooecial boundary results from intersection of longitudinal laminae and transverse laminae and occurs near dorsal edge of zooecial wall. A second, less distinct, boundary line may occur near ventral edge of zooecial wall. Main (dorsal) boundary line is thick and appears as a discontinuous, jagged zone in some walls. Exozone results from gradual thickening of zooecial wall. Distally cystose interspaces may be present.

Median plane distinct, bilaminate, continuous, and contains regularly spaced median tubuli that are not so distinct as in species of *Stictopora* Hall, *Cystostictopora, Eopachydictya* Ross, and *Pachydictya* Ulrich. Three or four median tubuli per zooecium. Median tubuli circular to oval in cross-section and number from 12 to 14 per 0.5 mm along median plane.

Remarks. — *A. kecius* differs from all other species of bifoliate cryptostomes in having the amalgamoporid wall structure. This species is named in honor of K. E. Caster.

Types and materials studied. — Holotype USNM No. 162103, paratypes USNM Nos. 162104 and 162105, from the Tulip Creek Formation, West Spring Creek (USNM locality 2146).

All specimens studied are from limestones between 371 feet and 383 feet above the top of the Tulip Creek sandstone at West Spring Creek (USNM locality 2146).

Occurrence and relative abundance. — Rare in the Tulip Creek Formation, West Spring Creek (USNM locality 2146), in limestones from 371 feet to 383 feet above the base of the Tulip Creek Sandstone.

Genus **CYSTOSTICTOPORUS**, n. gen.

Type species: *C. pachyphragmus*, n. sp.

Diagnosis. — Zoaria branching, large, may be self-encrusting in part; acanthopores present or absent; zooecia straight, commonly with several diaphragms; cystiphragm-like structures present in early exozone or late endozone and commonly result in either laterally or distally cystose interspaces in later exozone; zooecial boundary U-shaped in tangential view; median plane with straight or offset median tubuli.

Definition.—Zoaria irregularly branching, commonly large. May be partially self-encrusting. Zoarial surface either smooth, without surface ornamentation, or with acanthopores. Zoarial edges sharp to rounded. Zooecia arranged in both longitudinal and diagonal ranges at zoarial surface.

Zooecia oval to round at zoarial surface; intersect zoarial surface obliquely. Zooecia long and straight, gently curved, or slightly sigmoidal from median plane to zoarial surface. Angle of budding from median plane highly variable, alternate on opposite sides of median plane, not at constant intervals. Zooecia may contain diaphragms. Cystiphragm-like structures present in early exozone and may give rise to cystose interspaces. Interspaces may be laterally or distally cystose. Distally cystose interspaces may give rise to laterally cystose interspaces. Zooecia with keels and sinuses in forms with curved zooecial tubes (Boardman and Utgaard, 1966).

Zooecial walls thick, longitudinally laminate with steeply inclined inner portion. Boundary zones between zooecia distinct and may show inflections, U-shaped in tangential view. Zooecial walls thicken gradually in a distal direction. The endozone and exozone are not distinct in zooecia without cystiphragm-like structures. When cystiphragm-like structures present, the first such structure is taken as base of exozone.

Median plan may extend full width of zoarium. Edges of zoarium solid, without zooecia and median plane in larger forms. Median plane contains evenly-spaced median tubuli which may be arranged in a straight line or may be offset. Median plane may be straight or slightly curved.

Acanthopores present in some species and may be small or large, concentrated in zooecial boundary, or scattered at random in zooecial walls. Pseudoacanthopores occur in some forms and are restricted to zooecial boundary. They result from plane of tangential section passing through an inflection in zooecial boundary.

Diaphragms most commonly present and most species have several per zooecium. They are thin, planar, simply curved, or sigmoidal in longitudinal view. All diaphragms emplaced in exozone.

Remarks. — *Cystostictoporus* is most similar to *Phyllodictya* Ulrich in having cystose interspaces but it differs in having the cystiphragm-like structures in the proximal part of the zooecial wall which may or may not give rise to interspaces similar to those in *Phyllodictya*. *Phyllodictya* does not have the cystiphragm-like structures proximal to the cystose interspaces.

Cystostictoporus is related to *Stictopora* Hall in having similar wall structure (stictoporid), in having a distinct and single zooecial boundary, and in possessing median tubuli. But it differs in having well-defined cystiphragm-like structures in the proximal exozone which may give rise to distally or laterally cystose interspaces. *Cystostictoporus* is similar to *Ptilotrypa* Ulrich in possessing cystose interspaces but the latter genus lacks median tubuli. The name refers to the common cystose interspaces.

Cystostictoporus pachyphragmus, n. sp. Pl. 2, fig. 2; Pl. 3, fig. 1

Diagnosis. — Zoaria thick, with rounded edges and thick zooecial walls in exozone; acanthopores concentrated in zooecial boundaries; intersection of acanthopores and zooecial boundaries cause an inflection in zooecial boundary; endozone short; zooecia long.

Description. — Zoaria thick, with rounded edges. Branching irregular. Zoarial surface irregular but without well-defined monticules or maculae. Acanthopores present at zoarial surface but observed only in thin-sections where they are seen to be aligned in zooecial boundaries. When an acanthopore intersects zooecial boundary as seen in longitudinal section there is an inflection in zooecial boundary.

Zooecia oval at zoarial surface. They intersect zoarial surface obliquely at angles from 135° to 165°. Zooecia straight for most of their distance but may be slightly sigmoidal near point of origin from median plane. Endozone is short and is indistinguishable from early part of exozone. Zooecial length varies from 1.10 mm to 2.48 mm. Angle of budding from median plane varies from 35° to 75°, depending on shape of zooecium. Angle of exozone and median plane varies from 20° to 46°. Number of diaphragms per zooecium varies from two to four, always emplaced in exozone. Diaphragms either planar or slightly concave or convex. They are distinct diaphragm-wall units. Cystose interspaces present, but do not alternate with zooecia.

Zooecial wall thick and ranges in thickness from 0.065 mm to 0.25 mm. An apparent zooecial lining is caused by steeply dipping wall laminae adjacent to the zooecial void. Zooecial boundary distinct, serrate, and contains inflections.

Median plane continuous from one zoarial edge to another only in smaller specimens and contains evenly spaced centrally placed median tubuli. Median plane distinctly bilaminate with central dark line containing median tubuli. At about 65× in transverse view laminae of median plane are seen to continue into endozone of zooecia. Median tubuli number from eleven to eighteen per 0.5 mm along median plane.

Remarks. — *C. pachyphragmus,* n. sp. is distinguished by the thick zooecial wall, extremely short endozone, long zooecia, lack of distally emplaced cystiphragm-like structures in the endozone, and the inflections in the zooecial boundary. The specific name is derived from the Greek *pachys* (thick) and *phragmus* (wall) and refers to the nature of the zooecial walls.

Types and materials studied. — Holotype USNM No. 162154, paratype USNM No. 162112, from the McLish Formation, West Spring Creek (USNM locality 2126).

All specimens studied are from the McLish Formation from 123 feet to 307 feet above the top of the basal McLish sandstone; from 204 feet to 215.5 feet at West Spring Creek (USNM locality 2126); from 247 feet to 307 feet at U.S. Highway 77 (USNM locality 2114); from 123 feet to 178 feet at the west branch of Sycamore Creek (USNM locality 2129).

Genus **CRICODICTYUM,** n. gen.

Type species: *Cricodictyum ponderosum,* n. sp.

Diagnosis. — Zoaria dichotomously branching, annulate; annuli contain extensions of median plane with median tubuli. Zooecia gently curved, sigmoidal. Zooecial walls longitudinally laminate; boundary zones distinct, often serrate; pachydictyid wall structure. Zooecia in longitudinal ranges in endozone; at zoarial surface zooecia in curved diagonal ranges.

Definition. — Zoaria bifoliate, dichotomously branching, rarely encrusting, and have surface annuli which contain branches of median plane. Basal attachment not observed. Branching takes place at irregular intervals and branches straight, transversely biconvex, and bear transverse surface annuli. Monticules and maculae not observed. Zoarial margins sharp to rounded and contain median plane with median tubuli. Interspaces numerous and closed at zoarial surface. They occur between zooecia and are of three distinct types: (1) tabulate, (2) laterally cystose and (3) distally cystose. Tabulate interspaces contain planar or slightly curved tabulae which are continuous across interspace. They may contain a few isolated cystiphragm-like structures. Laterally cystose interspaces have cystiphragm-like structures which overlap in a direction roughly at right angles to zooecial growth direction. Distally cystose interspaces have cystiphragm-like structures which overlap in a distal direction. A laterally cystose interspace may begin as a distally cystose interspace.

Zooecia arranged in curved diagonal ranges at zoarial surface. Deep tangential views show zooecia arranged in longitudinal ranges in endozone. Interspaces between zooecia without pustules or acanthopores, and are usually either depressed below or raised above zoarial surface.

Zooecia gently curved, sigmoidal tubes which bud from either main median plane or its branches. Zooecia nearest annuli arise from branches of median plane. Annuli consist of secondary median planes from main median plane plus zooecia which have budded from secondary median planes and associated interspaces. Zooecia which bud from main median plane generally have high angle of budding as compared to low angle of budding from branches of the main median plane. Budding is alternate on opposite sides of median plane but alternate zooecia may bud close together.

Zooecial walls longitudinally laminate. Boundary zones between zooecia distinct, continuous, often serrate. They result from the abutting laminae of adjacent zooecia which intersect each other at a low angle. Exozone begins at level of interspaces. Zooecial walls thicken gradually in distal direction and with no sharp zooecial curvature.

Zooecial packing arranged so that in tangential view zooecia are surrounded by interspaces.

Dark line of endozone of a zooecium continues into exozone and forms dorsal boundary of interspace. Ventral boundary of interspace is formed by abutting laminae which are continuous with tabulae or cystiphragm-like structures and zooecial wall laminae. Proximal end of interspace is taken to be beginning of exozone.

Diaphragms thin, few, or absent, appear randomly spaced. They may be planar or slightly curved. Laminae of diaphragms merge with zooecial wall laminae.

Remarks. — *Cricodictyum* is related to *Pachydictya* Ulrich in the nature of the wall structure, especially as seen in tangential view, the continuous nature of the zooecial boundary as seen in tangential view, and the well-developed structure of the interspaces. It differs from *Pachydictya* and all other presently known bifoliate cryptostomes in having lateral branches of the median plane from which zooecia bud and which result in surface annuli roughly transverse to the direction of zoarial growth. It is further distinguished by having three distinct types of interspaces. The name refers to the Greek word *krikos* meaning ring and refers to the annuli which are characteristic of this genus.

Cricodictyum ponderosum, n. sp. Pl. 4-5

Diagnosis. — Zoaria bifoliate or encrusting, dichotomously branching, with surface annuli which contain branches of median plane. Zooecia may be surrounded by interspaces which may be of either of three basic types. Distal zooecial boundaries are continuations of dark line of endozone.

Description. — Zoaria typically bifoliate, rarely encrusting, dichotomously branching, and annulate. Large, ranging in width of a branch from 5 mm to 10 mm and in thickness of a branch from 0.6 mm to 2.0 mm. Surface annuli sharp to rounded. Median tubuli observed in median plane of each annulus in tangential section but are not seen to come to zoarial surface. Edges of annuli appear solid.

Zooecial angle with zoarial surface variable. Zooecia gently curved or sigmoidal from median plane to zoarial surface. Angle of budding variable, depending on zooecial shape, but averages about 45°. Angle of exozone to median plane ranges from 20.5° to 105°.

Diaphragms number from zero to three and emplaced in exozone. Diaphragms planar or curved in a proximal zooecial direction.

Zooecia commonly surrounded by interspaces which are closed at zoarial surface. Interspaces may be tabulated, laterally cystose, distally cystose, or a combination of these.

Individual zooecial laminae intersect zooecial boundary at high angle. Zooecial boundary distal to an interspace appears as a continuation into exozone of dark line of endozone. Boundary lines proximal to interspace due to intersection of laminae of interspace structures with zooecial wall laminae.

Maximum thickness of zooecial wall in exozone is 0.15 mm. Acanthopores or pustules not observed.

Median plane appears as a dark line with regularly spaced median tubuli ranging from nine to eleven per 0.5 mm along median plane. Diameter of median tubuli ranges from 0.025 mm to 0.045 mm.

Remarks. — *C. ponderosum,* n. sp. shows the characters of the genus.

Types and materials studied. — Holotype USNM No. 162129, figured paratype USNM No. 162130 from the McLish Formation, West Spring Creek (USNM locality 2126).

All specimens studied are from the McLish Formation, West Spring Creek (USNM locality 2126) and show a stratigraphic range of from 98 to 116 feet from the top of the McLish sandstone.

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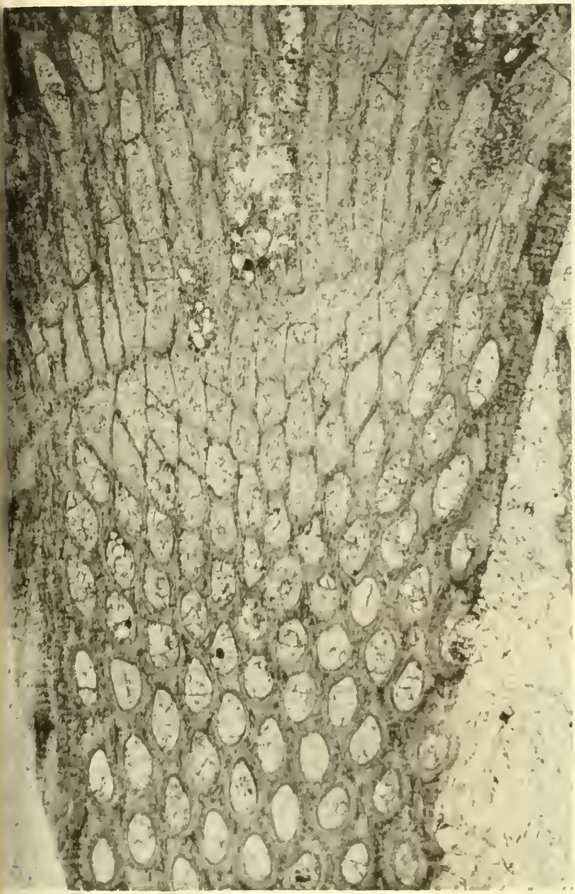
EXPLANATION OF PLATE 1

Figure

1, 2. **Amalgamoporus kecius,** n. sp.

1a. Oblique tangential view of holotype, USNM No. 162103, cutting the median plane in the upper left hand portion of the illustration. Note median tubuli in the median plane, amalgamate appearance of the zooecial walls, and dark patches in the zooecial walls; × 30. Tulip Creek Formation, West Spring Creek, Okla. 1b. Longitudinal view of same showing zooecial curvature, one diaphragm emplaced in the early exozone, and nature of the zooecial boundary; × 30.

2a. Tangential view of paratype, USNM No. 162104, showing a concentration of dark patches in the area of branching. Zooecia in lower part of illustration appear larger and elongate because section is passing parallel to the zooecial curvature; × 30. Same locality and horizon as above. 2b. Longitudinal view of same showing zooecial curvature, nature of zooecial walls, and diaphragms. A poorly developed tabulated interspace is seen in the lower right-hand portion of the illustration; × 30. Same formation and locality as above.



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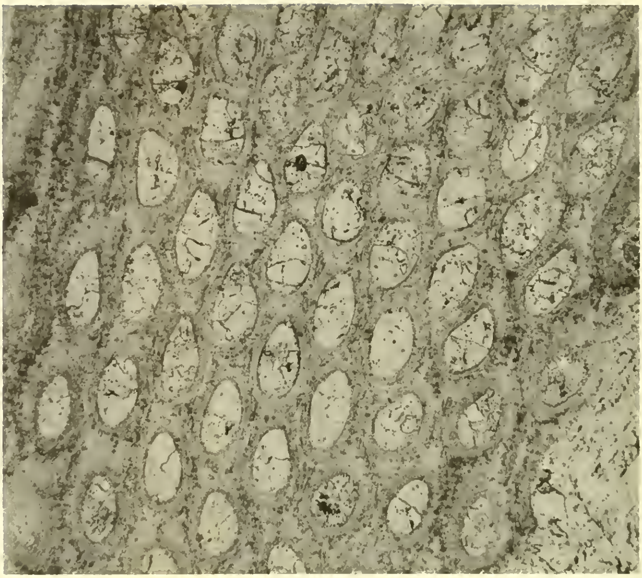

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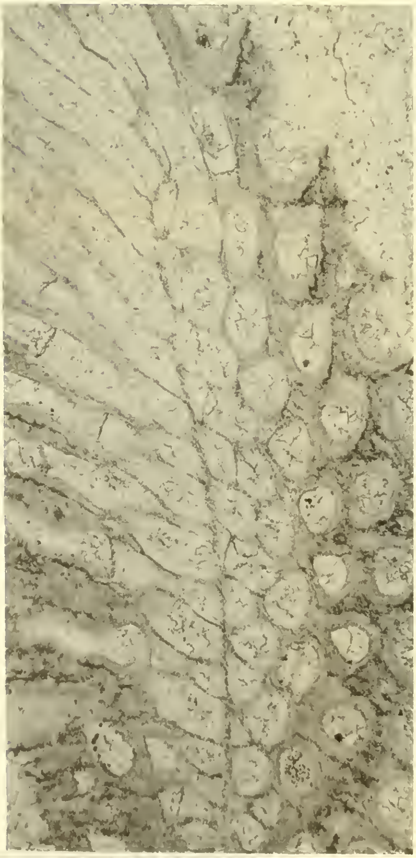

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EXPLANATION OF PLATE 2

Figure

1. **Amalgamoporus kecius,** n. sp.

   1a. Tangential view of holotype, USNM No. 162103, showing amalgamate appearance of walls, mural lacunae, and zooecial shape near zoarial surface; × 63. Tulip Creek Formation, West Spring Creek, Okla. 1b. Oblique transverse view of holotype showing small median tubuli in median plane and wall structure in exozone; × 63. Tulip Creek Formation, West Spring Creek.

2. **Cystostictoporus pachyphragmus,** n. sp.

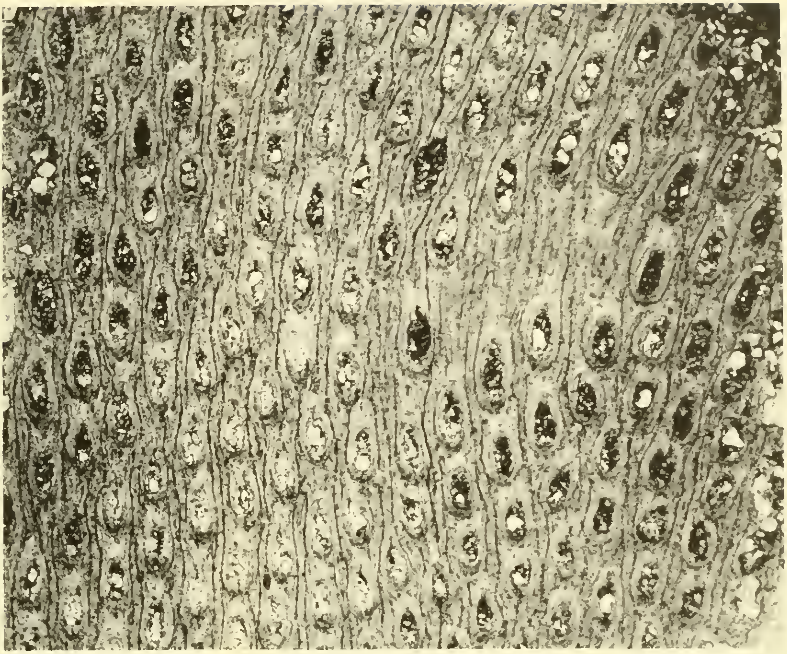
   Longitudinal view of paratype, USNM No. 162155, showing nature of zooecial origin from median plane and distally cystose interspaces; × 63. McLish Formation, West Spring Creek, Okla.

EXPLANATION OF PLATE 3

Figure

1. **Cystostictoporus pachyphragmus,** n. sp.

   1a. Shallow tangential section of holotype, USNM No. 162154, showing zooecial shape near the zoarial surface, horseshoe-shaped boundary lines around zooecia, and inner zooecial lining; × 30. McLish Formation, West Spring Creek, Okla. 1b. Slightly oblique longitudinal section showing diaphragms in zooecia and distally and laterally cystose interspaces; × 30. 1c. Transverse section showing massive nature of zoarium, low angle of zooecial budding, and nature of the median plane and zooecial boundaries; × 30.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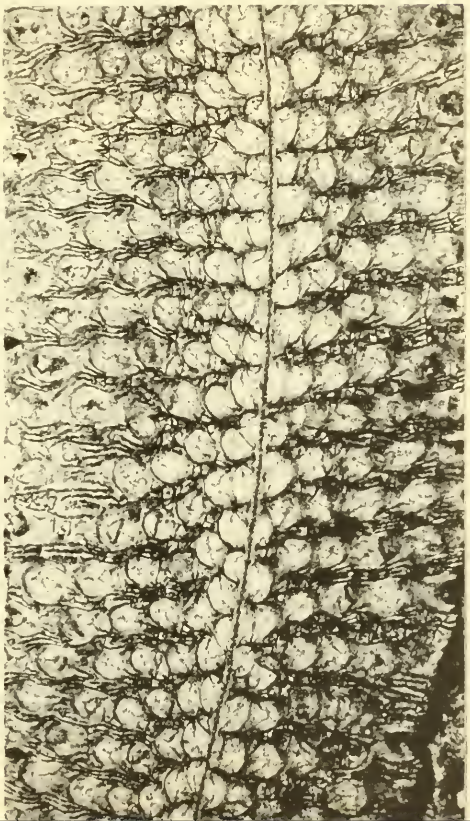
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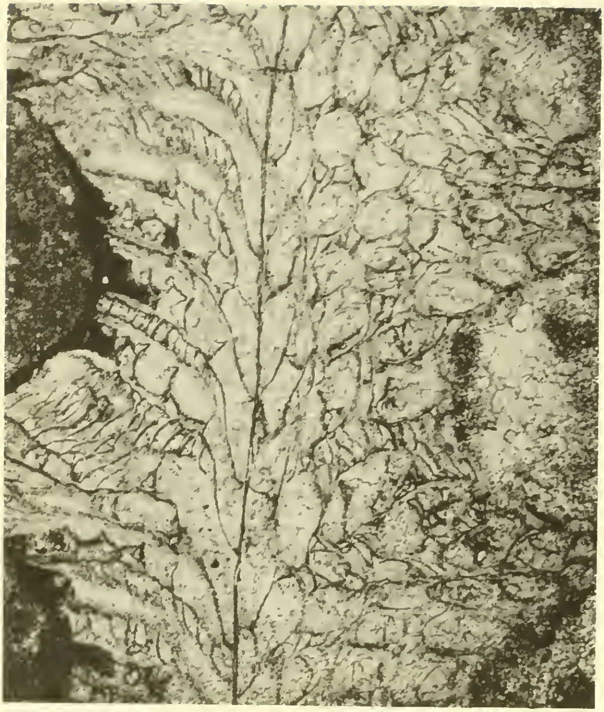
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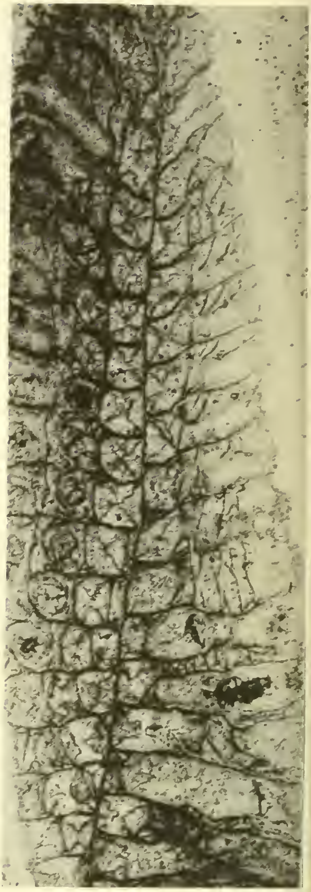
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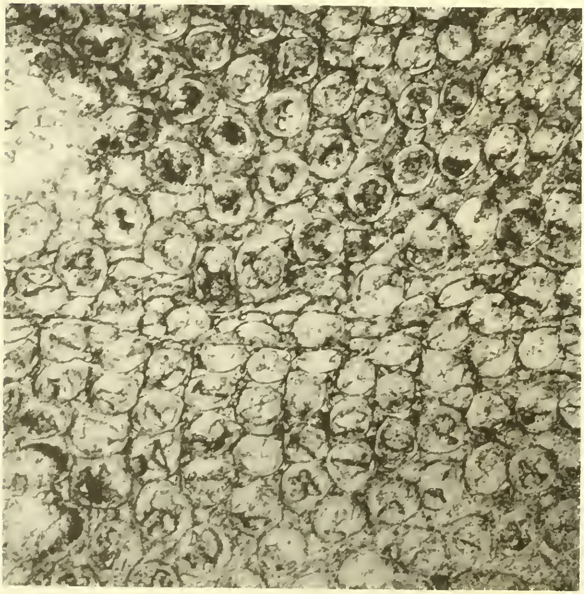
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2b

EXPLANATION OF PLATE 4

Figure

1, 2. **Cricodictyum ponderosum,** n. sp.

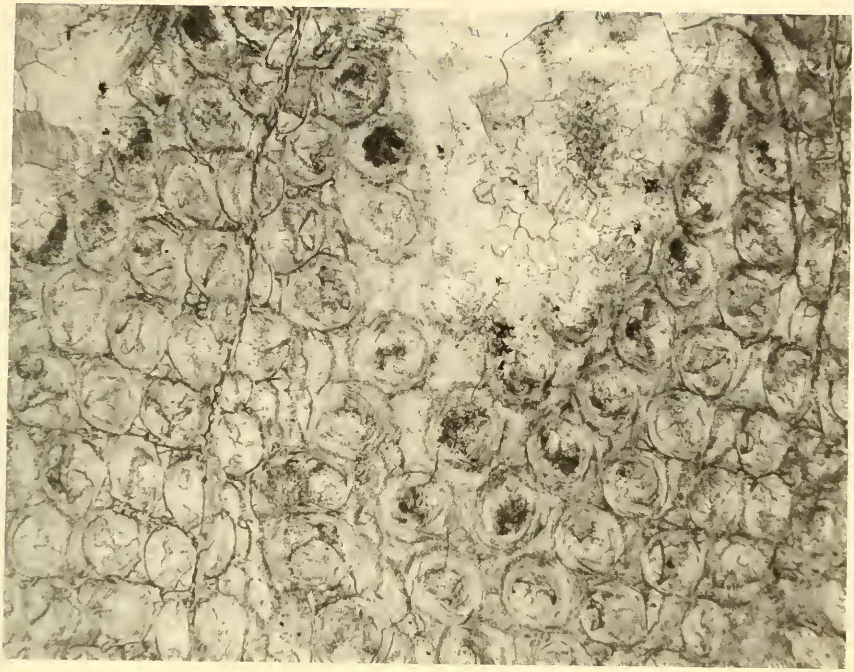
1a. Longitudinal view of holotype, USNM No. 162129, showing lateral branches of the median plane, median tubuli in the lateral branches, cystiphragm-like zooecial diaphragms, and the three basic types of interspaces. Two zooecial annuli are shown; × 30. McLish Formation, West Spring Creek, Okla. 1b. Tangential view of same specimen showing two annuli with branches of the median plane bearing median tubuli. Note inter-zooecial areas (interspaces) and the fact that zooecial walls are thinner near annuli and thicker between annuli due to the zooecial wall being elevated by the annuli and subtended at earlier growth stages by the plane of the section; × 30.

2a. Transverse view of paratype USNM No. 162130, showing lack of keels and sinuses, zooecial packing, and the evenly spaced median tubuli of the median plane; × 30. Same locality as above. 2b. Oblique transverse section showing large median tubuli in median plane; × 30.

EXPLANATION OF PLATE 5

Figure

1. **Cricodictyum ponderosum,** n. sp.
   1a. Shallow tangential view of holotype, USNM No. 162129, showing thick zooecial linings, median plane in annuli, and median tubuli in median plane; × 63. McLish Formation, West Spring Creek, Okla. 1b. Longitudinal view showing two annuli with branches of median plane and zooecia which have budded from these branches; × 63.



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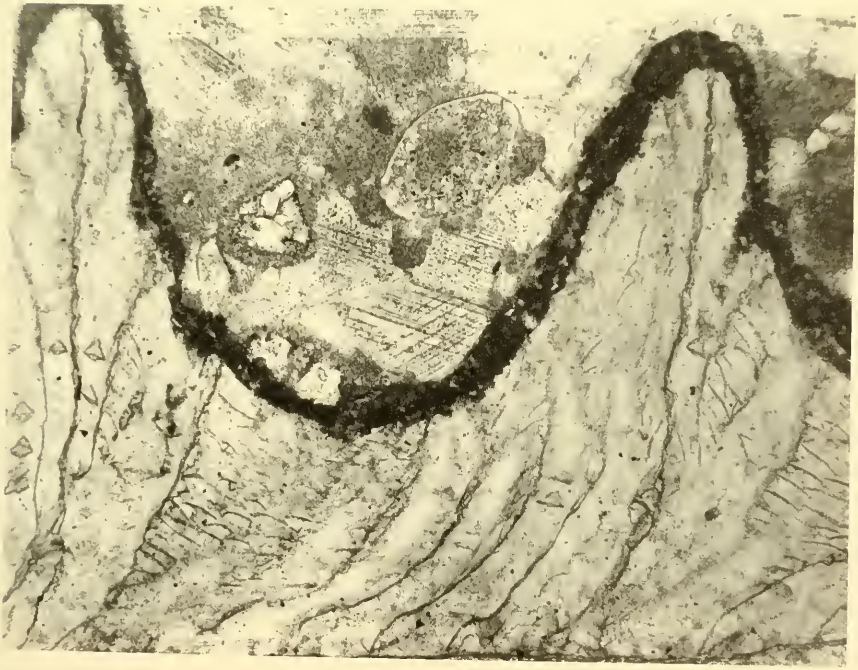

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AMERICAN LITUITIDAE (CEPHALOPODA)

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INTRODUCTION

Lituites is a nautiloid of distinctive form, with a small coiled apical part followed by a later part which may be faintly sigmoid at first but is finally straight. It is a genus long considered as characteristic of the "*Orthoceras* Limestone" of the Balto-Scandinavian region and has been figured widely in geological and paleontological works as a genus characteristic of the Ordovician of northern Europe. With it are grouped other genera, making up the Lituitidae, of which a good summary is found in Teichert, *et al.*, 1964. These shells range from *Cyclolituites,* with a coiled part of about two and a half volutions and only a short anterior part in which coiling is reduced, through genera with small coils and fairly long straight parts, to *Ancistroceras* in which the coil is greatly reduced and the straight shell is conically expanded, to *Rhynchorthoceras* in which the apex is cyrtoconic and the anterior straight part is generally more slender than in *Ancistroceras*. Growth lines show typically ventrolateral crests separating lateral sinuses from the ventral hyponomic sinus. The siphuncle is commonly slightly dorsad of the center. Camerae contain episeptal and hyposeptal deposits of characteristic form (Dewitz, 1880; Holm, 1885) which may pass through perforations in the siphuncle; deposits of adjacent camerae may join (Sweet, 1958).

Significant contributions to the knowledge of the family are found in Dewitz (1880), Remelé (1880, 1881, 1881a, 1882, 1886), Noetling (1882, 1883), and Lossen (1860). Hyatt (1894) reviewed the family and added the genera *Angelinoceras* and *Holmiceras*.

Two views of the affinities of the family have been proposed: (1) that the Lituitidae are descendants of coiled ancestors (Hyatt, 1894, 1900; Flower and Kummel, 1950; Flower, 1955; Sweet, 1958; Furnish and Glenister, *in* Teichert, *et al.*, 1964), and (2) an origin in straight-shelled ancestors variously named the Orthoceratida, Orthoceroidea, and Michelinoceratida (Schindewolf, 1942). Flower (*in* Flower and Kummel, 1950) first placed the Lituitidae with the Barrandeoceratida, but Sweet (1958) showed reason to place them instead with the Tarphyceratida. It now seems probable that the Lituitidae developed from the Trocholitidae. In both families the siphuncle is ventral in the first half whorl but later assumes a position dorsad of the center. The Trocholitidae develop cameral deposits, notably in *Curtoceras* (Ulrich, Foerste, Miller, and Furnish, 1942) which may well be ancestral to those of the Lituitidae.

Although not so stated at the time, Flower was influenced in assigning the Lituitidae to the Barrandeoceratida by the similarity between young stages of *Lituites* which are compressed shells with lateral lobes and growth lines with a hyponomic sinus but without yet the development of the lateral sinuses and ventrolateral crests, with the adult features of *Barrandeoceras*. Origin in the Barrandeoceratidae is opposed not only by the morphological evidence presented by Sweet, 1958 but by the fact, not then clear, that the great expansion of the Lituitidae lies within the Kunda, Aseri, and Lasnamägi stages of northern Europe, and that these beds, formerly considered broadly as Chazyan, represent the middle and upper parts of the Whiterock Stage of Cooper (1956) of North America, a matter dealt with more extensively elsewhere (Flower, 1974). Also, much confusion surrounded the stratigraphic position of most of the Lituitidae; they were described largely from glacial erratics of the north German plains, and only recently (notably Sweet, 1958 and Jaanusson, 1960) has the stratigraphic position of many of the species been ascertained. Of the six genera lying in beds of Whiterock equivalence, only one, *Ancistroceras,* continues into the overlying Uhakuan Stage, and the late Middle Ordovician is marked by the appearance of *Tyrioceras* which appears first in the Lower Chasmops Limestone of Norway and continues well on into the Upper Ordovician.

Some further resolution of some problems of correlation and faunal succession was made possible by NSF grant CB6809 which permitted observation and collecting from the Swedish section, examination of various significant collections, and fuller discussion with colleagues on questions of correlation within the Ordovician.

The conclusion of the writer was that beds inclusive of the Volkhov, Aseri, and Lasnamägi represented the Whiterock Stage. The fauna was, however, provincial, and for many years was thought to be confined to the Balto-Scandinavian region of northern Europe. The Pagoda Limestone of central China has yielded (Yu 1930, Lai Chai-Geen, 1965, Kobayashi 1969) cephalopods of Baltic affinities, suggesting somewhat different ranges but within the limits of the Kunda, Aseri, and Lasnamägi, while the underlying Kuniutan Limestone contains the *Sinoceras rude* fauna, which suggests that of the Volkhov of Sweden. Interestingly, faunas from Spitzbergen, now in the process of study yield (1) an early Middle Canadian cephalopod association (2) a Cassinian cephalopod succession, both of North American aspect, succeeded by (3) a fauna with Table Head types of trilobites (Whittington and Fortey, personal communication) but with cephalopods allied to those of the Volkhov and Kunda of the Baltic faunas.

The North American material here described includes Hyatt's (1894) type and only known specimen of *Cyclolituites americanus,* which is here redescribed and illustrated; it is a good member of that genus and is from the lower part of the Table Head Formation. *Holmiceras bennetti,* n. sp. was collected by the writer from the lower part of the Table Head Limestone, made possible by NSF grant CB 6809. The first indication of the Lituitidae in western North American faunas came from the form here described as *Trilacinoceras undulatum,* submitted for study by Lehi Hintze. Material collected by Reuben Ross added two more species; all are from the Antelope Valley beds of Ikes Canyon, Nevada. The writer collected there the holotype of *Ancistroceras magnum*, n. sp. Material from collections of the U.S. Geological Survey and from the University of Oklahoma, the last lent by Patrick Sutherland, supplied specimens here referred to *Ancistroceras* from the Oil Creek Formation and McLish Formation of Oklahoma. Some vexations and taxonomic problems surround generic assignments of these species, discussed more fully below.

Early references to *Lituites* or to the Lituitidae (Miller, 1889, 1891, 1897) were erroneous, Bassler (1915) noted removal of all American species formerly assigned to *Lituites* to other genera. Hyatt (1894) described a species from the Niagaran Group near Chicago, Illinois, as *Ancistroceras ? dyeri;* the description is brief and the species has never been figured. Bassler (1915) is of no help. The species is of uncertain position until the type can be studied; from its Silurian age and from its description, assignment to *Bickmorites, Jolietoceras,* or even to *Cliftonoceras* or *Cummingsoceras* all seem possible. Hyatt's (1894) *Cyclolituites americanus* seems to be the only early species of North America which had been assigned to any of the genera of the Lituitidae which has not been changed to another genus and another family, though doubt as to its affinities with *Cyclolituites* has been expressed, as noted under the discussion of the species.

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RANGE AND EVOLUTION OF THE TARPHYCERATIDA

The writer (*in* Flower and Kummel, 1950) in distinguishing the Tarphyceratida from the Bassleroceratida considered that the Tarphyceratidae constituted a dominantly Canadian stock, except for surviving Trocholitidae, characterized by thick-layered rings like those of the Ellesmeroceratina and the primitive Endoceratida. Whereas the Barrandeoceratida were a stock which began in the Chazyan and extended into the Devonian, with thin and apparently homogeneous rings. Subsequently Flower (*in* Flower and Teichert,

1957) suppressed the small order Bassleroceratida, containing then two families of exogastric cyrtocones with ventral tubular siphuncles. The Bassleroceratidae, possessing thick-layered rings like those of the Tarphyceratidae, were placed as the archaic family of that order, and the family Graciloceratidae, with thin homogeneous rings was placed as the archaic family of the order Oncoceratida, higher families of which possessed dominantly expanded siphuncle segments. The Russian Treatise (Ruzhentsev, *et al.*, 1962) overlooked this proposal and placed both the Bassleroceratidae and Graciloceratidae, with the unrelated endogastric Shideleroceratidae in the "Basslerocerataceae" of the Ellesmeroceratida. Teichert (*in* Teichert, *et al.*, 1964, p. K69,) accepted the conclusions of Flower, but in the systematic descriptions the Bassleroceratidae are assigned to the Ellesmeroceratida. The writer considers that the Bassleroceratidae are the first family of the Tarphyceratida. With minor and dubious reports of a few Lower Canadian species (mainly from dolomitized sections where the distinction between Lower and Middle Canadian faunas is obscured) the Bassleroceratidae begin in the early Middle Canadian and extend to the close of the period. The family is dominantly American; there are only two exceptions known at present, a *Bassleroceras* described from the Upper Canadian of Australia (Teichert and Glenister, 1954) and a new genus (Flower, ms.) from the late Canadian *Teiichispira* fauna of part of the Setul Limestone of Malaysia. Evolution in the family progressed from primitive compressed shells with prominent lateral lobes, to forms of broader whorl and transverse sutures; there are a few minor contractions of the aperture, but the family remains relatively simple. The family disappears at the close of the Canadian.

The Tarphyceratidae in North America are coiled shells, dominantly with ventral siphuncles. Primitive forms are loosely coiled and compressed in section; more advanced forms show closer coiling, broadening of the whorl and some development of costae. Two genera, *Moreauoceras* and *Pilotoceras,* have curiously constricted apertures at maturity. In *Centrotarphyceras* the siphuncle becomes subcentral at maturity. The family appears in the early Middle Canadian and was formerly thought to disappear in North America at the close of the Canadian. Two apparent survivors are known; one is an undescribed genus and species from the Table

Head Formation of Whiterock age in Newfoundland, the other is *Deltoceras vaningeni* Ruedemann (1906) of the Chazyan of the Champlain Valley. I have found it impossible to separate coiled shells with and without impressed zones and merge the Deltoceratidae or Estonioceratidae with the Tarphyceratidae.

The Trocholitidae comprise coiled shells in which the siphuncle, beyond the first whorl or half-whorl, is dorsad of the center, and commonly close to the dorsum. The oldest known forms are of Jefferson City age. The family continues into the Cassinian, the dominant genera there are *Curtoceras* and *Trocholitoceras,* continuing and expanding in the Whiterock Stage, where they are the dominant and nearly the only coiled cephalopods. Here the characteristic genera *Litoceras, Plectolites, Jasperoceras,* and *Crenuloceras* (now known to belong to this family from new material yet unpublished), are joined by three more genera now in manuscript. Only *Trocholites* is recognized as extending from the Chazyan to the Maysville beds. *Graftonoceras* is a Middle Silurian survivor of the stock; I have yet to find specimens and species connecting it stratigraphically with the latest known *Trocholites.*

Flower, as noted above, first placed the Lituitidae with the Barrandeoceratida, a view which is now abandoned. Sweet (1958) showed morphological evidence connecting the family with the Tarphyceratidae, and later it became evident that the acme of the Lituitidae lay in the Kunda, Aseri, and Lasnamägi stages, and that these intervals together with the underlying Volkhov Limestone, are equivalent to the Whiterock Stage of Cooper. Thus the great expansion of the Lituitidae is older than the first appearance of the Barrandeoceratida.

Thanks to NSF grant CB 6809, it was possible for the writer to see the faunal succession of cephalopods in the "*Orthoceras* Limestone" section of Sweden, to collect material, to study specimens in various collections, and to discuss problems of correlation of Ordovician faunas in North America, Europe, and Asia more widely with various colleagues. Much of the uncertainty that had surrounded the ranges and stratigraphic occurrences of the Lituitidae, and many other "*Orthoceras* Limestone" cephalopods as well, has been greatly reduced by the publications of Sweet (1958) and of Jaanusson (particular 1960). Balashov (1953) supplied evidence of the succession of the coiled cephalopods on the Russian side of the Baltic Sea.

The writer for reasons discussed more fully elsewhere (Flower, 1974) concluded that the Volkhov through the Lasnamägi represented the Whiterock Stage, and that reasonably the overlying Uhaku Stage is equivalent to the Chazy of North America.

As shown in Text-figure 1, the distribution of the coiled cephalopods in Norway, Sweden, and the Baltic provinces has been found to be surprisingly different from that of North America. No Bassleroceratidae are known. Tarphyceratidae are certainly known only in the Kunda Stage where the distinctive genera *Estonioceras, Tragoceras (= Planctoceras), Falcilituites,* and *Eichwaldoceras* occur. In Sweden (Jaanusson, 1960) the first Trocholitidae appear in the Lasnamägian, as *Trocholites* or *Paleonautilus,* while *Discoceras* is the dominant coiled genus of the later half of the Middle and all of the Upper Ordovician.[1]

In Sweden the Lituitidae appear first in the Kunda Formation, where *Holmiceras praecurrens* (Holm) is known. One wonders whether a reported *Ancistroceras* (Bohlin, 1955, p. 128) might also be a *Holmiceras.* It has not been figured or described, and *Holmiceras* has long been an all-but-forgotten genus. The Aserian Segerstad Limestone yields the zone of *Angelinoceras latum* (Angelin), the only species of the genus. The Lasnamägian is divided into the Skarlov Limestone, with the zone of *Lituites (Trilacinoceras) discors,* the Seby Limestone with the zone of *Lituites lituus,* and the Folkeslunda Limestone with the zone of *Lituites perfectus. Rhynchorthoceras angelini* is listed from the upper Aserian. *Ancistroceras* is listed from the Folkeslunda, which is also the source of *Cyclolituites applanatus.* The Uhakuan above, an old name for which is the *Ancistroceras* Limestone, yields *Ancistroceras* sp. and doubtfully, *A. undulatum.* Jannusson tells me that *Ancistroceras* is not uncommon there, but that specimens are commonly poorly preserved.

In Norway a comparable but somewhat different succession is recorded by Sweet (1958). *Holmiceras kjerulfi* Sweet is either from the upper *Asaphus* shales or from the overlining *Endoceras* Lime-

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[1] A *Discoceras canadense* was described from the Red River beds of Manitoba. I have not investigated the species, but it is unusually stout-whorled and rapidly expanding for the genus.

stone, both of Kunda equivalence. The *Ogygiocaris* shales are the source of *Lituites lituus* (Modeer), *L. perfectus, Trilacinoceras discors* (Holm), and *T. norvegicum* Sweet; these cephalopods suggest mixed affinities within the Aserian and Lasnamägian of Sweden.

The Ampyx Limestone is the source of *Ancistroceras undulatum* Boll, *Angelinoceras latum* (Angelin), and *Trilacinoceras* sp. Again mixed affinities with parts of the Swedish Ordovician are suggested by these cephalopods.

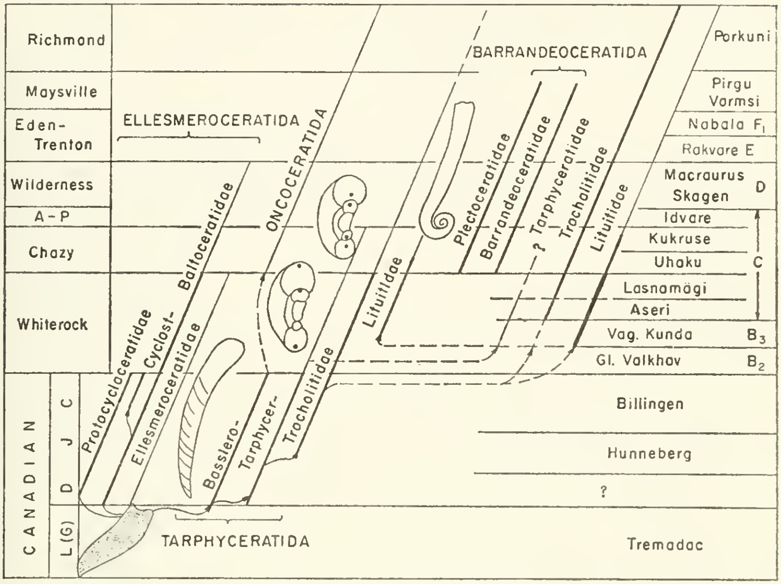
The Cephalopod Shale, which Sweet indicates as ranging in age through the *Ogygiocaris* beds, the Bronni beds (sandstones which have yielded no cephalopods) and the Ampyx beds, have yielded *Ancistroceras undulatum* (?), *Trilacinoceras discors, Cyclolituites lynnensis,* and *C. kjerulfi.* Here again the cephalopods suggest mixed affinities in stratigraphic terms of the Swedish section, suggesting horizons ranging from the Lasnamägian through the Uhakuan but not farther. Interestingly, some genera from the Cephalopod Shale suggest the Chazyan of North America, notably *Ruedemannoceras* and *Valcouroceras,* and first appearances of *Oncoceras* and *Allumettoceras.*

Interestingly there are no Tarphyceratidae known from the Norwegian section, and the first *Trocholites* occurs in the upper *Didymograptus* shales, probably materially older than the first occurrence in Sweden.

The first *Discoceras,* a genus which ranges into the Upper Ordovician, is in the *Ogygiocaris* shales and the dominantly Upper Ordovician lituitid, *Tyrioceras,* appear in the Lower Chasmops Limestone.

On the Russian side of the Baltic, Balashov (1953) cited from Cl, *Lituites perfectus, L. procerus, L. tenuicaulis, Ancistroceras torelli,* and *Ancistroceras undulatum;* the fauna is similar to that of the Lasnamägian. Balashov's (1955) genus *Eichwaldoceras,* a member of the Tarphyceratidae, is from the Kunda beds (B3); the writer has obtained a fragment of this genus from the Kunda of Oland.

The situation is expressed in Text-figure 1, which shows the ranges of the families of the Tarphyceratida on the left, in terms of the American Column, and on the right in terms of the Swedish and Russian terminology. Cognizance is taken of the Norwegian suc-



Text-figure 1. Ranges of the families of the Tarphyceratida in terms of the American section, on the left, and the Swedish and Baltic sections combined on the right. Family names are largely abbreviated by elimination of the -atidae endings. Symbols on the left are L (G), Lower Canadian, Gasconadian; D, Demingian; J, Jeffersonian; C, Cassinian; A-P indicates the Ashby-Porterfield intervals; I consider the Eden a shaly phase of limestone beds of the late Trenton.

On the right, the Tarphyceratidae are largely confined to the Kunda, with a few doubtful records from higher beds. The Trocholitidae are nearly as old in Norway. The acme of the Lituitidae is in the Kunda-Lasnamägi interval, declining in the Uhaku, and persisting higher only as *Tyrioceras*. The range of the Barrandeoceratida is represented in terms of the first appearances in North America; the order is yet unknown in the Baltic region until *Apsidoceras* and *Charactoceras* of the Apsidoceratidae (not represented) appear in the Upper Ordovician.

cession, but no attempt is made to review its precise correlation with the section in Sweden, beyond the above remarks.

EASTERN ASIA

Much recent work, largely published in Chinese with Russian or English summaries, was summarized by Kobayashi (1969), a great help as many of these publications are not available in this country. The cephalopod faunas suggest that in central China the Kuniutan Limestone, formerly considered the lower Pagoda Limestone, has a fauna suggesting that of the Volkhov. The higher restricted Pagoda Limestone contains genera suggesting varied correlations within the limits of the Kunda; an *Estonioceras, Lituites leei,* and *L. ningkiangense,* (which can be *Lituites, Trilacinoceras,* or possibly *Angelinoceras*) and *Ancistroceras angelini,* a species which is properly assigned to *Rhynchorthoceras* are cited. These forms sugest varied Aserian and Lasnamägian affinities (Yu, 1930, Lai Chai-Geen, 1965, and Kobayashi's summary of 1969). The faunal successions and problems of correlation are discussed more fully by Flower, 1974.

GENERA OF THE LITUITIDAE

Some difficulty has been encountered in assigning species to genera in the present work largely because the available literature is ambiguous on some features of the genera. The family is characterized by nautiloids, typically coiled initially, straightening adorally, with a siphuncle at or dorsad of the center, and growth lines in which a pair of lateral sinuses are separated by crests from a ventral sinus. Generic distinctions have emphasized the shape of the shell, but have given little attention to other features, such as cross section, suture patterns, or internal features. The genera may be summarized as follows:

Lituites Bertrand — One and a half whorls coiled, slender, compressed, with lateral lobes; growth lines here fail to show the lateral sinuses. In the straight or sigmoid part lateral lobes develop, but at late maturity an additional pair of dorsolateral crests appear, beyond which the dorsum may have low dorsolateral lobes separated by a broad low median saddle. The siphuncle is slightly dorsad of the center beyond the first half whorl.

Trilacinoceras Sweet — Similar to *Lituites* but lacking the dorsolateral "lappets."

Holmiceras Hyatt — The early part is gyroconic and slender, followed by a rapidly expanding sigmoid part as coiling is lost, becoming more slender in the anterior, straighter part. Growth lines as in *Trilacinoceras;* Holm's figure shows shallow ventral lobes.

Ancistroceras Boll — The early part is tightly coiled and moderately slender; the shell expands rapidly as coiling is reduced; the shell remains conically expanding as far as it is known.

Rhynchorthoceras Remelé — The early part is moderately expanding and only faintly exogastric; the shell then is gently conical, and may be slender anteriorly. Growth lines may show only obliquity; in some species the lateral lobes are not clearly developed.

Cyclolituites Remelé. — Small shells of about two or two and a half whorls, the later part fairly rapidly expanding vertically and showing anterior vestigial reduction of coiling.

TAXONOMIC PROBLEMS SURROUNDING AMERICAN SPECIES

In attempting assignment of the American material described here to the Lituitidae, no problems were encountered. However, assignment of such fragmentary specimens presented problems at the generic level, encountering uncertainties as to the shape of the shells except for our *Cyclolituites* and *Holmiceras.* Anterior straight parts of three species have the ornament pattern of *Trilacinoceras,* but all three of them have cross sections wider than high, and one of the species has transverse sutures. Two others show lobes on the venter, a feature known previously only in *Holmiceras praecurrens* (Holm). On one hand, a new genus could be made for such species; on the other, this would seem to proliferate genera in the Lituitidae unnecessarily. We face the additional problem that while surfaces of these forms resemble species of *Trilacinoceras* closely, we cannot be certain that the aperture at late maturity might not be that of true *Lituites,* or, on the other hand, that early stages might have the features of *Angelinoceras.*

Several species here assigned to *Ancistroceras* present other and different problems. *A. magnum* has the conically expanding phragmocone of *Ancistroceras,* whereas late parts of *Rhynchorthoceras* are more slender, but is compressed in section, whereas typical specimens of both genera in Europe are subcircular in section. The pattern of cameral deposits is that of *Ancistroceras,* and is unknown in any of the Michelinoceratida, showing openings of the connecting rings through which episeptal and hyposeptal deposits may pass and those of adjacent camerae may join. Such features were shown also by three species, each represented by rather short pieces of phragmocones from the Simpson Group of Oklahoma. One, *Ancistroceras oklahomae* is a part of a phragmocone with oblique sutures, compressed in section and slightly curved; records are indecisive, but it is probably from the Oil Creek Limestone. A second fragment representing a later growth stage is straight and has shorter camerae, and is probably another species; this is figured as *Ancistroceras* (?) *sp.* A third more slender part of a phragmocone is described as *Ancistroceras? deckeri;* it is from the McLish Limestone, which we regard as equivalent to the Chazyan of the Champlain Valley and to the Uhaku Stage of Sweden, thus suggesting survival of *Ancistroceras* in both North America and Europe, beyond the close of the Whiterock into the Chazyan. It is subcircular, very faintly depressed in section, straight, with simple transverse sutures. It also has the internal pattern of *Ancistroceras,* though from its very slender form, I was tempted first to place it in *Rhynchorthoceras.*

Flower (1968) described as *Nevadaceras conicum* a short fragment of a late growth stage of a straight cephalopod, conical, compressed in section, and with an eccentric siphuncle. Its siphuncle and camerae were empty. This is comparable to our *Ancistroceras* ? *magnum.* If future work shows it advisable to separate compressed shells here included in *Ancistroceras,* the name *Nevadaceras* may be used, and to it might be assigned *Ancistroceras oklahomae* of the present work. If not, it may be suggested that *Nevadaceras* might be placed as a synonym of *Ancistroceras.* The *N. conicum* specimen lacks evidence of organic cameral deposits or of openings in the connecting ring, and was considered a member of the Michelinoceratidae and the siphuncle was regarded as ventral in position. There is, however, no material connecting this form with other known members of the Michelinoceratidae, and its interpretation as a compressed, anterior, straight part of a lituitid is eminently more reasonable.

SYSTEMATIC PALEONTOLOGY

Genus **HOLMICERAS** Hyatt

Hyatt, 1894, Amer. Phil. Soc., Proc., vol. 32, p. 512.
Sweet, 1958, Norsk Geol. Tiddskr., Bd. 38, p. 125.

Holmiceras was originally separated from *Ancistroceras* on the basis of the loose rather than the tight coil of the early coiled part of the shell. Hyatt also noted that the adoral loss of lateral and ventral sinuses was paralleled by *Rhynchorthoceras* but did not note the ventral lobes of the sutures. From Holm's (1892) illustration the reduction of lateral and ventral sinuses is less extreme than in typical *Rhynchorthoceras*. Sweet (1958) further emphasized the sigmoid profile of the shell which is wanting in typical *Ancistroceras*.

The type species *Lituites praecurrens* Holm is from the Kunda of Sweden; Sweet added *Lituites kjerulfi* from either the upper *Asaphus* Shale or the lower *Endoceras* Limestone of the Oslo area. The *Endoceras* Limestone is currently regarded as equivalent to the lower Kunda. Kunda equivalence of the lower Table Head Limestone is suggested by other evidence.

Holmiceras bennetti Flower, n. sp. Pl. 4, figs. 1-6

Description. — This is a small lituitid, with an early coiled part imperfectly known, less than the last half whorl being observed, the shell becoming rapidly expanding where the curvature disappears, rapidly expanding, then straight and slender, but not sigmoid.

The holotype (Pl. 4, figs. 1-2) expands from 7 mm in width and 6 mm in height to 9 mm wide and 10 mm high, in the early curved part, then to 14 and 14 mm in the next 20 mm, where the rate of expansion becomes reduced. The shell continues for another 17 mm but is incomplete, attaining an estimated adoral width of 13 mm and a height estimated at 16 mm. Adoral camerae average 3 mm in length, the adoral 17 mm are aseptate. Growth lines are rugose, showing the ventral lobe, low lateral lobes, and a broad shallow lobe on the dorsum. The siphuncle is obscure. Adorally the cross section is slightly more narrowly rounded dorsally than ventrally.

A paratype (Pl. 4, figs. 4-6) is a somewhat distorted specimen, showing a quarter volution of the curved part increasing in height from 4 to 7 mm, the following part rapidly expanding for 10 mm, attaining a height of 13 and an exaggerated width of 15 mm, increasing to a height of 15 mm and width of 11 mm in the next 15 mm and extending for another 15 mm and showing a small part of the matrix-filled living chamber adorally, where the height is estimated at 16 mm, the width at 15 mm. The siphuncle is obscure, but appears to lie slightly dorsad of the center.

A second paratype (Pl. 4, fig. 3), is a small part of the rapidly expanding part of the shell 24 mm long increasing from 11 to 17 mm in diameter in a length of 24 mm. Adorally a clear septal surface is seen in which one side is slightly more narrowly rounded than the other, the siphuncle 1.5 mm in diameter is 6 mm from the narrowly rounded side, 10 mm from the other, and extending from the siphuncle toward the broadly rounded side the specimen shows a narrow elevated ridge, evidently a phenomenon of the cameral deposits. Only the septal surface at the anterior end of the specimen is figured (Pl. 4, fig. 3).

Discussion. — All three of the known specimens are largely calcite-filled phragmocones, and two were so weathered as to be friable, a matter which forbade any attempt to remove the specimens more perfectly from the matrix. The shell is characterized by its proportions, notable features of which are the slender curved part, followed by a region of rapid expansion in which rugose growth lines are close, then a more slender portion, with more distant rugose elevations of the shell. The adoral reduction in expansion gives the shell a faintly fusiform aspect in dorsal or ventral view; indeed, there is a suggestion of faint lateral contraction adorally which is apparently real, in spite of the incompleteness of the specimens. Absence of clearly preserved early stages led to some doubt as to whether this species should be assigned to *Holmiceras* or to *Ancistroceras*. The general form is more like *Holmiceras* in the adoral reduction of the rate of expansion, and it resembles *Holmiceras praecurrens* (Holm) also in the close spacing of rugose markings over the rapidly expanding part of the shell. There is no indication of the adoral loss of dorsal and ventral sinuses in the anterior part of the shell as is reported for *Holmiceras praecurrens,* but there is no anterior part showing the growth lines clearly. I have named the species for Paul Bennet in recognition of his exceptionally able help in collecting in western Newfoundland.

Types. — Holotype NMBM 1541 and paratypes NMBM 1542, 1543, all from the base of the upper third of the lower Table Head Limestone, Table Head, Newfoundland. All three specimens were found in a narrow zone, a 15 foot interval, by the large natural rock shelter in the Table Head section.

Genus **TRILACINOCERAS** Sweet

Sweet, 1958, Norsk Geol. Tiddskr., Bd. 38, H. 1, p. 147.

The features of this genus were summarized in the above summary of the genera of the Lituitidae. In placing the following three species in the genus, it is expanded to include forms in which the whorl may be slightly broader than high; two of the species, *T. undulatum* and *T. costatum* have sutures developing lobes on the venter; in *T. reubeni* the suture is transverse ventrally. In *T. reubeni* the siphuncle is very slightly closer to the venter than to the dorsum; in *T. undulatum* it is, as is usual in the Lituitidae, slightly closer to the dorsum than to the venter.

Trilacinoceras undulatum Flower, n. sp. Pl. 1, figs. 1-4

Description. — The holotype and only known specimen is a part of a living chamber 35 mm long, incomplete adorally and apically, and slightly distorted, expanding from 6.5 and 8.0 mm to 11.0 and 13.0 mm in 20 mm. A septum at the base shows a siphuncle 1 mm across and slightly dorsad of the center. The basal suture shows a broad low ventral lobe but is transverse dorsally and over most of the lateral surfaces. The surface shows smoothly rounded moderately elevated annuli separated by broader flat interspaces; increasing from 1 mm apart in the apical part, to 4 mm from crest to crest adorally. Growth lines are transverse dorsally, show lateral lobes of somewhat different conformation on the two sides which I believe to be the result of distortion, rising to rounded ventrolateral crests flanking a hyponomic sinus.

Discussion. — Although I have only part of a living chamber of this form, it is important in showing the surface features of *Trilacinoceras* Sweet, and a surface with features like those of *Trilacinoceras discors* (Holm) as figured by Sweet (1958, pl. 13, figs. 1, 4). Unevenness of the lateral lobes on the two sides is regarded as the result of slight distortion of the shell which is not otherwise clearly evident. Unlike *T. discors,* the section of the specimen is slightly broader than high, and the sutures show ventral lobes.

Type and occurrence. — Holotype, to be deposited in the U.S. National Museum (USNM 208992) from the Sponge beds of the Antelope Valley Limestone from the main exposures at Ikes Canyon, Toquima Range, Nevada; collected and submitted for study by Lehi Hintze.

Trilacinoceras costatum Flower, n. sp. Pl. 2, figs. 1-3; Pl. 4, figs. 7-9

Description. — This is a lituitid known only from moderately small parts of the straight part of the shell. The lituitid growth lines are evident, showing the usual ventral sinus, ventrolateral crests, lateral sinuses, deepest near the crests, smoothing out to transverse markings on the dorsum. Good surfaces are not preserved, but the internal molds show the growth lines reflected in rather distant low costae. The section is slightly broader than high; the somewhat flattened venter exhibits broad shallow lobes, shallower than the ventral sinus of the exterior.

The holotype (USNM 166175) is a fragment 27 mm long, expanding from 8 and 9.5 mm to 11 and 13.5 mm in a length of 27 mm. Costae are 4-5 mm apart, the length of the camerae increases from 2.5 mm to 3.0 mm. Neither septa nor siphuncle are apparent at the breaks at either end of the specimen.

A paratype, (USNM 166176) representing a slightly earlier part of the shell has a maximum length of 29 mm, expands from 7 and 8 mm to 10 and 11 mm in 18 mm, showing three camerae in a length of 5 mm and apically eight costae in an equal length. The anterior 8 mm is aseptate. In this specimen the ventral lobes of the sutures are slightly deeper than the ventral sinuses of the growth lines.

Discussion. — This species differs from *T. undulatum* in proportions, the rather low, more widely spaced costae, which are expressed on the interior by low rounded transverse ridges showing the lituitid pattern of lateral and ventral lobes. It is also a more gently expanding shell, and shows the ventral lobes rather deep. That the cross section is broader than high distinguishes this species from described *Trilacinoceras* of the Balto-Scandinavian region.

Types and occurrence. — Holotype and paratype, USNM Nos. 166175, 166176, from the Antelope Valley Limestone, USGS collection D2283-CO (71-RJ-18) about 25 feet below the highest exposure on hill 8937. Nevada coord., central zone: E. 473,950 ft; N. 1,565,700 ft., Wildcat Peak Quadrangle, Nevada. This locality is far up into Ikes Canyon, where the Antelope Valley Limestone is seen in a separate thrust mass from that nearer the mouth which is the well-known sponge collecting locality.

Trilacinoceras reubeni Flower, n. sp. Pl. 1, figs. 5-8

Description. — The holotype is a straight portion of a shell, 44 mm long, of which the anterior 16 mm represents the basal part of a living chamber. The shell expands from a width of 8 mm and a height of 7 mm to a width of 15 mm and a height of 12 mm. The surface shows narrow sharply elevated growth lines separated by narrow interspaces which are generally flat and slightly broader than the elevated markings. Apically ten ridges occupy a length of 5 mm, the number is reduced to eight in that length at the base of the adoral two-thirds of the specimen, and become closer again at mid-length of the type. They possibly widen at the extreme adoral end, where the shell surface is wanting. Growth lines are transverse across the dorsum, develop faint lateral lobes, higher ventrolateral crests, and a broad shallow hyponomic sinus. Sutures, visible only near the base of the living chamber, are transverse; the last camera is 2.5 mm long, the previous one 2.1 mm. A section at the base (not figured) shows the siphuncle 1 mm across, 2 mm from the venter and 3 mm from the dorsum; an unusual condition as the siphuncle is usually slightly dorsad of the center in the Lituitidae. The cross section is slightly more flattened ventrally than dorsally.

A cross section was cut near the base, apicad of which are 3 more mm of the shell, partly covered; the limestone was weathered and friable and further extraction of this part was unsafe.

Discussion. — The extremely narrow close transverse ridges distinguish this species from the allied American forms, as does also the absence of a good ventral lobe and the rather broad shallow hyponomic sinus. Species of the Balto-Scandinavian region are narrower in cross section, and none have been figured showing such fine close transverse ridges.

Type and occurrence. — Holotype, USNM No. 166177, from USGS collection D2283-CO, 25 feet below the highest exposure on hill 8937, Nevada coord.: central zone. E 473,950 feet, N 1,565,700 feet, Wildcat Peak Quadrangle, Nevada; this locality is far up in Ikes Canyon, Toquima Range, Nevada, exposing a thrust sheet distinct from the section near the mouth of Ikes Canyon containing the familiar Sponge beds. The horizon is believed to represent either the *Nileus* beds or the Sponge beds.

Genus **ANCISTROCERAS** Boll

The characters of this genus have been noted above. Particular perplexity surrounds distinction of this genus from *Rhynchorthoceras,* which differs typically in having the early part of the shell cyrtoconic, in having the growth undulations of the growth lines, smoothed, and particularly, with the reduction of the lateral lobes. When only parts of the straight part of the shell are available, as in the specimens described here, separation of the genera presents difficulties almost impossible to surmount. It is some comfort that Sweet (1958) suggested that such changes in shell form as have been accepted as distinguishing *Rhynchorthoceras* from *Ancistroceras* might take place independently in several species groups. The writer had considered separating *Ancistroceras deckeri* from *Ancistroceras* and placing it in *Rhynchorthoceras* on the basis of the very gentle rate of expansion but finally concluded that certain separation could not be made on this basis. It may be noted that Holm (1885) made known the striking pattern of the cameral deposits in *Ancistroceras,* and Sweet (1958, p. 121) emphasized the thick rings with perforations in *Rhynchorthoceras helgoeyense.* In this respect the two genera are similar, and Holm's figure of *Lituites lituus* (1885, pl. 5, fig. 2,) shows that there is a similar internal pattern in *Lituites.*

Ancistroceras magnum Flower, n. sp. Pl. 5, figs. 1, 2; Pl. 6, figs. 2, 3

Description. — This species is known from a part of a phragmocone, evidently from a late growth stage, expanding from 40 and 44 mm to 65 and 84 mm (slightly restored) in 100 mm. The lateral rate of expansion of 5 mm in 40 mm, is abruptly increased in the adoral part to 15 mm in an equal length. Apically the specimen is bounded by an oblique break, and even the siphuncle was not evident. Adorally the septum shows the siphuncle 10 mm in diameter, 35 mm from one side, 37 mm from the other. The specimen lacks growth lines and septa are not apparent externally; the compressed rather than depressed nature of the cross section is an inference, but one supported by the outlines.

A longitudinal section slightly oblique to the vertical plane shows recrystallized calcite considerably obscuring the siphuncle outline. The anterior camera is matrix-filled and shows no cameral deposits. The other camerae are calcite-filled, and show a pattern of episeptal and hyposeptal deposits strongly reminiscent of the sections Holm (1885) illustrated for *Ancistroceras*. These are shown most strikingly in the lower right of our illustrated section in the apical three camerae. The penultimate camera shows a vertical line longitudinal, slightly irregular, outside the limits of the siphuncle, from which a slightly sinuate tube (?) seems to extend in a sinuate pattern apicad and outward farther into the camera.

Discussion. — Though I have only a small piece of this form, it is clearly a lituitid, with cameral deposits like those of *Ancistroceras*. A remarkable feature of the shell is the marked flaring at the anterior end of the specimen, the flaring being lateral. The fragment is straight, and I am uncertain as to identification of dorsal and ventral sides except that in lituitids the siphuncle is commonly dorsad of the center. The anterior cross section shows one of the narrow ends slightly more broadly rounded than the other; the siphuncle is slightly nearer this side than the other. Apically, the apical angles are 15° laterally and 20° vertically, but in the adoral 30 mm the lateral apical angle is increased to 20-25°.

Type and occurrence. — Holotype, NMBM 1582, from the Sponge beds, Ikes Canyon, Toquima Range, Nevada.

Ancistroceras ? oklahomae Flower, n. sp. Pl. 2, figs. 4, 5; Pl. 3, figs. 1, 2

Description. — The holotype and only known specimen (USNM 208993) is a part of a phragmocone slightly compressed in section, and slightly curved. The cross section is more broadly rounded on the convex side, which I regard as ventral, and the siphuncle lies slightly dorsad of the center. The specimen is 60 mm long and increases from 20 and 15 mm to 31 and 25 mm. Apically the siphuncle is 3 mm across, 10 mm from the convex and 7 mm from the concave side; adorally the siphuncle is 5 mm across, 14 mm from the convex and 11 mm from the concave side. No surface markings are shown. One side is weathered, exposing what appear as rather thick annular markings; these are septa widened by episeptal and hyposeptal deposits; they slope slightly orad from the concave to the convex side.

A nearly vertical section shows camerae which are 7 mm long apically and shorten gradually orad; adorally five occupy a length equal to the shell height; apically four camerae occupy a similar length. The siphuncle is tubular, the septal necks long, straight adorally, pointing faintly inward in the apical segments, and ranging from one-third to nearly one-half the length of the segment. Straight thin connecting rings can be seen in some parts, but in many segments the ring is incomplete, leaving the siphuncle open into the camerae, a condition like that figured by Sweet (1958, text fig. 15 B and Pl. 20, fig. 3) for *Rhynchorthoceras helgoeyense,* except that here the openings are larger.

Episeptal and hyposeptal deposits are developed; on the venter they pass through the openings in the siphuncle wall and may fuse; on the ventral side they join and occupy a considerable part of the ventral side of the siphuncle. In this section, cavities within the siphuncle on the ventral side do not enter the siphuncle adorally, but such a connection is seen apically. On the dorsal (concave) side these openings are in some cases occupied by light calcite with conspicuous white borders, as on the venter, but in several anterior segments matrix penetrating the siphuncle passes through a narrow aperture in the siphuncle wall, and widens, filling the cavity between episeptal and hyposeptal deposits in the camerae.

In the apical part of the specimen inorganic calcite fills the original cavity of the siphuncle and also in the camerae. One section, all that was possible, is insufficient to show the detailed nature of the openings of the siphuncle; apparently some parts of the section cut such openings while others do not; there is probably a regular radial pattern, but its details cannot be ascertained without more material.

Discussion. — Reference of this species either to *Ancistroceras* or to *Rhynchorthoceras* is somewhat venturesome without knowledge of the apical part of the shell; assignment to *Ancistroceras* is suggested by the slight concavity of the dorsum and convexity of the venter, and by the compressed cross section. Interestingly, the openings of the siphuncle into the camerae, the large siphuncle with exceptionally long necks and the pattern of the cameral deposits are features diagnostic of the Lituitidae. They are apparently common to at least *Rhynchorthoceras*, from Sweet's (1958) evidence, and *Ancistroceras* and *Lituites* from Holm's (1885) evidence.

Type and occurrence.—Holotype, USNM 208993 from the Simpson Group, the label reads "3 miles east of Pooleville, Oklahoma." The locality is certainly from exposurers in West Spring Creek on what is now the Virgil Snyder Ranch. The horizon must remain doubtful, unless further records can be found, but this is either from the Oil Creek Formation or the McLish Formation. The yellow hue of the weathered limestone suggests the Oil Creek Limestone rather than the McLish, from observations of the writer, but these observations are limited and probably not conclusive. The McLish is generally a light gray white-weathering limestone.

Ancistroceras (?) deckeri Flower, n. sp. Pl. 2, fig. 6; Pl. 3, fig. 3

Description. — This is based upon a part of a straight phragmocone, slightly depressed in section, 60 mm long expanding from 31 and 32 mm to 39 and 40 mm. Adorally the siphuncle is 7 mm across, 11 mm from one side and 17 mm from the other. Sutures are straight and transverse, rather obscure; camerae vary rather irregularly in length, largely from 7 to 9 mm, but the last complete camera is 12 mm long. A section was made, oblique to the plane of symmetry. The siphuncle has long septal necks, averaging one-third the length of a camera. Connecting rings are varyingly incomplete. On the left of the figured section, in the third and again in the fifth camera, matrix has penetrated the siphuncle, being narrow at its passage through the siphuncle openings, and widening between episeptal and hyposeptal deposits in the camerae. As in the preceding form, episeptal and hyposeptal deposits may penetrate the siphuncle and join. On the right side, the adoral end of the first complete camera shows a triangular patch of matrix between the anterior septum and the cameral deposits. The next segment shows matrix penetrating the camerae, widening slightly beyond its passage through the siphuncle. The section fails to cut cavities in the next three segments, and cavities in the camerae show a lining which is not only episeptal and hyposeptal but extends along the outer surface of the connecting ring. Without evidence of other parts of the specimen and of the allied *Ancistroceras* (?) *oklahomae,* these deposits would have been considered inorganic, but it may well be that, as there is evidently some considerable complexity in the radial pattern of the deposits, that this condition may be attained by organic deposits in some parts of the camerae. The last segment shows the episeptal deposit extending apicad for one segment, and beyond it more calcite extends for two more segments.

Discussion. — The perforate siphuncle wall and the pattern of cameral deposits are those characteristic of the Lituitidae. As noted in the generic discussions, there is some difficulty in assigning this species to either *Ancistroceras* or *Rhynchorthoceras* to the exclusion of the other.

Type and occurrence. — Holotype, Univ. of Oklahoma No. 51 from the McLish Limestone (label by C. E. Decker), Sec. 35, Township 1 S, Range 2 E., Murray County, Oklahoma, north of the John's Ranch.

Ancistroceras ? sp. Pl. 3, figs. 5, 6

Description. — This is based upon a badly weathered bit of phragmocone 55 mm long, so weathered and incomplete that orientation was uncertain when the specimen was cut. Adorally the section is 34 by 38 mm, and is believed to be depressed. The sectioned surface expands in width from 32 to 38 mm, and contains ten and parts of two more camerae which are 4 mm long throughout, failing to show the irregularities or ontogenetic differences shown in the preceding two specimens. As in those specimens, necks are long, openings in the rings are frequent, where they occur matrix may penetrate the camerae, narrow at the region of the necks, widening in the camerae. As also in the preceding forms, episeptal and hyposeptal deposits may join through the openings in the siphuncle. Where the section cuts siphuncle walls that are complete, a lining in the siphuncle, from evident penetration of the cameral deposits, and occasional development of cameral deposits against the outside of the ring can be seen. One side of the section is figured here ×2; the opposite side of the section, which misses the siphuncle apically, is also shown.

Discussion. — I had considered whether this specimen might represent a later growth stage of *A. oklahomae* than is shown by the type, but there are too many differences. Septa are closer, the siphuncle is smaller in proportion to the shell diameters, sutures are transverse rather than oblique, the section is depressed instead of compressed. Conceivably the closer septa and the small diameter of the siphuncle might be developed in a later stage of *A. oklahomae,* but that other differences might be achieved in ontogeny seems most unlikly. *A. deckeri* is known from a commensurate fragment and is widely different in the very long camerae and the more nearly circular cross section.

Figured specimen. — USNM 208994 from USGS locality 200 i (old series) 3 miles east of Pooleville, Oklahoma, Reed's West Spring Creek section. This is from the same locality as *Ancistroceras* (?) *oklahomae* but probably from somewhat higher in the section. Lithology suggests the Oil Creek Limestone rather than the McLish Limestone.

Genus **CYCLOLITUITES** Remelé

Remelé, 1886, Deutsch. Geol. Gesell., Zeitschr., Bd. 38, pp. 467-8; 1890, Untersuchungen u. Verst. Diluvialgeschieben, Bd. 1, sec. 3, p. 101.
Schroder, 1891, Palaeont. Abhandl., n. f., Bd. 1, H. 4, p. 45.
Hyatt, 1894, Amer. Phil. Soc., Proc., vol. 32, p. 505.
Sweet, 1958, Norsk Geol. Tiddskr., Bd. 38, p. 153.
Furnish and Glenister, 1964, Treatise on Invert. Paleontology, Part K, Mollusca 3, p. K 366.

This genus was erected for small shells with lituitid growth lines, in which a coiled part of about two and a half volutions, in contrast to one and a half in most other lituitids, is followed by an anterior portion which is departing from the coil. Apparently no complete living chambers were known from the Balto-Scandinavian specimens, but probably the anterior part with reduced coiling was of no great length.

C. applanatus Remelé (1886) was described from a drift specimen, but Holm (*fide* Jaanusson) examined the type, and was able to conclude that the specimen came from the Folkeslunda Limestone, to which it was attributed by Jaanusson, 1960. *C. lycnus* Holm is also from the Folkeslunda Limestone. The two Norwegian species, *C. lynnensis* Kjerulf and *C. kjerulfi* Sweet are both from the Cephalopod Shale of Norway (Sweet, 1958).

It may be noted that while *Cyclolituites americanus* is larger than the previously known Scandinavian specimens, it is typical in ornament and form, notably in the shallow grooves flanking the hyponomic sinus (Sweet, 1958, fig. 18,) but I do not find such extreme sinuosity of the growth lines as Sweet represents, in the same illustration, for *Cyclolituites lynnensis*.

Cyclolituites americanus Hyatt
Pl. 3, fig. 4; Pl. 4, fig. 10; Pl. 5, figs. 3, 4; Pl. 6, figs. 1, 4

Cyclolituites americanus Hyatt, 1894, Amer. Phil Soc., Proc., vol. 32, pp. 505-6; Foerste, 1929, Denison Univ. Bull., Sci. Lab., Jour., vol. 24, p. 57; Foerste, 1930, *ibid.*, vol. 24, pp. 269, 271.

Cyclolituites? americanus Hyatt, Ulrich, Foerste, Miller and Furnish, 1942, Geol. Soc. Amer., Spec. Papers, No. 37, p. 75.

Description. — The type and only known specimen preserves three-fourths of a volution, the early part being missing. At the earliest point the whorl is 16 mm high and 14 mm wide, slightly more narrowly rounded ventrally than dorsally, the greatest width dorsad of the center, with slight ventrolateral flattening, and a slight flattening of the rounded ventral face. The spiral at this point is 19 mm across, increasing, by the addition of the next half whorl to 29 mm. Adorally the spiral is 37 mm, the whorl 16 mm high. Both sides are incomplete, and the width can only be estimated as 12 mm. Here the width is greatest at the umbilical shoulders. In the three fourths of the whorl preserved, the height increases more rapidly than the width, and flattening of the ventral face becomes increasingly evident.

Septa can be seen through the shell; apically they are nearly transverse, showing vestigial lateral lobes which slope slightly forward from the umbilical to the abdominal shoulders; adorally the lobes become more prominent but are no more inclined forward from dorsum to venter. The shell is largely smooth on one side; on the other it shows growth lines, but even here the relief is gentle, and clearly the surface exposed is an inner layer of the conch, from which the external layer, which we would expect to show sharper relief of surface features, has been exfoliated. Growth lines show lateral sinuses, deepest in the dorsal half of the shell, rising to high ventrolateral crests where the lateral surface rises to low rounded longitudinal ridges, followed by shallow rounded grooves, between which the venter is then gently convex in outline, more flattened adorally than adapically.

The specimen fails to show the siphuncle clearly, but it is clearly not close to the venter, and it must be central or slightly dorsad of the center. Sutures can be seen obscurely as color variations on the unwhitened surface; they are nearly transverse apically; adorally faint lateral lobes develop (Pl. 5, fig. 4). Camerae lengthen adorally, being 3.5 mm long at the base of the specimen and 5.0 mm long adorally, both as measured on the venter. Matrix in the adoral end of the type suggests that it includes the base of the living chamber.

Discussion. — Bypassing several early works which assigned coiled cephalopods to *Lituites,* all incorrectly, and long ago corrected, the description of *Cyclolituites americanus* has remained as the only report of a lituitid in North America to which some credence could be given. The species had not been figured, and there was naturally some doubt as to whether it was a true lituitid, expressed by Ulrich, Foerste, Miller, and Furnish (1942) and Sweet (1958), and which the writer had shared. Restudy of Hyatt's type shows that the species is a *Cyclolituites,* and one very close in proportions to *Cyclolituites lycnus* Holm, though somewhat larger in size. It is probable, that with restoration of the living chamber as occupying a quarter of a volution, the shell was 40-45 mm across, rather than 74 or 75 mm as Hyatt (1894) stated (the 7 could easily be a misprint for a 4). The siphuncle is not clearly shown, but it is clear that it does not lie ventrad of the center. Growth lines are typical in the pattern of crests and sinuses. The two revolving ridges flanking the dorsum are found in other species of *Cyclolituites* as noted above. The smoothing of the faintly rounded growth lines is peculiar, but it may be that the outer shell layer, showing stronger and more rugose growth lines, has been lost by exfoliation. Our illustration shows what appears to be a sharp umbilical angle at the anterior end of the specimen which is false; the effect is produced by some matrix adhering to the specimen, which I did not attempt to remove in view of possible fragility of the specimen, and the fact that it was not mine. Actually the umbilical shoulder is rounded. Calcite fills the preserved camerae, but there is not clear evidence of cameral deposits or "pseudosepta" which are properly junctures between such deposits. The real septa are visible, being differentiated by color. Gentle relief of the growth lines offered particular difficulties in their photography, and one figure (Pl. 6, fig. 1,) is taken of a whitened specimen from the surface of which the ammonium chloride was partly wiped away, leaving the depressions white, the elevations dark.

Hyatt cited the specimen as from Gargamelle Cove, without assignment to any formation. At Gargamelle Cove only the lower Table Head Limestone is exposed; the lithology of the type is consistent with such an origin. My recollection of the absence of lower beds attributable to the St. George group has been kindly confirmed by L. M. Cumming (*fide litt.*), whose examination of the region has been thorough.

Type and occurrence. — Museum of Comparative Zoology, No. 5138, from limestones of the lower part of the Table Head Formation, Gargamelle Cove, just southeast of the Port-au Choix Peninsula, (the southwestern side of which is Pointe Riche) Newfoundland. The section on the north side of Gargamelle Cove is continuous with that at Point Riche.

CONCLUSIONS

In summary, it may be noted that the Lituitidae are reasonably derived from the Trocholitidae by (1) development of lateral as well as ventral lobes (2) perforations of the siphuncle wall permitting intrusion of episeptal and hyposeptal deposits into the siphonal cavity (3) reduction of coiling to the apical part of the shell, and finally its near obliteration in *Rhynchorthoceras.*

The great expansion of the Lituitidae is in the interval of the Kunda, Aseri, and Lasnamägi, regarded as Middle and Upper Whiterock in age. The Volkhov, the lower member of the Swedish succession, and zone L of western Utah (Ross 1951, Hintze, 1951, 1952) lack known lituitids. Occurrence of lituitids in the lower Table Head Limestone, of Newfoundland, the Antelope Valley Limestone of Nevada, and the Oil Creek Limestone of Oklahoma, serve to strengthen this correlation further, while *Ancistroceras* in the Chazyan McLish Formation is consistent with Chazyan correlations suggested elsewhere (Flower, 1974) for the Uhaku Stage, the *Ancistroceras* Limestone of earlier usage.

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EXPLANATION OF PLATE 1

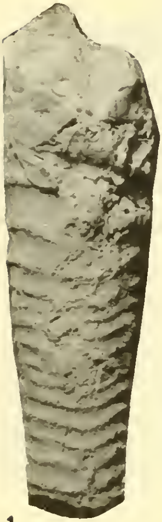
Figure

1-4. **Trilacinoceras undulatum** Flower, n. sp.

Holotype, USNM 208992, a slightly distorted living chamber, × 2. 1. Lateral view, venter on right. 2. Ventral view, showing crests flanking the hyponomic sinus. 3. Lateral view, venter on left, showing a somewhat different conformation of growth lines than in fig. 1. 4. Dorsal view. Sponge beds, Antelope Valley Limestone, Ikes Canyon, Toquima Range, Nevada.

5-8. **Trilacinoceras reubeni** Flower, n. sp.

Holotype, USNM 160777, × 2. 5. Dorsal view; showing narrow close costae. 6. Lateral view, dorsum on left. 7. Ventral view showing hyponomic sinus and lateral crests; note the transverse condition of the suture. 8. Left lateral view, venter on left. Antelope Valley Limestone, from a thrust plate high in Ikes Canyon, Toquima Range, Nevada, USGS collection D2283-CO.



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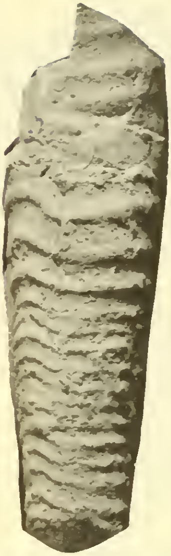

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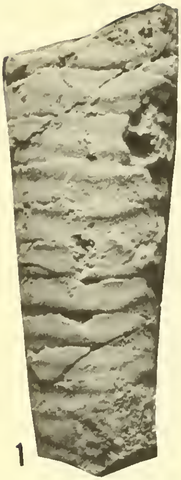
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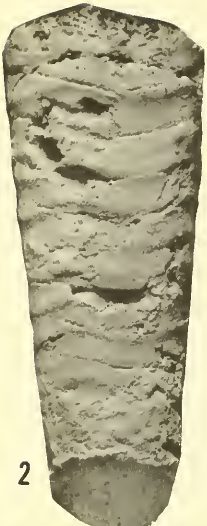
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EXPLANATION OF PLATE 2

Figure

1-3. **Trilacinoceras costatum** Flower, n. sp.

Holotype, USNM 166175, × 2. 1. Right lateral view. 2. Ventral view; note shallow sinuses and deeper lobes. 3. Dorsal view. Antelope Valley Limestone, high in Ikes Canyon, Toquima Range, Nevada, USGS collection D2283-CO. See also Pl. 4, figs. 7-9.

4-5. **Ancistroceras ? oklahomae** Flower, n. sp.

Holotype, USNM No. 208993. 4. Vertical section, × 1. 5. Same, × 2, extreme apical part missing. From either the Oil Creek or Simpson Limestones, West Spring Creek, 3 miles east of Pooleville, Oklahoma. See also Pl. 3, figs. 1, 2.

6. **Ancistroceras ? deckeri** Flower, n. sp.

Holotype, Univ. of Oklahoma, No. 51, nearly vertical section, × 1.4, venter on left; See also Pl. 4, fig. 3. McLish Limestone, Murray Co., Oklahoma.

EXPLANATION OF PLATE 3

Figure

1, 2. **Ancistroceras ? oklahomae** Flower, n. sp.

Holotype, USNM 208993, × 1. 1. Lateral view, venter on right, showing weathered surface exposing septa widened by cameral deposits. 2. Doral view, venter on right. Oil Creek Formation or Simpson Formation, 3 miles east of Pooleville, Oklahoma. See also Pl. 2, figs. 4, 5.

3. **Ancistroceras ? deckeri** Flower, n. sp.

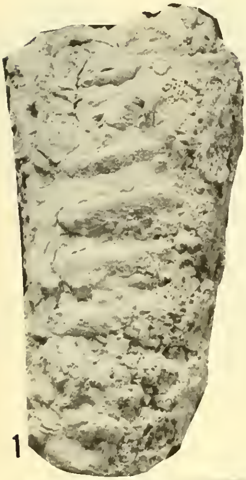
Holotype, × 1, Univ. of Oklahoma No. 51, dorsum on left, exterior of an internal mold; McLish limestone, Murray Co., Oklahoma, See also Pl. 2, fig. 6.

4. **Cyclolituites americanus** Hyatt

Holotype, Museum of Comparative Zoology 5138, Harvard University, ventral view × 2.5, showing hyponomic sinus, faint growth lines, and grooves and ridges flanking the sinus. See also Pl. 4, fig. 10; Pl. 5, figs. 3, 4; Pl. 6, figs. 1, 4.

5, 6. **Ancistroceras ?** sp.

5. USNM 208994, one side of a section oblique to the vertical plane, × 2, showing incomplete rings and cameral deposits extending into the siphuncle. 6. Opposite side of the same section × 1. From the Oil Creek or McLish Limestones, West Spring Creek, 3 miles east of Pooleville, Oklahoma.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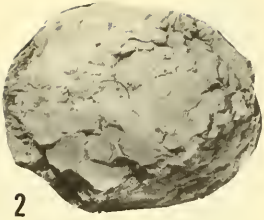
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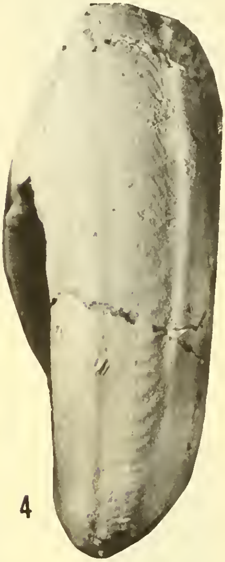
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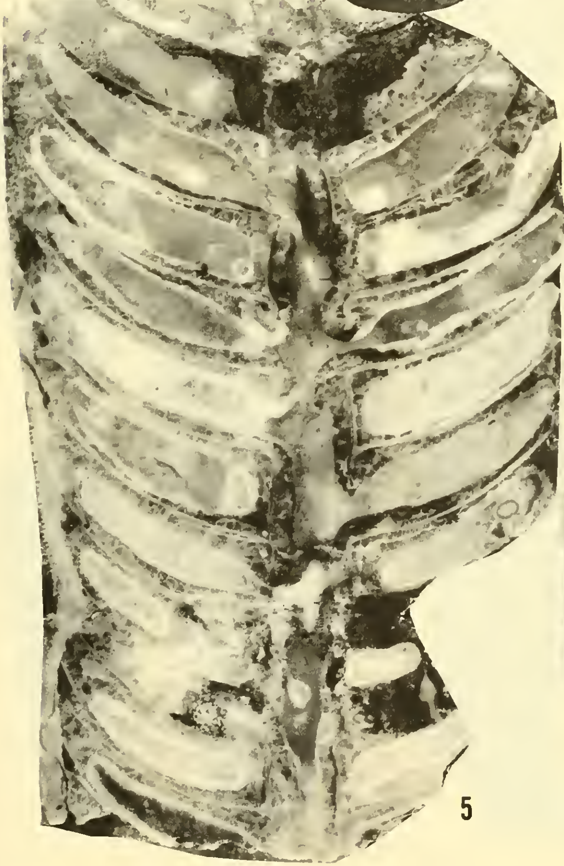
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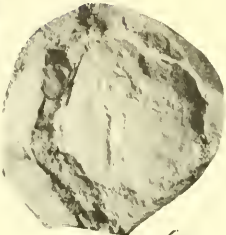
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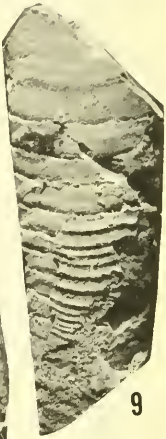
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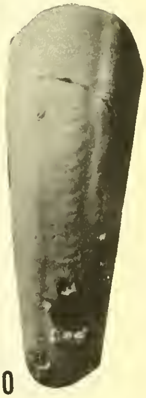
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EXPLANATION OF PLATE 4

Figure

1-6. **Holmiceras bennetti** Flower, n. sp.

Holotype, NMBM 1541, × 2. 1. Ventral view. 2. Lateral view, venter on left. 3. Anterior (septal) view of paratype NMBM No. 1543, showing dorsum above, groove formed by cameral deposits extending from the siphuncle to the venter; Paratype, NMBM No. 1542, × 2. 4. Dorsum. 5. Lateral view, dorsum on left. 6. Ventral view. Table Head Limestone, Table Point, Newfoundland.

7-9. **Trilacinoceras costatum** Flower

Paratype USNM 166176, × 2. 7. Lateral view, venter on left. 8. Dorsum. 9. Venter, showing hyponomic sinus and shallow lobes. Antelope Valley Limestone from high in Ikes Canyon, Toquima Range, Nevada, USGS collection D2283-CO. See also Pl. 2, figs. 1-3.

10. **Cyclolituites americanus** Hyatt

Holotype, Museum Comparative Zoology, 5138, ventral view of a slightly earlier stage than Pl. 3, fig. 4. See also Pl. 3, fig. 4; Pl. 5, figs. 3, 4; Pl. 6, figs. 1, 4. Table Head Limestone, Gargamelle Cove, Newfoundland.

EXPLANATION OF PLATE 5

Figure

1, 2. **Ancistroceras magnum** Flower, n. sp.

Holotype, NMBM 1582. 1. Anterior end, × 1, venter below. 2. Lateral view, venter on left. Antelope Valley Limestone, Sponge beds, Ikes Canyon, Toquima Range, Nevada. See also Pl. 6, figs. 2, 3.

3, 4. **Cyclolituites americanus** Hyatt

Holotype, Museum Comparative Zoology 5138, lateral views, × 2; fig. 3 is whitened, showing the growth lines, lost by weathering adorally; fig. 4 is unwhitened, showing spacing and form of the sutures. Table Head Limestone, Gargamelle Cove, Newfoundland. See also Pl. 3, fig. 4; Pl. 4, fig. 10; Pl. 6, figs. 1, 4.

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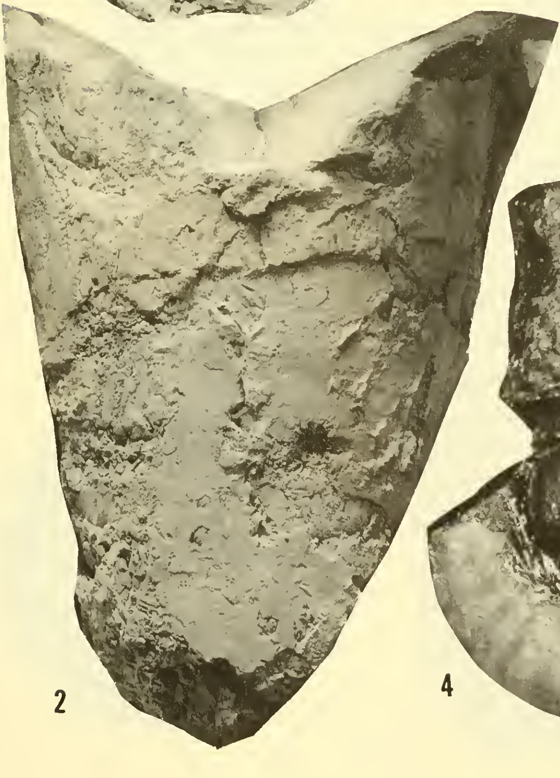

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EXPLANATION OF PLATE 6

Figure

1, 4. **Cyclolituites americanus** Hyatt

Holotype, Museum of Comparative Zoology 5138, Harvard University, × 2. 1. Ventral view, whitened, then with whitening rubbed off, accentuating the growth lines and ventrolateral ridges and grooves. 4. Oblique lateral view, whitened, showing growth lines, revolving grooves on the ventrolateral region, and part of the venter with the growth lines outlining the hyponomic sinus. Table Head Limestone, Gargamelle Cove, Newfoundland. See also Pl. 3, fig. 4; Pl. 4, fig. 10; Pl. 5, figs. 3, 4.

2, 3. **Ancistroceras magnum** Flower, n. sp.

Holotype, NMBM 1582, 2, vertical section, venter on left, × 1. 3. Ventral (antisiphonal side), × 1. See also Pl. 5, figs. 1, 2. Sponge beds, Antelope Valley Limestone, Ikes Canyon, Toquima Range, Nevada.

SOME PROBLEMS IN CORAL PHYLOGENY AND CLASSIFICATION

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PREFACE

When Flower (1961) published on the corals of the Montoya Group of New Mexico and adjacent areas it was stated that the help of Miss Helen Duncan was so extensive that she should have been named as joint author. She declined, largely because she felt U.S. Geological Survey procedures would have delayed the publication further. Subsequently a few significant finds were made by us and the publications of others (Sokolov, 1962) modified and elaborated the taxonomy of the Ordovician corals materially. The present work is a summary of some of our discoveries and of our discussions on matters of coral taxonomy and phylogeny which extended through her long illness from 1968 to her death in 1971. Our main concern here is discussion of phylogeny and descriptions of some new structures found in some new species which solve some problems but augment others.

Rousseau H. Flower

ACKNOWLEDGMENTS

The New Mexico Bureau of Mines and Mineral Resources contributed to the expense of publication of this work. We have profited from discussion with colleagues, mainly William Oliver and David Budge. Stephen Hook gave valuable assistance in the closing phases of preparation of this paper, as did Lois Devlin, for whom one of the species is named.

PHYLOGENY OF ORDOVICIAN CORALS

The study of the Montoya corals (Flower, 1961) led to conclusions as to phylogeny shown there in figure 4 on page 33, and shown here with some additions and modifications in Text-figure 1. It presupposes the antiquity of *Lichenaria,* ceroid colonies with fibrous walls, tabulae, and no septa. From it are derived phaceloid

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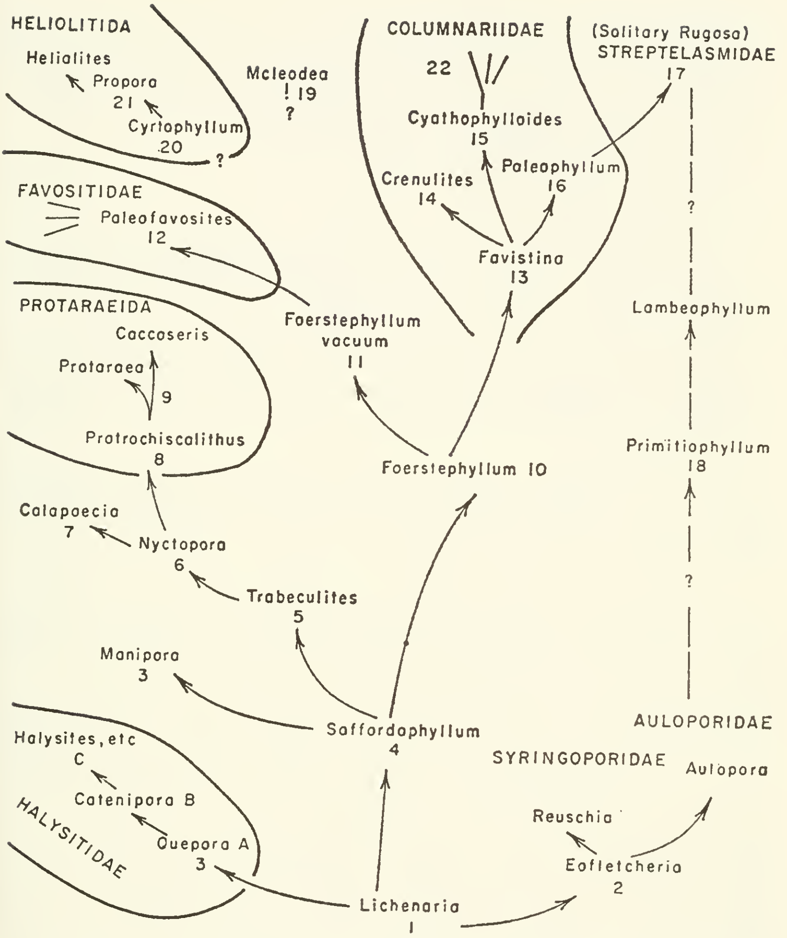
*Deceased.

forms, *Eofletcheria,* probably leading to *Reuschia* and the Syringoporidae, on the one hand, and to *Aulopora* and the Auloporidae on the other. A distinct lineage leads to the Halysitidae; here are shown *Quepora* without septal structures, *Catenipora* with septa and balken in some species, leading to *Halysites* and derived forms where mesocorallites containing tabulae are substituted for balken.

Saffordophyllum is derived from *Lichenaria* by crenulate walls and the beginning of septal ridges or spines. Here lineages split. One line leads to *Nyctopora,* with more prominent septal structures, and from there on one hand to *Calapoecia* with development of a porous coenenchyme; another leads to the Protaraeida of Sokolov (1962); here walls are of solid baculae and septa appear as independent bacular structures, extending with or without modification into the columella; in simpler forms tabulae form in spaces between the septa; in advanced forms septa widen and there is no room for tabulae.

Foerstephyllum is a genus containing species both with simple fibrous walls with only axial planes, and forms with axial plates, solid dark structures which we believe to be epithecae. They are probably a modification of holothecae which we believe to be present from *Lichenaria,* evident in the Halysitidae and in *Manipora* but commonly destroyed as the outer covering of cerioid corals; colonies being commonly abraded before burial.

Through *Foerstephyllum vacuum* (Foerste) where pores become prominent and septal structures are reduced, one passes to *Paleofavosites* and to the Favositidae. Longer septa develop in *Favistina* [shown here as a distinct genus, though Ruth Browne's (1965) conclusion that it grades into *Cyathophylloides* with longer septa is certainly correct] from which develops the amplexoid genus *Crenulites* on one hand and the phaceloid *Paleophyllum* on the other; both are developed from forms with short (*Favistina*) rather than long (*Cyathophylloides*) types of septa. From *Paleophyllum* it is no great step to corals with fewer buds and shorter more conical corallites in which division is less frequent, corallites become shorter, leading to the solitary *Streptelasma* and Streptelasmidae. Probably another line is the colonial rugosan group leading to the Columnariidae, and perhaps further. It is remarkable that in the *Foerstephyllum-Cyathophylloides-Paleophyllum* lineage no cardinal or



Text-figure 1.—Evolutionary relationships of Ordovician coral genera.

1. Cerioid corals; fibrous walls, tabulae, no septal structures.
2. Phaceloid colonies.
3. Cateniform colonies.
    - A. Simple fibrous walls.
    - B. Septal spines; balken develop in the genus.
    - C. Balken replaced by mesocorallites containing tabulae.
4. Crenulate walls: convexities show the beginning of septal structures.
5. Fibrous walls with axial planes broken up into bacular (trabecular) units.
6. Baculae shorter, septa more prominent.

Continued next page

7. Corallites separated by perforate coenenchyme.
8. Walls and septa of solid bacular structure; columellae bacular or of twisted fibres; tabulae between septa.
9. Septa widen, join, leaving no space for tabulae.
10. Numerous septal spines; within the genus the axial plane is replaced by the axial plate, development of epithecae around individual corallites.
11. Septal structures reduced; pores become numerous.
12. Septal structures generally lost; pores extensive.
13. Septa longer, major and minor septa.
14. Septa amplexoid.
15. Septa longer, joining in center of corallite.
16. Phaceloid colonies; septal fibres become specialized.
17. Budding reduced, corallites shorter, more conical, finally, solitary forms.
18. Conical corallites with short septal ridges, deep calices with funnel-shaped layers (tabulae?) at the base.
19. Heliolitid pattern but with corallite walls.
20. Heliolitid pattern, tabulae modified to form apparent corallite walls; beginning of heliolitid "trabeculae".
21. Heliolitid, coenenchyme cystose with prominent heliolitid "trabeculae", commonly radiating from corallites.
22. Continuation of cerioid corals with long septa, but without apparent cardinal or counter areas.

Only some specialized families are indicated; the dotted lines running from *Aulopora* to the *Streptelasmidae* indicate the origin of the Rugosa suggested by Sokolov, 1962.

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counter regions can be recognized, and the same seems to be true of cerioid forms extending to the Devonian *Columnaria* and beyond. On the other hand, the tetracoral symmetry is developed in the Streptelasmidae (or Streptelasmatidae) and is to be seen in one of the earliest solitary rugosan genera of North America, *Lambeophyllum*. However, Sokolov (1962) and Iwanowsky (1972) apparently had not seen Flower (1961), and Sokolov proposed a different relationship involving the concept that (1) the Auloporidae are the common ancestors of the Rugosa and Tabulata (2) that from the Auloporidae a connection can be traced through *Primitophyllum* and *Lambeophyllum* into the Rugosa. *Lambeophyllum* shows cardinal and counter regions but is anomalous; calices are deep, septa are ridges on its interior, and *Primitophyllum* has funnel-like structures instead of tabulae; another possible interpretation is that these funnel-shaped structures are tabulae, conforming to the calices. Here are two divergent hypothesis for the origin of the Rugosa. Can it be that the group is polyphyletic?

We note with approval that Sokolov (1962) removed the Chaetetidae from the corals, and considered them related to the Hydrozoa. Indeed, differences in wall texture between the Tabulata and the Tetradiidae suggest that the Tetradiidae might be a group more related to the Hydrozoa than to the Anthozoa. We have also had reservations concerning the assignment of *Labyrinthites* to the Tabulata, a matter which we must leave for others to investigate.

Sokolov (1962) separated the Heliolititoidea from the Tabulata but retained as a group of equivalent rank within the Anthozoa. This group he divided into three major groups, the Protaraeida, the Heliolitida, and the Proporida. Our observations suggest that the Protaraeida of Sokolov developed from the Tabulata with bacular skeletons. We suggest that the primitive forms are those with tabulae, including *Protrochiscolithus* and *Pycnolithus* which have solid walls, septa, and coenenchyme, and perhaps *Paleoporites* and *Trochiscolithus,* in which these structures are porous. Flower (1961) noted in encrusting forms assigned to *Protrochiscolithus* two types of structure, one in true *Protrochiscolithus,* in which some of the oblique baculi of the septa become vertical centrally and comprise the columella, and another *P. alemanensis,* in which the columella is composed of nonbacular bands forming an intricate and seemingly irregular meshwork. A similar columellar pattern is reported in *Cosmiolithus,* of which we have not had adequate material or illustrations, but if the illustrated vertical spaces with tabulae crossing them are, as we suspect, spaces between bacular septa, *Protrochiscolithus alemanensis* Flower might be assigned to that genus, which would extend its range downward into beds of Middle Richmond (Upper Ordovician) age. More specialized forms are regarded as those in which septa widen and join, leaving no room for tabulae. In *Coccoseris astomata* Flower baculi of the septa become vertical and corallites as such cannot be recognized from sections alone, probably corallites remain as indentations of the surface of the colony, although we have no unabraded surfaces. An investigation was contemplated to inquire whether these forms might be the ancestors of the Alcyonaria.

The true heliolitids, which term we extend broadly to include the Order Heliolitida as used by Sokolov (1962) and including at least part of the Proporida of Sokolov, are corals of a different nature. Instead of having massive trabecular elements the skeleton is seemingly composed of very thin vertical and horizontal elements comprising tabulae, and apparently the corallite walls. A coenenchyme is composed at one extreme of domelike plates, and at the other, instead of such curved plates, a rectilinear pattern of essentially vertical and horizontal elements. Trabeculae are reported as sparse and confined to the younger species of *Propora* and may constitute the thick "stereoplasm" of the distal parts of *Siberiolites* (Sokolov, 1962). Such trabeculae as we have seen in *Propora lambei* (Schuchert) consist of seeming bacular elements, but the fibers are horizontal to an axis and not arranged in a funnel-shaped pattern as in the trabeculae as we know them from *Nyctopora* to *Coccoseris*. These "trabeculae" are honey-yellow in appearance, very fine in texture, and are new structures developed in *Propora*.

Our material is limited, and it is hoped that present investigations can be expanded with more material. Our concern with these forms began with two new corals from the Montoya Group of New Mexico. Of these one, from the Second Value Formation, has the pattern of *Cyrtopora* and is related to the *Cyrtopora* (here named *C. troedssoni*) which Troedsson (1929) figured as *Plasmopora lambei*. It is apparently on the basis of this form that Sokolov (1962), Iwanowski (1972), and Kaljo and Klaaman (1973) recognized *Cyrtophyllum* in North America. Our species are distinct on the basis of several features, but both of these forms show corallites subcircular in section and only faintly angled where a halo of vertical elements in the coenenchyme join the corallite wall. These halos, composed of rays ranging from 20 to 22 in number, end some distance from the corallite walls. Longitudinal sections show a coenenchyme in which there is some variation between uparched domelike plates, between straight vertical linear plates, which may continue for some length but are actually discontinuous, and regions in which the domelike plates change to simple horizontal bands.

We have not been able to find septal structures in our species. However, the apparent corallite walls are finely porous, and some such pores enter the thin dark elements of the halos while others enter the cells of the coenenchyme. We were puzzled by our inability to differentiate corallite walls texturally from the rest of the colony. Some sections show that the tabulae, which are generally transverse, but peripherally may be downcurved into shallow scallops (Pl. 2, fig. 5) actually swing forward and fuse to form the apparent wall. In some parts of the section this fusion is found to be incomplete (Pl. 1, fig. 4). In the coenenchyme the tabulae may divide to form the dome-shaped plates, whose margins apparently fuse again to form the thin vertical elements. From these observations, *Cyrtophyllum* is a colony in which there are no true corallite walls, but that walls are simulated by an amazing forward extension of structures which are completely modified tabulae and which branch to form a coenenchyme. It is a far cry from this form to our oldest corals in which fibrous walls are primitive, and septa develop from them. *Cyrtophyllum* is certainly not related to any tabulate corals as we know them. To what extent can this generalization be applied to other genera of the Heliolitida? Our material is too limited to permit us to say, and the problem is probably more intricate than it first appears. Material of *Plasmopora lambei,* which has the general features of *Propora,* also shows corallites in which there is certainly no wall that can be distinguished from tabular structures, but we have found no region in which, as in parts of our *Cyrtophyllum,* the tabulae can be seen as imperfectly fused entities forming the apparent corallite wall. However, cross sections on the earliest stages of this form show corallites which are less stellate than in later parts and suggest the crenulated margins of the tabulae seen in our *Cyrtophyllum.*

In *Cyrtophyllum devlinae,* n. sp., distal parts of the colony show vertical elements in the coenenchyme which, basally, might be derived from the tabular structures, the dome-shaped plates becoming rectilinear in pattern, but the vertical elements thicken in the distal parts of the colony and in some parts the vertical elements turn into "trabeculae" similar to those of *Propora lambei.* These structures have no relevance to the baculi or "trabeculae" which are composed of fibres arranged in a funnel-shaped pattern, found in the lineage (Text-fig. 1) beginning in *Trabeculites* and continuing through *Nyctopora, Calapoecia* and into the Protaraeida of Sokolov. They are instead textural modifications of vertical elements in the coenenchyme which we believe to be developed from tabular structures.

Our material suggests that the true Heliolitida have hard parts that are completely derived from tabulae. First tabulae swing forward to form a corallite wall and divide in the coenenchyme to form cysts. Second, the dome-shaped cysts become rectilinear or cubical. Third, the vertical elements in the coenenchyme may widen and take on the aspect of the heliolitid "trabeculae." Our observations are incomplete but suggest that *Proheliolites* is related to *Saffordophyllum,* and not to the Heliolitida, for it has fibrous, crenulate corallite walls.

On the other hand *Mcleodea* seems an apparent heliolitid, but it has good corallite walls from which the tabulae of the corallite and the cysts of the coenenchyme are completely distinct (Pl. 2, figs. 1-4).

Our sections show *Plasmopora lambei* Schuchert to be a *Propora,* with some minor reservations. Reasonably, like *Cyrtophyllum,* it has no true corallite wall, but the coenenchyme is composed of dome-shaped plates interrupted by broad "trabeculae". Sokolov (1962) considered *Propora* as a heliolitid genus in which "trabeculae" develop only in Devonian species; yet he figured such structures in the Silurian *Propora conferta* (1962, p. 280, fig. 4). We find this condition in *Propora lambei* of the Ordovician.

Helen Duncan (1956) noted in the Tank Hill Limestone of the Pioche District of Nevada, the earliest coral fauna in North America in which there was some differentiation beyond the limits of *Lichenaria* of the Canadian (Lower Ordovician). The position of this fauna, collected long ago by Edwin Kirk, was uncertain. Lehi Hintze, Ronald Jensen, and Rousseau Flower visited the north end of this range. Later Flower augmented this section slightly from observations at the south end of the same range. A composite summary of these observations involves (1) zone M of Hintze (1952) in black limestones rather than shales, (2) lighter nonresistant weathering beds comparable to the middle and upper Kanosh, low zone N, (3) darker limestones, bluish weathering, with the fauna of the Lehman Limestone, (4) lighter weathering beds containing the coral fauna in two thin bands. [This coral fauna is certainly that of zone O, represented in western Utah by more dolomitic beds in which the corals are more poorly preserved.] (5) yellowish silty beds probably equivalents of the Copenhagen Limestone (6) the Eureka Quartzite.

SYSTEMATIC DESCRIPTIONS

Cyrtophyllum devlinae Flower and Duncan, n. sp.
Pl. 1, figs. 1-4; Pl. 2, fig. 5

Description. — The type and only known colony is mound-shaped, the base missing, 65 mm high and 90 mm from the center to one margin. Corallites radiate slightly; one oblique corallite is 80 mm long.

Corallites are circular in section, 1.5 to 1.8 mm in diameter, with smaller immature individuals rare, separated by a coenenchyme which, between adjacent corallites is between one third and one half the corallite diameter, broader in spaces surrounded by three or four corallites. Rays extend from the corallite walls, 15-22 in number forming radiating halos, but those stemming from adjacent corallites rarely fuse, and in the wider spaces the meshwork is incomplete and tabulae are imperfectly separated. No septal structures have been seen. The rays of the halos are imperfectly hollow, and pores extend in them for short distances, probably continuing, but not uniformly in the plane of any one cross section. Pores also open, though infrequently, into the cells of the coenenchyme.

Tabulae are generally simple or transverse but may curve either up or down in the corallite centers. Tabulae average 16 in a length of 5 mm, and rarely anastomose, but there are zones of crowded tabulae, 1 mm in length, widely spaced, from 6 to 10 mm apart. There tabulae commonly anastomose. As they approach the corallite margin tabulae become crenulate, as in *Crenulites*. The coenenchyme is composed variously of dome-shaped cysts, but where there are vertical linear processes, the cysts become less curved, transverse, and a rectilinear meshwork results. At high magnification it is apparent that the tabulae swing forward, fusing, to form an apparent corallite wall; in some regions (Pl. 1, fig. 4) this fusion is imperfect, as noted in the general discussion. Tabulae divide to form the transverse elements of the coenenchyme, which vary between (1) dome-shaped plates and (2) horizontal plates between solid vertical structures. The vertical bands are long, generally persistent but break up where the section cuts into the incomplete meshwork of the broader areas of the coenenchyme.

Horizontal plates in the coenenchyme are about twice as numerous as are the tabulae, but in the narrow zones of crowded tabulae their number is not increased correspondingly. Basally, the vertical elements of the skeleton resemble the plates, and there seems to be a rectilinear bending and dividing of the tabulae. Distally, the vertical structures become thicker, and in some parts of the corallite they take on a yellow color, have dark axes, and resemble the "trabeculae" of *Propora lambei.* Plate 1, figure 2 is a cross section in which, in the lower part of the figure, the zone of widely-spaced tabulae is encountered, but above, this section passes through one of the zones of crowded tabulae; here some corallites show the scalloped downturned edges of the tabulae.

Discussion. — As noted above, the amazing features of this colony are that its apparent corallite walls are composed of forward projections of the tabulae, that tabulae divide further to form the dome-shaped plates of the coenenchyme which may next form a rectilinear meshwork of horizontal and vertical elements, but that anteriorly the vertical structures widen, and in places take on the aspect of the "trabeculae" of *Propora lambei.*

Only one North American species is known to us which is congeneric and comparable in structure. This is a *Cyrtophyllum* here named *Cyrtophyllum troedssoni.* It is based upon the specimen which Troedsson (1929, pl. 31, figs. 1a, b; pl. 33, figs. 1a, b) figured as *Plasmopora lambei.* The colony which he illustrated has corallites like those of our species in general aspect but ranging slightly smaller, 1.2 to 1.4 mm in diameter. From them extend halos similar in aspect and number to those of *C. devlinae,* but the tendency toward developing a mesh of incompletely separated cells is less marked. In vertical section the coenenchyme is made up of more consistently quadrate cells, plates are more consistently horizontal and vertical elements, and the vertical bands are more consistently continuous, and generally thicker than the horizontal plates. Tabulae are much closer, 28 to 32 in length of 5 mm, and more commonly anastomosing; they are not crenulate peripherally. The type, No. 469 of Troedsson. Mineral. Mus. Univ. Copenhagen, is from the Cape Calhoun beds (Ordovician) of Cape Calhoun, Greenland.

Type and occurrence. — Our holotype, New Mexico Bureau of Mines (NMBM) No. 1607, was collected by David LeMone from the Second Value Formation of the Montoya Group in the southern Franklin Mountains at the edge of El Paso, Texas, near the crest of the Scenic Drive.

Propora lambei (Schuchert) Pl. 3, fig. 1-7

Plasmopora lambei Schuchert, 1900, U.S. National Mus., Proc., vol. 22, p. 154; Roy, S. K., 1941, Field Museum Nat. Hist., Geol., Mem., vol. 2, p. 70, figs. a-f.

Description. — The following description is based upon USNM No. 28140d, the largest of the four syntype colonies. The colony is mound-shaped, 40 mm high, 110 mm across. Corallites are small, averaging 1.2 to 1.5 mm in diameter, subcircular near the base of the colony, but the outlines are indistinct, the margins being cystlike and suggestive of the crenulated margins of tabulae in *Cyrtophyllum;* there the coenenchyme is cystose and narrow; less than half the diameter of the average corallite. Adorally the corallites become increasingly stellate in cross section, but the outlines are indistinct, as it is difficult to separate the cysts of the coenenchyme from possible tabular structures. Corallites remain of the same size, but there is a slight increase in the thickness of the coenenchyme, which in cross section consists of an irregular meshwork of curved plates. Within the coenenchyme, sparse basally, more abundant in distal parts of the colony, are "trabeculae" which in cross section are somewhat irregular in pattern, in general radiate from the corallites, but are irregular, and those of adjacent corallites commonly fail to join. In cross section the "trabeculae" are honey-yellow, and show dark linear axes which are probably nothing more than the axes from which the fine fibers radiate. In longitudinal section, the corallites contain up-arched, rather irregular curved dissepiments commonly anastomosing; corallite walls are not distinct, but nowhere here can we find such incomplete fusion of tabular elements as was observed in *Cyrtophyllum.* The coenenchyme is composed of thin dark domelike plates, intersected by the vertical "trabeculae," but the plates fail to become regular transverse structures producing, with the vertical elements, a rectilinear meshwork such as is common in the higher heliolitids.

We have found 28-34 cystose tabulae, many incomplete, in a length of 5 mm; in the coenenchyme there are more than twice that number of arched plates in an equal length.

Discussion. — The above description is based upon one of Schuchert's syntypes. The largest of these colonies was chosen in order to ascertain whether basal and distal parts of the colony differed, as is reported in some heliolitid corals. Sokolov (1962) reported some significant differences of this sort in the younger species of *Propora* (he mentioned trabeculae in the Devonian forms only, but his text figure shows trabeculae in a Silurian species, *Propora conferta*).

As noted above, the "trabeculae" shown here are unlike true baculi (often called trabeculae also) in the corals from *Trabeculites* through *Nyctopora, Calapoecia* and into the Protaraeida of Sokolov (1962).

Plasmopora lambei was correctly identified by Roy (1941) who added an allied species, which he called *Plasmopora pattersoni.* Troedsson's *P. lambei* (1929, p. 119, pls. 31, 32, 33) is a *Cyrtophyllum.* Teichert's *P. lambei* (1937, p. 53, pl. 4, fig. 13; pl. 5, figs. 1, 2) is a different form, with a narrow coenenchyme, more like early stages of *Siberiolites* or our genus *Mcleodea.* Hume (1925) identified *P. lambei* from the Ordovician Liskeard Formation of the Lake Timiskaming region but his description and illustration do not afford enough evidence to determine the generic position in the current more elaborate classification of the heliolitids (Sokolov, 1962). Bolton (1972) figured several heliolitids which he referred to *Propora* spp. scattered throughout the formations from the Vaureal to the Jupiter (Ordovician-Silurian) but illustrations are of too small a magnification for evaluation, and there are no descriptions.

In some respects *P. lambei* has a coenenchyme and corallites more like those of *Plasmoporella kiaeri* as figured by Sokolov (1962) than *Propora conferta* or *P. magna* but is closer to *Propora* in the development of the remarkable trabeculae.

Type and occurrence. — Syntypes, USNM No. 28140-a-d. Of these, we select No. 28140-d as the lectotype, as this is the largest colony and the only one in which cross sections were taken both of basal and distal parts of the colony. From Ordovician beds of Silliman's Fossil Mount (Miller, *et al.,* 1954), Frobisher Bay, Baffin Island, Canada.

Genus **MCLEODEA** Flower and Duncan, n. gen.

Type species: *Mcleodea loisae* Flower and Duncan, n. sp.

Description. — This is an apparent heliolitid in which corallites are subcircular, angled slightly outward where rays extend, commonly joining one corallite to another; spaces between adjacent corallites are one-fourth to one-third the diameter of the corallites; but are slightly broader at the corners surrounded by three or four corallites. There are sparse septal spines, short, evidently distant. Longitudinal sections show tabulae transverse, or slightly curved upward in the centers. The coenenchyme at its narrowest shows close horizontal dissepiments between two corallites; but, in the widest spaces, form irregular columns of anastomosing dome-shaped plates. Corallite walls appear granular (direction of fibres may be lost by recrystallization.) The transverse elements terminate at the corallite walls, do not swing forward as in *Cyrtophyllum,* forming a false corallite wall. Cysts of the coenenchyme are slightly thicker and darker but again terminate at the corallite wall.

Discussion. — As suggested by David Budge (personal communication), this coral resembles *Siberiolites* Sokolov in the large rounded corallites and the narrow coenenchyme. However, *Siberiolites* forms high mound-shaped to ramose colonies, and distally the coenenchyme widens and seems to be composed of solid linear elements, possibly true trabeculae or possibly the very different "trabeculae" seen in *Propora lambei* (Schuchert).

Mcleodea loisae Flower and Duncan, n. sp. Pl. 2, figs. 1-4

Description. — The holotype is an incomplete cerioid colony with a maximum height of 60 mm, and 56 mm across but was probably over 100 mm in diameter. Corallites are circular in cross section, faintly angled outward, where 10 to 13 rays extend into the coenenchyme. Corallites average from 1.5 to 1.7 in diameter, but extremes range from 1.2 (obviously immature, smaller budding individuals), to 1.8 mm. Short septal spines occur but are scarce; evidently they are widely spaced vertically; the number of columns of spines cannot be readily estimated; one corallite suggests that there may be as many as 24 columns. Ten to 13 rays extend from each corallite. They are irregular in position and do not form a prominent halo as in *Cyrtophyllum;* they outline cells. Ordinarily there is only one cell between adjacent corallites, but more are developed in the centers of groups of three, four, or five corallites.

Tabulae are transverse or may arch upward slightly in the centers of the corallites. Anastomosing of tabulae is rare; tabulae occur six to nine, rarely ten in a length of 5 mm. No zones of crowded tabulae were noted. The coenenchyme consists of horizontal thin plates where the corallites are closest together, but in widened spaces, is surrounded by three to five corallites. The coenenchyme is composed of dome-shaped plates, irregular, fusing erratically, and spaced 19 to 22 in length of 5 mm.

Under high magnification (Pl. 2, fig. 3) the longitudinal sections show corallite walls of granular texture; presumably an original fibrous structure was lost by recrystallization. In some parts of the colony a thin dark axis is seen in the wall; in other parts this band lies on or close to the outside of the corallite wall. Tabulae are thinner and darker, distinct in texture, and terminate where they join the corallite wall. Diaphragms of the coenenchyme behave in the same way; they are slightly thicker and darker than the tabulae.

Discussion. — As noted in the generic discussion, this coral shows true walls from which tabulae and cyst plates of the coenenchyme are distinct, in contrast to the condition of *Cyrtophyllum,* in which there is no true corallite wall. Only one specimen has been figured previously to which our form seems at all similar. This is the specimen figured by Teichert (1937, p. 53, pl. 4, fig. 13; pl. 5, fig 1, 2,) as *Plasmopora lambei.* His plate 5, figure 13 is apparently inverted as corallites diverge below and tabulae are arched down rather than up in the centers of the corallites. His form has tabulae closer and more commonly anastomosing, and from measurements indicated, the corallites average 1.08 mm instead of 1.5 to 1.7 mm. Teichert's form is from the Ordovician of Iglulik Island, Canada, representing beds of either Red River or Richmond age.

Type and occurrence. — Holotype NMBM No. 1608, from the coral bed of the Aleman Formation, Montoya Group, from exposures below the crest of the Scenic Drive, El Paso, Texas.

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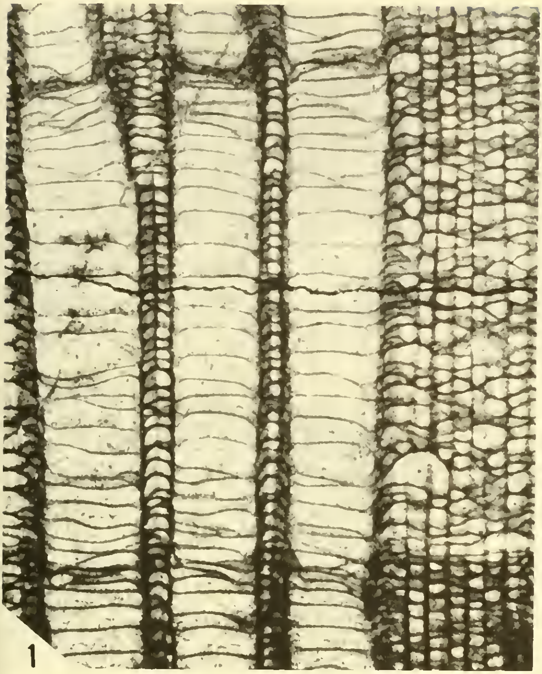
EXPLANATION OF PLATE 1

Figure

1-4. **Cyrtophyllum devlinae** Flower and Duncan, n. sp.

1. Vertical section, × 10, showing corallites with distant crowded zones of tabulae, the coenenchyme in which dome-shaped plates merge into more consistently horizontal structures between vertical plates, the vertical plates are discontinuous where the section passes through the wider parts of the coenenchyme. Two of the narrow zones of crowded tabulae are shown.
2. Cross section, × 9, showing corallites with halos. The darker upper part of the figure represents a part of the section passing through the narrow zone of crowded tabulae; here some indication of the peripheral scalloping of the tabulae can be seen.
3. Cross section, × 14, showing homogeneity of apparent corallite walls with the halos of the coenechyme. Some pores are seen extending a short way into the rays of the halos. The section intersects some of the peripheral scallops of the tabulae in the lower corallite.
4. Vertical section, × 21, showing a region in which the forward marginal projections of the tabulae forming an apparent corallite wall are incompletely fused. See also Pl. 2, fig. 5.

All from the holotype, NMBM No. 1607, Second Value Formation Montoya Group, southern Franklin Mountains near El Paso, Texas.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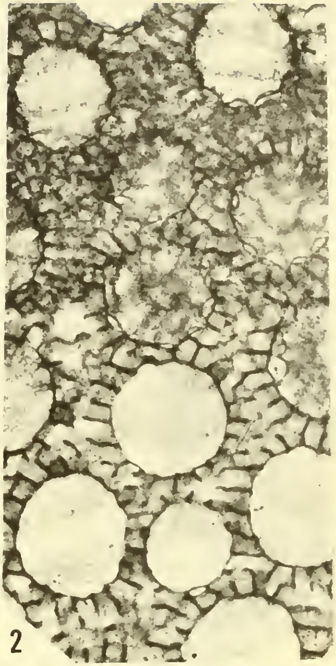
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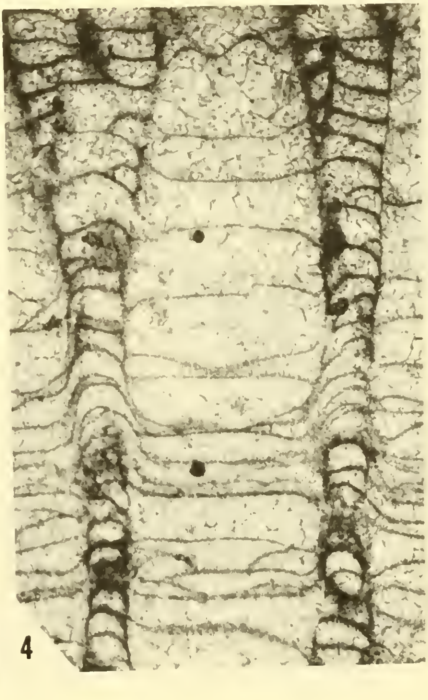
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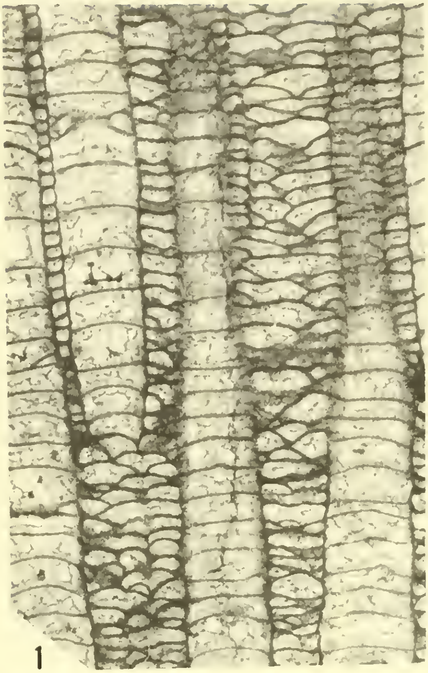
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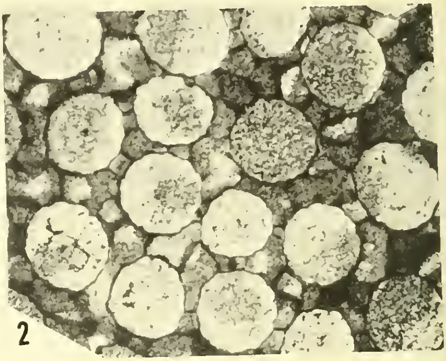
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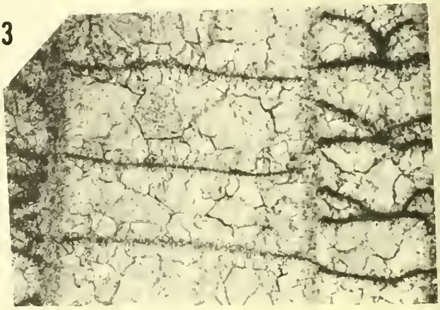
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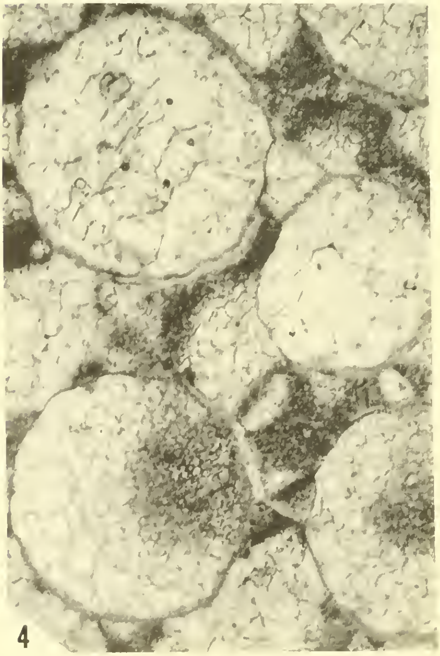
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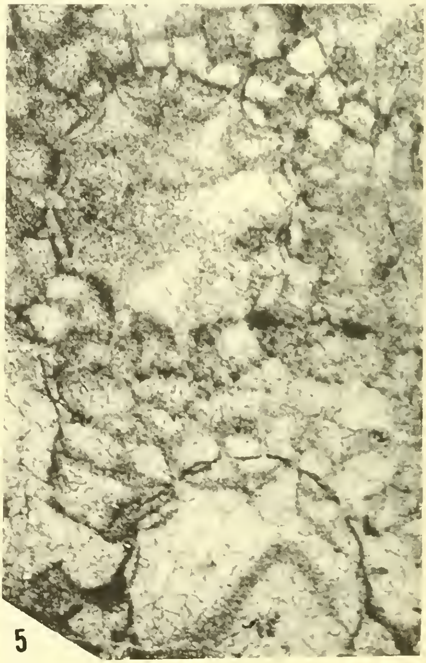
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EXPLANATION OF PLATE 2

Figure

1-4. **Mcleodea loisae** Flower and Duncan, n. sp.

1. Vertical section, × 7, showing typical tabulae, plates of the coenenchyme domelike in the broader areas, more horizontal in the narrower regions between corallites, but lacking consistent vertical bands in the coenenchyme.
2. Cross section, × 7, showing typical corallites some showing septal spines and narrow coenenchyme.
3. Longitudinal section, × 22.5, showing tabulae and cysts of the coenenchyme terminating at corallite wall, which differs from both in greater thickness, lighter color, and different texture.
4. Cross section, × 21, showing significant thickness of the corallite wall, some septal spines, and texture of plates in the coenenchyme. NMBM no. 1608, Coral zone of the Aleman Formation, from near the Scenic Drive, El Paso, Texas.

5. **Cyrtophyllum devlinae** Flower and Duncan, n. sp.

Cross section through one of the zones of crowded tabulae, × 14, showing crenulate edges of the tabulae and some pores extending into the rays of the halos. See Plate 1.

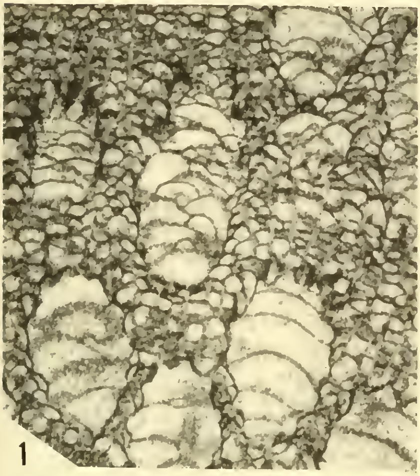
EXPLANATION OF PLATE 3

Figure

1-7. **Propora lambei** (Schuchert)

1. Nearly longitudinal, slightly oblique section, × 7, showing anastamosing tabulae, irregular cystose coenenchyme with a few "trabeculae".
2. Longitudinal section, × 21, with corallite on left, and coenenchyme with cystose plates and a few vertical "trabeculae".
3. Cross section, × 21, through the latter part of the colony, showing a corallite with an irregular stellate and indistinct boundary, with, below the corallite, some "trabeculae".
4. Cross section, × 31, with the edge of a corallite on the left, and showing "trabeculae" extending from it, with light outer parts and thin, dark, linear axes.
5. Cross section, × 10, taken near the base of the corallite; here corallites are more nearly circular in section, cystose margins suggest the crenulated margins of tabulae, as in *Cyrtophyllum devlinae,* and cystose coenenchyme with few "trabeculae".
6. Two corallites, × 17, from the mature part of the colony showing indistinct stellate outline, cystose coenenchyme, and "trabeculae" radiating from the corallites.
7. Cross section of a corallite, taken near the base of the colony. Showing more circular outline, one "trabecula" on the upper right, cystose boundary of the corallite, and traversing several tabulae.

All sections from lectotype, USNM No. 28140d, from Mt. Silliman, Frobisher Bay, Baffin Island, Canada.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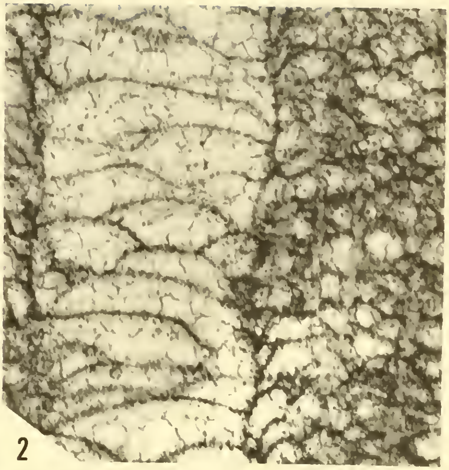
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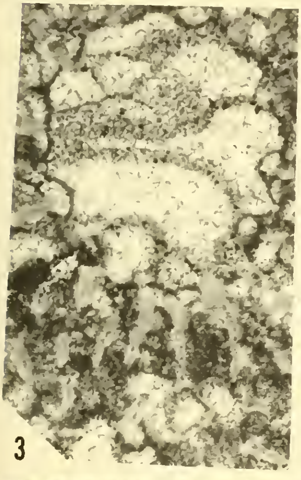
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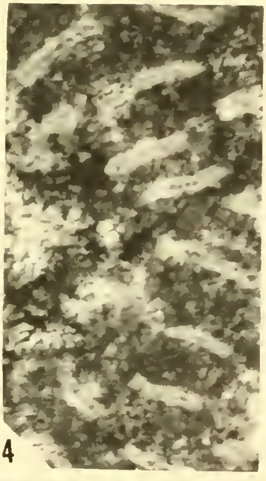
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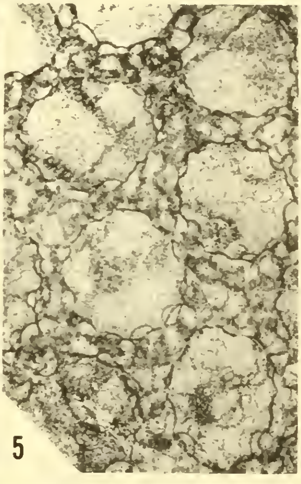
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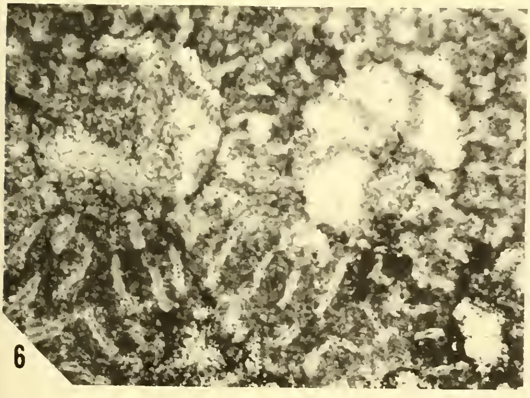
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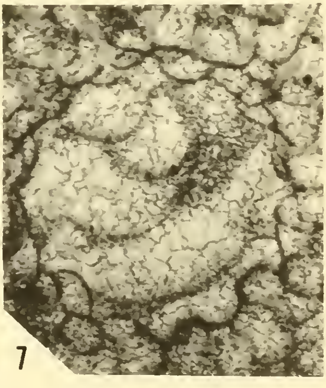
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A MAQUOKETA-LIKE MOLLUSCAN COMMUNITY IN THE BRASSFIELD FORMATION (EARLY SILURIAN) OF ADAMS COUNTY, OHIO

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ABSTRACT

A diminutive fauna composed primarily of molluscs has been found in the Brassfield Formation (Early Silurian) of Adams County, Ohio. This fauna is similar in size and taxonomic composition to the Late Ordovician Maquoketa "Depauperate Zone" fauna from Illinois, Iowa, and Missouri. In addition, the dominant species of these two fauna are the same—*"Plagioglypta" iowaensis* (James), *Palaeoneilo fecunda* (Hall), *Nuculites neglectus* (Hall), and *Liospira micula* (Hall).

Several species were previously unknown from the Brassfield and from rocks younger than Upper Ordovician: *Deceptrix scofieldi* (Ulrich), *Nuculites neglectus* (Hall), *Palaeoneilo fecunda* (Hall), *Praenucula albertina* (Ulrich), and *Lyrodesma* sp.

The community structure of the diminutive Brassfield and basal Maquoketa faunas is also similar. They both contain a majority of detritus feeders and browsers with some predatory cephalopods. The major taxonomic groups are palaeotaxodont bivalves, archeogastropods, hyolithids, "scaphopods" and, orthoconic cephalopods. Because the major adaptive types and taxonomic composition of these two communities are so similar, the environments must have also been similar. That these environments were not synchronous is supported by the presence of the Early Silurian conodont *Icriodina irregularis* Branson and Branson in the Brassfield and the stratigraphic position of the Brassfield Formation which unconformably overlies Upper Ordovician formations such as the Preacherville and Elkhorn, usually time correlated with the Maquoketa (Berry and Boucot, 1970).

The basal Maquoketa fauna is thought to be ancestral to the diminutive Brassfield fauna.

INTRODUCTION

The Brassfield Formation (Early Silurian) of Ohio, Indiana, and Kentucky is sparsely fossiliferous at most of its outcrops and usually yields few mollusks. However, in Adams County, Ohio, several outcrops of alternating shales and carbonates contain an abundant, diminutive molluscan fauna. This fauna has not been found elsewhere in the known outcrop area of the Brassfield. Most of these fossils range from 1 to 5 mm in greatest dimension, occurring abundantly only in the carbonates. This fauna is continuous laterally within the narrow outcrop belt of the Brassfield from Jacksonville to West Union, Ohio, and is distributed through a 4.5 m vertical sequence.

The most abundant faunal elements are molluscan — bivalves, gastropods, "scaphopods" (see discussion of *"Plagioglypta" iowaensis* (James)), and hyolithids. These fossils are strikingly similar in size and taxonomic composition to the so-called Depauperate fauna of the basal Maquoketa (Late Ordovician) which crops out primarily in Illinois, Iowa, and Missouri. Several authors (Ladd, 1925, 1929; Ojakangas, 1959; Bretsky and Bermingham, 1970; Snyder and Bretsky, 1971) have studied the fauna from the basal Maquoketa; this is the first study reporting this type of fauna from the Brassfield.

This investigation attempts to analyze these two faunas to determine the extent of their similarity, to make paleoecological inferences from the fauna, and to evaluate the significance of these two heterochronous, but taxonomically homogeneous communities.

William Harrison authored the systematic paleontology of the bivalves; and Linda Harrison, the archeogastropods and hyolithid. The remainder is jointly authored.

ACKNOWLEDGMENTS

We both are grateful to Kenneth E. Caster for continued encouragement and constructive criticism. William Harrison's work on the bivalves of the Brassfield was part of his Ph.D. dissertation, conducted under Caster's guidance at the University of Cincinnati. John Pojeta, Jr., of the United States Geological Survey, also served as an adviser and generously gave his time and assistance at the United States National Museum. Linda Harrison wishes to thank Ellis L. Yochelson of the U.S. Geological Survey for his advice and assistance at the United States National Museum. His knowledge and enthusiastic support were invaluable. Peter Bretsky and Jeffrey Levinton of the State University of New York at Stony Brook assisted us in trying to interpret survivorship curves. Bretsky also critically reviewed the manuscript. Richard Bambach thoughtfully reviewed the manuscript.

We would also like to thank the following people and institutions for lending us type and study specimens: R. L. Batten of the American Museum of Natural History (AMNH); F. S. Collier of the United States National Museum (USNM); R. A. Davis of the University of Cincinnati (UCGM); B. M. Bell of the New York State Museum; H. L. Strimple of the University of Iowa and R. L. Ethington of the University of Missouri (UMMG).

Text-figure 1. — Known outcrop areas of the basal Maquoketa and diminutive Brassfield faunas.

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COMPARISON OF THE BRASSFIELD AND BASAL MAQUOKETA DIMINUTIVE FAUNAS

The dominant species of the diminutive Brassfield fauna (primarily molluscan) are markedly smaller than congeneric specimens of the same age in central and eastern North America. Most specimens measure 1 to 5 mm in greatest dimension. This is also true of the basal Maquoketa fauna (Snyder and Bretsky, 1971; Ladd, 1929).

There are a few notable exceptions to the smallness of the population. Orthoconic cephalopods 10 cm in length were found in the basal Maquoketa beds (Snyder and Bretsky, 1971, p. 234); in the diminutive Brassfield fauna, specimens 4 cm long were found.

Diminutive faunas are not unique and have been described by several authors (Ball, 1935; Branson, 1930; Fisher, 1951; Loomis, 1903; Tasch, 1953; Trechmann, 1913). At the specific level, the basal Maquoketa fauna is unique; however, it has been shown to be similar at familial and superfamilial levels to several later Paleozoic faunas (Bretsky and Bermingham, 1970, p. 919, Table 2).

Both the basal Maquoketa and the Brassfield diminutive faunas are characteristically dominated by a few molluscan species which occur in abundance. In both communities, palaeotaxodont bivalves, archeogastropods, orthoconic cephalopods, "scaphopods", and hyolithids are the primary faunal constituents. Secondary constituents include trilobites, crinozoans, bryozoans, ostracodes, tentaculites, and sponges. Only the basal Maquoketa is known to contain polyplacophorans.

The two most abundant palaeotaxodonts in the Brassfield diminutive fauna are *Palaeoneilo fecunda* (Hall) and *Nuculites neglectus* (Hall) both infaunal deposit feeders. These two species are also the two most abundant nuculoids in the basal Maquoketa fauna and were extensively sampled and analyzed by Snyder and Bretsky (1971). Several other writers have described the basal Maquoketa fauna (Ladd, 1925, 1929; Ojakangas, 1959; Wang, 1949; Bretsky and Bermingham, 1970).

Species of the primary fossil groups listed above which have been found in the basal Maquoketa and diminutive Brassfield faunas are listed in Table 1. Those which are dominant faunal elements (that is, those which occur most abundantly), are indicated by an asterisk.

Table 1. Basal Maquoketa and diminutive Brassfield species of primary fossil groups

Taxa	Maquoketa				
	Ojakangas (1959)	Ladd (1929)	Johnson (1939)	Snyder and Bretsky (1971)	Brassfield (this study)
"Ctenodonta" pulchella Ulrich				x	
Deceptrix scofieldi (Ulrich)					x
**Nuculites neglectus* (Hall)	x	x	x	x	x
Lyrodesma sp.					x
Orthdesma approximatum Foerste	x				
"Palaeoconcha?" hamburgensis (Walcott)				x	
Palaeoconcha obliqua (Hall)	x	x	x	x	
Palaeoconcha ohioensis (Bassler)					x
**Palaeoneilo fecunda* (Hall)	x	x	x	x	x
Praenucula albertina (Ulrich)				x	x
Praenucula sp.				x	
Genus A aff. *"Ctenodonta" longa* (Ulrich)					x
Michelinoceras sociale (Hall)	x	x	x		
Orthoconic cephalopod					x
**"Plagioglypta" iowaensis* (James)	x	x	x		x
"Bellerophon" lirata Hall		x	x		
"Bellerophon" patersoni Hall		x	x		
Bucanella (Plectonotus) conradi Hall		x	x		
Bucanella (Plectonotus) sp.					x
Bucania? sp.					x
Cyclonema (Cyclonema) humorosum Ulrich			x		
Cyclonema (Cyclonema) bilex Conrad			x		
Cyclonema (Dyeria?) sp.					x
"Cyclora" depauperata (Hall)		x	x		x
"Cyclora" minuta Hall	x				
"Cyclora" sp.		x			
"Cyclora" cf. *"C." pulchella* Miller					x
Cyrtolites carinatus Miller	x				
Cyrtolites retrorsus var. *fillmorensis* Ulrich and Scofield	x				
Holopea symmetrica Hall	x				
Holopea? sp.					x
Holopea cf. *H. symmetrica* Hall					x
**Liospira micula* (Hall)	x	x	x		x
Loxoplocus (Donaldiella) sp.					x
Loxoplocus (Lophospira) tropidophora Meek	x				
Loxoplocus (Lophospira?) sp.					x
Murchisonia (Hormotoma) trentonensis Ulrich and Scofield	x				
Murchisonia (Hormotoma) sp.		x			
Murchisonia (Murchisonia) sp.					x
Raphistomina rugata Ulrich and Scofield	x				
Tropidodiscus subacutus Ulrich	x				
Tropidodiscus sp.					x
Elegantilites? sp.					x
"Hyolithes" parviusculus (Hall)	x	x	x		

The apparent total greater diversity of the basal Maquoketa is in large part due to the larger outcrop area and the greater number of studies.

COMPARISON OF THE LITHOLOGIES OF THE DIMINUTIVE BRASSFIELD AND BASAL MAQUOKETA BEDS

The lithology, paleontology and stratigraphy of the Brassfield Formation were first investigated extensively by Foerste (1885, 1888, 1895, 1896, 1901, 1906, 1909, 1919, 1923, 1931, 1935). His remained the only authoritative work on the unit until the 1960's. More recently, O'Donnell (1967), Rexroad (1965), and Gray and Boucot (1972) have described the Brassfield Formation as it crops out in Indiana, Ohio, and Kentucky.

The Brassfield Formation is considerably thicker in its eastern exposures in Ohio and Kentucky (generally between 7 and 10 m, exceeding 15 m in several sections near Adams County, Ohio,) than in the western outcrops in Indiana and Kentucky (generally between 1 and 3 m, rarely greater than 5 m).

The stratigraphic terminology used to describe the Brassfield lithology follows O'Donnell (1967). The lithology of the Brassfield varies laterally and vertically. In Adams County, Ohio, the lowermost Belfast Member consists of calcareous or dolomitic thinly bedded shales and siltstones. Overlying the Belfast the "lower massive unit" lithology is thickly bedded limestone or dolomite with occasional nodular chert beds. The "upper thinly bedded unit" overlies the "lower massive unit" and consists of alternating beds of shale and limestone or dolomite; these beds are overlain by the uppermost Brassfield Member, the Noland, with alternating shale and carbonate beds.

It is within the "upper thinly bedded unit" that the diminutive Brassfield fauna occurs. The bottom of the beds containing this fauna is approximately 10 m above the base of the Brassfield. The fauna is found in shale but most abundantly in coarsely crystalline or ferruginous carbonates containing small quantities of pyrite, and varying amounts of clay. In the ferruginous carbonates, limonite occurs as fossil replacement and small pellets which give the rock an oolitic appearance.

The fauna of the crystalline carbonates is preserved as recrystallized shells which have been filled with phosphatic sediment. Preservation in the ferruginous carbonates is by limonitic infiltration of shells (particularly bivalves) and some phosphatic steinkerns (especially gastropods and "scaphopods"). Fossils thus preserved were removed from the matrix by solution with 15% acetic acid.

In most coarsely crystalline carbonates, the fauna comprises the allochemical constituents, there being only little or no terrigenous sediments. The coarseness of the carbonates is primarily due to recrystallization of the fine-grained lime mud matrix. Most of the fauna ranges in size from 0.25 mm to 5 mm in the ferruginous carbonate, with cephalopods measuring to 40 mm in length. The fauna of the coarsely crystalline carbonates is similar in size; however, uncommon accumulations of slightly larger brachiopods occur (5-12 mm) which are probably not sympatric with the diminutive fauna.

Some post-mortem movement of the fossils occurred. Evidence of such movement is found in primary sedimentary structures. The only horizon which shows large primary sedimentary structures characteristic of wave or current action is one coarsely crystalline carbonate which is ripple marked, with wave lengths of approximately one meter. One ripple set measured 93 cm from crest to crest, 7.5 cm from trough to crest. The ripples are symmetrical. Several of the thicker limestone beds show low angle cross-stratification. Some fossils such as bryozoans show preferred orientation on some ferruginous carbonate surfaces. There is, then, evidence for current action.

The stratigraphy and lithology of the Maquoketa have been investigated by several authors, including Ladd (1925, 1929) Johnson (1939) Bromberger (1968), and Ojakangas (1959). According to Ladd (1929, p. 44) the basal Maquoketa crops out primarily in Iowa, Illinois, and Missouri, but also occurs in parts of Wisconsin, Michigan, Kansas, Arkansas, and Oklahoma (Text-figure 1). Varying from shales to carbonates, it consistently contains phosphatic minerals, pyrite, and limonite.

In Missouri, the basal Maquoketa is a pyritic, limonitic shale (Johnson, 1939, p. 127). In Iowa and Illinois, Ojakangas (1959, p. 15) described the basal Maquoketa as a dark shale with pyrite and phosphatic pebbles. At Scales Mound, Iowa, he found "excessive amounts of pyrite, not only as isolated crystals, but also as the cementing agent of the rock." In Fayette and Clayton counties, Iowa, Glenister (1957, p. 716) described these beds as "slightly calcareous, highly ferruginous clay, and they contain numerous phosphatic pebbles and pyrite crystals." Snyder and Bretsky (1971, p. 228) described the lithology of the basal Maquoketa in Iowa and Illinois as "a highly phosphatic (hydroxylapatite) and ferruginous carbonate (mostly dolomitic)". They felt that the fauna was deposited in place, with fairly little post-mortem winnowing. They acknowledged (p. 912) that the preservation of "scaphopods" is patchy and clumped but suggested that only moderate bottom currents would be needed to remove the shells from the sediments and "wash them into shallows and hollows." They attributed the disturbed nature of the beds to biogenetic reworking. Tasch (1953) emphasized the possibility of size sorting as it might reflect current activity.

Some current action is evident in both the basal Maquoketa and the Brassfield beds. Because the Brassfield ripple marks are symmetrical about the crests, the currents producing them may well have been oscillatory, capable of abrading and disarticulating specimens and perhaps removing some larger specimens by breakage or selective transport, but did not remove most of the small mollusks far from their living environment.

COMMUNITY STRUCTURE OF THE DIMINUTIVE FAUNA

In Walker and Laporte's (1970) comparison of Ordovician and Devonian communities, the similarity of the fossil assemblages at high taxonomic levels was attributed to environmental control of the major adaptive types. Considering that the Brassfield and Maquoketa faunas contain the same species as dominant faunal elements, and that other members of the molluscan community are congeneric, it is reasonable to assume that they both evolved in response to very similar environmental conditions. Following the format of Walker and Laporte (1970, p. 935), Table 2 lists the genera and species common to both the Maquoketa and Brassfield faunas along with their inferred modes of life. Modes of life are inferred by analogy with living relatives and on the basis of functional morphology (Yonge, 1939; McAlester, 1968; Walker, and Laporte, 1970; Marek and Yochelson, 1964).

The taxonomic composition of the two communities is similar to those of Bretsky's (1968, 1969) stable nearshore environment and Ziegler (1965) and Ziegler, Cocks, and Bambach's (1968) *Lingula* community.

For both the basal Maquoketa and diminutive Brassfield communities, the most diverse group of organisms is the archeogastropods, and most of the taxa are detritus feeders and browsers. This diverse gastropod assemblage suggests the presence of plants (Johnson, 1964, p. 123) which Bretsky and Bermingham (1970) interpreted as algal stands.

Ladd (1929, p. 366) described a similar nearshore fauna in Michigan. He found the fauna of the Bill's Creek Shale in the lowermost Richmondian (Upper Ordovician strata) of Michigan so similar to the "depauperate zone" that he believed it represented an "upward continuation" of it. Comparing the Bill's Creek and "depauperate" Maquoketa fauna, he stated, "To be sure, there are minor faunal and lithologic differences but such are to be expected in areas so widely separated. The differences total less than the differences existing between certain sections in different parts of the Iowa belt." He listed the following species (names do not reflect current taxonomic philosophy) from the Bill's Creek Shale but did not figure them:

Table 2.—Brassfield and Maquoketa community members and their inferred modes of life.

Major Taxon	Community Members Maquoketa/Brassfield	Relationship to Substrate			Feeding Type		
		Nektobenthonic	Epifaunal	Infaunal	Deposit feeder	Browser	Predator
"Scaphopoda"	*"Plagioglypta" iowaensis/"P." iowaensis*			x	x		
Cephalopoda	*Michelinoceras sociale/cephalopod*	x					x
Palaeotaxodont Bivalvia	*Nuculites neglectus/N. neglectus*			x	x		
	Paleoconcha/Paleoconcha			x	x		
	Palaeoneilo fecunda/P. fecunda			x	x		
	Praenucula albertina/P. albertina			x	x		
Archeogastropoda	*Bellerophon/Bucania?*		x			x	
	Bucanella (Plectonotus)/B. (Plectonotus)		x			x	
	Cyclonema (Cyclonema)/ C. (Dyeria?)		x			x	
	"Cyclora" depauperata/ "C." depauperata		x			x	
	Cyrtolites/Cyrtolites		x			x	
	Holopea/Holopea		x			x	
	Liospira micula/L. micula		x			x	
	Murchisonia (Murchisonia)/M. (Murchisonia)		x			x	
	Tropidodiscus/Tropidodiscus		x			x	
Hyolithida	*"Hyolithes" parviusculus/Elegantilites?* sp.		x		x		

Glossograptus sp.
Lingula changi Hussey
Dalmanella sp.
Ctenodonta fecunda (Hall)
Bellerophon patersoni Hall
Pleurotomaria (Lophospira) depauperata? (Hall)
Hormotoma sp.
Liospira micula (Hall)
Coleolus sp.
Orthoceras sociale Hall
Isotelus cf. *I. iowaensis* (Owen)
Drepanodus acinociformis, n. sp.

Ladd (1929) also discussed the similar diminutive fauna of the Arnheim Formation [oldest unit in the Richmondian (Upper Ordovician)] in Ohio. He listed these species as having been identified by Shideler:

Cornulites, n. sp.
Dalmanella sp.
Zygospira modesta Hall
Ctenodonta sp.
Clidophorus faberi Miller
Clidophorus fabula (Hall)
Microceras inornatum Hall
Cyclora depressa Ulrich
Cyclora hoffmanni Miller
Cyclora minuta Hall
Cyclora parvula (Hall)
Hyolithes parviusculus (Hall)

Ladd stated that this was suggestive of the Maquoketa. Shideler pointed out that there were "similar but patchy occurrences, [of this diminutive fauna] locally developed . . . in the Mt. Auburn, the Corryville, the Mt. Hope [all Maysvillian] and down as far as the Mohawkian in Kentucky" (written communication with Ladd, 1927). None of these faunas so closely resemble the Maquoketa "depauperate" fauna as does the Brassfield diminutive fauna.

PALEOECOLOGY OF THE BRASSFIELD AND BASAL MAQUOKETA DIMINUTIVE FAUNAS

Based on the faunal associations and sedimentary characteristics, Bretsky and Bermingham (1970) and Snyder and Bretsky (1971) interpreted the environmental setting of the basal Maquoketa as a shallow, warm epeiric sea, with somewhat restricted circulation. They interpreted the substrate as a "soft, gently undulating, organically-rich carbonate mud, undergoing penecontemporaneous replacement by dolomite and phosphate" (p. 229). Snyder and Bretsky cited the paleomagnetic data concerning the position of the Ordovician paleoequator of Opdyke (1962), Ma (1962), and Fell (1968) in support of their warm water interpretation.

Following Johnson's (1964, p. 123) suggestion, that the fairly diverse gastropod fauna, dominated by a few species, indicates the presence of plants, Bretsky and Bermingham (1970) thought that algal stands might be expected because of the shallow water, subtropical environment. They noted that algal stands might have locally produced higher organic content, limited water circulation, and thereby increased the possibility of locally higher salinities and oxygen deficient environments in which very small amounts of sulfides precipitated.

Parts of the Brassfield beds indicate current action. Most of the bivalves are disarticulated, and some show abrasion, especially *Nuculites neglectus* (Hall). Some of this breakage undoubtedly occurred in the disaggregation and sieving of the delicate remains. The number of left and right valves of bivalves in the Brassfield are similar (Table 3). This suggests that the currents which affected this fauna may have been oscillatory. Kornicker, Wise and Wise (1963), Martin-Kaye (1951), and Boucot, Brace, and DeMar (1958) discussed the behavior of bivalve shells.

Table 3. — Comparison of number of left, right, and articulated palaeotaxodont valves. (Combined data from four separate carbonate horizons in the Brassfield Formation.)

Species	Right	Left	Articulated
Deceptrix scofieldi	9	19	45
Palaeoneilo fecunda	654	640	109
Nuculites neglectus	40	40	0
Lyrodesma sp.	131	107	23
Palaeoconcha ohioensis	14	14	13
Praenucula albertina	18	19	0
Genus A. aff. "*Ctenodonta*" *longa*	14	11	0

The Brassfield fauna seems to have lived in an area of somewhat better circulation (at least at times) than the Maquoketa. We feel that the limiting factors of a high stress environment in the warm, shallow, nearshore epeiric sea were as significant as those of the Maquoketa basal beds, as evidenced by the similar faunal response. With so many faunal similarities, it is unlikely that the living environments of the basal Maquoketa and diminutive Brassfield faunas were grossly different.

The only Brassfield species studied which is not related to specimens found in the Maquoketa are the conodonts. *Icriodina irregularis* Branson and Branson and several species of *Paltodus* are part of the diminutive Brassfield fauna and were reported by Rexroad (1965) from the Brassfield in Adams County, Ohio. They have not been found in strata older than Early Silurian. The conodonts of the Maquoketa described by Glenister (1957) do not include these forms.

Except for the conodonts, the Brassfield diminutive fauna is similar to the Upper Ordovician faunas in taxonomic composition. Apparently in response to similar environments, both faunas are similar in community structure and diminutive size. What were the environmental causes which produced the small size of such faunas? Suggested physical causes include current sorting and selective shell breakage (Tasch, 1953). Excess hydrogen sulfide, iron, and phosphate, too little oxygen, and fluctuations in salinity as well as post-depositional solution of larger shells have been suggested as chemical agents (Ladd, 1925, 1929; Ojokangas, 1959; Bretsky and Bermingham, 1970).

Snyder and Bretsky (1971) suggested a genetic size control, whereby in such a high-stress environment, those species having characteristics of early maturity and high fecundity would be selected for, producing a paedomorphic community. They have suggested that other "dwarfed" or diminutive faunas may also be paedomorphic. Age-selective predation may have contributed to the lack of large shells.

COMPARISON OF GROWTH-MORTALITY DATA

Many investigators have discussed the use of size-frequency distributions in reconstructing faunal characteristics and environmental settings (Boucot, 1953; Boucot, Brace, and DeMar, 1958; Olson, 1957; Craig and Hallam, 1963; Craig and Oertel, 1966; Hallam, 1967; Kornicker, Wise, and Wise, 1967).

Snyder and Bretsky (1971, p. 236) constructed size-frequency distributions and survivorship curves (for populations of palaeotaxodonts obtained by bulk sampling the basal Maquoketa) using the growth-rate relationship derived by Levinton and Bambach (1970, p. 99):

$$D = s \ln(T+1)$$

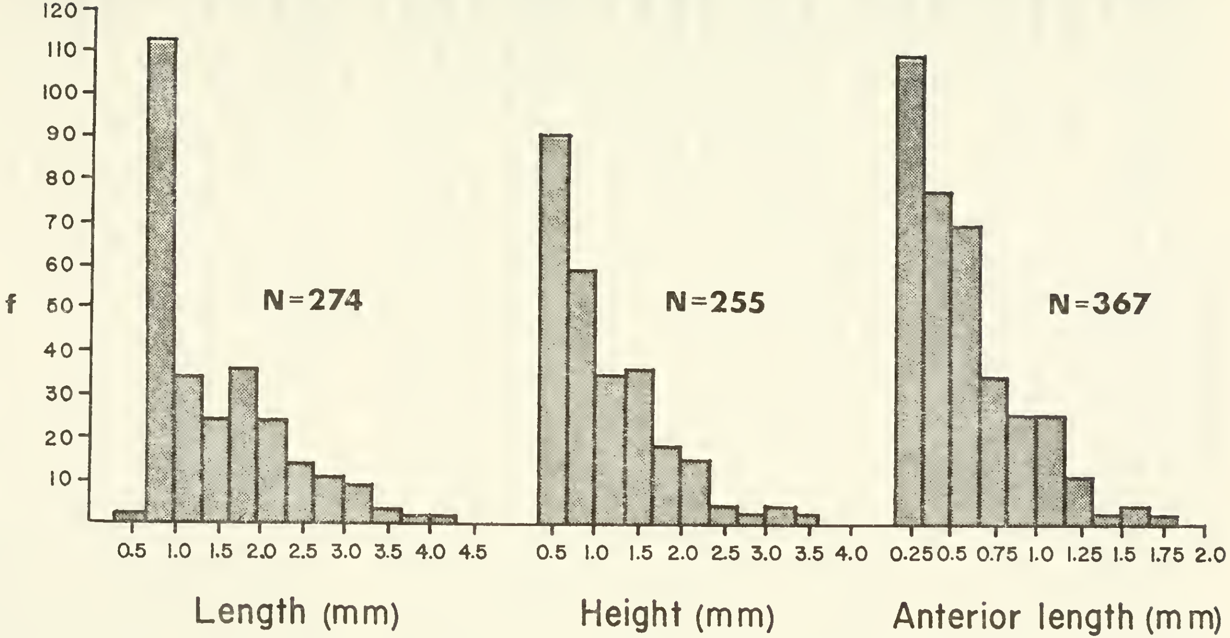
where D is size, T is time and s is a constant. The constant s is determined from the equation by using the maximum size for D, and selecting a value for T. The larger the value selected for T, the smaller the resulting s. It is clearly important that the selection of

T be consistent if two populations are to be compared. Bretsky was unable to make the Snyder and Bretsky (1971) values for T (and consequently, s) available to us. Following Levinton's (personal communication and Levinton and Bambach, 1970) instructions, we could not determine a constant value for s in all of Snyder and Bretsky's (1970) survivorship curves for *P. fecunda.* Because we can not be sure that the survivorship curves which we could construct from our data would have been constructed as Snyder and Bretsky's were, we do not present them here. Rather, only the histograms are presented for their comparison with those of Snyder and Bretsky's. The Brassfield population of *Palaeoneilo fecunda* is more like the Scales Mound than the Mt. Carroll populations of Snyder and Bretsky. *Nuculites neglectus,* although the second most abundant palaeotaxodont was generally not well enough preserved to determine size-frequency distribution.

RECURRENT NEARSHORE COMMUNITIES

Among those who have described recurrent communities, Bayer (1967) found a benthonic community in the Elgin Member of the Maquoketa (stratigraphically higher than the basal Maquoketa beds) in 49 "shell beds" within a 45′ vertical sequence. Each community was similar to the others in numbers and proportions. The beds were traceable laterally for only a few feet. The most important environmental control operative upon this community was thought to be periodically increased rate of terrigenous sediments accompanied by shoaling. In other words, the facies-dependent fauna simply migrated with the environment to which it was adapted. This is also true for the diminutive faunas in the Brassfield. Occurring in alternating beds, the fauna could not survive in the environment in which the shale was deposited, an environment of increased terrigenous sedimentation.

The recurrence of the Maquoketa community in the Brassfield Formation is also a facies phenomenon. That this fauna is recurrent stratigraphically is a reflection only of the geographic movement of the facies through time. The specific and generic similarities of these two communities suggest that the Maquoketa fauna is ancestral to the Brassfield fauna. Greater detail of the sequence of events producing this record is lacking because of the lack of knowledge of intervening stratigraphy.



Text-figure 2.—Size frequency distributions of length, height, and anterior length of *Palaeoneilo fecunda* (Hall) from the diminutive Brassfield beds.

CONCLUSIONS

The diminutive faunas of the Early Silurian Brassfield and Late Ordovician basal Maquoketa Formations are similar in size (both consisting of specimens usually ranging in size from 1 to 5 mm), taxonomic composition at the specific and generic levels, dominant faunal elements (*"Plagioglypta" iowaensis, Palaeoneilo fecunda, Nuculites neglectus,* and *Liospira micula*), and community structure. The abundance of detritus feeding palaeotaxodont bivalves, hyolithids, and archeogastropods, together with predatory cephalopods indicates a nearshore, shallow-water environment. Because these faunal communities are so similar, the environments to which they were adapted could not have been very different.

Both formations contain phosphatic, ferruginous carbonates in which the fauna is found. We interpret the environment of the Brassfield diminutive fauna to be similar to that of the Maquoketa as described by Snyder and Bretsky (1971). That is, the environment was a nearshore, warm, epeiric sea with a carbonate mud bottom. Current activity in the Brassfield, however, was probably more vigorous than in the Maquoketa and may have removed some of the very fine carbonate mud. The presence of symmetrical ripple marks and similar numbers of right and left bivalve shells suggest oscillation currents rather than unidirectional currents were present. Such currents could effect minor sorting as well as disarticulate specimens and cause some abrasion but are not thought sufficiently competent to completely remove the fauna from the environment in which it lived.

That these communities are heterochronous is supported by the stratigraphic positions of both formations and conodont biostratigraphy. *Icriodina irregularis* Branson and Branson, an Early Silurian conodont, is found in the Brassfield; Maquoketa conodonts indicate a Late Ordovician age for that formation (Glenister, 1957), as do the larger fossils, including graptolites.

Because these two faunas are so similar at the generic and specific level, it is reasonable to assume that they represent the same faunal associations through time, the basal Maquoketa fauna being ancestral to the diminutive Brassfield fauna. The sequence of events producing this record cannot be ascertained because of the lack of knowledge of intervening stratigraphy.

SYSTEMATIC DESCRIPTIONS

Class BIVALVIA Linné

Subclass PALAEOTAXODONTA Korobkov

Order NUCULOIDA Dall

Superfamily **NUCULACEA** Gray

Family **PRAENUCULIDAE** McAlester

Genus **DECEPTRIX** Fuchs

Deceptrix scofieldi (Ulrich) Pl. 1, figs. 1-6

1894. *Ctenodonta scofieldi* Ulrich, Final Rept. Minnesota Geol. Nat. Hist. Sur.) vol. 3, part 2, Paleont., p. 593, pl. 42, figs. 53-58. Reprinted in 1897.

1893 [1895]. ?*Ctenodonta perminuta* Ulrich, Ohio Div. Geol. Sur. Rept. Inv., vol. 7, part 2, p. 680, pl. 46, figs. 11-14.

Description. — Shell outline subovate; beak prominent, high and erect, located in posterior third of the shell. Anterior region is elongate and somewhat attenuated at the anterior tip. Dentition on a gently arched hinge plate, consisting of three to five chevron-shaped anterior teeth and twice as many posterior teeth that are smaller than the anterior ones (Pl. 1, fig. 5). Muscle scars distinct. Adductors oval and located at the anterior and posterior margins just above midheight. Elongate, anterior pedal protractor and retractor scars are dorsal to and confluent with the adductor (Pl. 1, fig. 6). Posterior retractor is nearly circular and separated from the posterior adductor, but dorsal to it (Pl. 1, fig. 5). Two or three pairs of umbonal scars are usually preserved. Exterior marked by uniform, fine varices of growth (Pl. 1, fig. 4).

Remarks. — *Deceptrix scofieldi* has not been specifically reported from the Maquoketa Formation; however, Snyder and Bretsky (1971, p. 229) reported the occurrence of "*Praenucula* spp." *Praenucula* and *Deceptrix* are often difficult to differentiate without internal features which are usually not found in Maquoketa specimens. The author has also seen several specimens from samples collected at Scales Mound, Illinois, that are referrable to *D. scofieldi*. *Deceptrix perminuta* may be synonymized here as the range in morphology of some small Brassfield specimens encompasses that of *D. perminuta*.

Although the relative abundance of this species is variable in the samples collected from the Brassfield Formation, it usually comprises about 1 percent of the total bivalve population. The rarity of *D. scofieldi* may explain why it has not been reported from the Maquoketa. The size range for Brassfield specimens is from 0.6 mm to 7.1 mm in length.

Figured specimens. — *Deceptrix scofieldi* (Ulrich) UCGM 42619, 42620, 42621, 42625, and 42626.

Genus **PRAENUCULA** Pfab

Praenucula albertina (Ulrich) Pl. 1, fig. 7

1847. [*Non*] *Nucula levata* Hall, Paleont. of New York, vol. 1, p. 150, pl. 34, figs. 1a-c.
1875. [?]*Tellinomya levata* (Hall), Hall and Whitfield, Ohio Geol. Sur. Rept., Paleont. vol. 2, pt. 2, p. 82.
1894. *Ctenodonta abertina* Ulrich, Final Rept. Minnesota Geol. and Nat. Hist. Sur., vol. 3, pt. 2, Paleont., p. 598, pl. 42, figs. 76-82. Reprinted in 1897.
1894. *Ctenodonta filistriata* Ulrich, Final Rept. Minnesota Geol. and Nat. Hist. Sur., vol. 3, pt. 2, Paleont., p. 599, figs. 44a-e. Reprinted in 1897.
1920. *Ctenodonta albertina* Ulrich, Stewart, Ontario Dept. Mines Ann. Rept. vol. 29, No. 6, pt. 1, p. 9.
1970. *Praenucula levata* (Hall), Bretsky, Peabody Mus. Nat. Hist., Yale Univ., Bull. 34, p. 114.

Description. — Shell outline subtrigonal to subquadrate, anteriorly elongate with beak in posterior third of valve. Valve margin rounded anteriorly and posteriorly with posterior margin nearly vertical. Orthogyrous beak low and rounded. Small uniform chevron-shaped teeth occupy the anterior and posterior hinge plates that meet beneath the beak at an obtuse angle, anterior teeth more numerous. Oval adductor scars situated just below hinge plate at shell margins. Other musculature is not well preserved on Brassfield specimens. Shell surface marked by fine growth varices.

Remarks. — *Praenucula albertina* was reported from the Maquoketa by Snyder and Bretsky (1971, p. 227). It is a rare faunal element in the Brassfield, usually less than 1 percent of the total bivalves. The variation in morphology exhibited by the type specimens of *P. albertina* and *P. filistriata* seems minor and within acceptable variation within a single species.

Figured specimen. — *P. albertina* Ulrich UCGM 42627.

Genus **PALAEOCONCHA** Miller

Palaeoconcha ohioensis (Bassler) Pl. 1, figs. 9-13

1894. [*Non*] *Ctenodonta socialis* Ulrich, Final Rept. Minnesota Geol. Nat.

Hist. Sur., vol. 3, pt. 2, Paleont., p. 594, pl. 42, figs. 59, 60. Reprinted in 1897.

1893 [1895]. *Tellinomya (Nucula?) socialis* Foerste, Ohio Div. Geol. Sur. Rept. Inv., vol. 7, pt. 2, p. 563, pl. 37, figs. 12a-c.

1915. *Ctenodonta ohioensis* Bassler, United States Nat. Mus., Bull. 92, pt. 1, p. 308 (new name for *Tellinomya socialis* Foerste).

Description. — Shell outline triangular in dorsal half and semicircularly rounded ventrally. Shell equidimensional or higher than long. Posterior-dorsal auricle developed to varying degrees but less prominent than in *P. faberi* Miller. Beaks low, rounded, erect and located near mid-line of shell. Valves are inflated as compared to *P. faberi.* Dentition and musculature with exception of deeply impressed anterior adductor poorly preserved. Dentition consists of anterior and posterior straight, blocky taxodont teeth, relatively small and distributed uniformly throughout the dental series (Pl. 1, fig. 10). Anterior adductor is circular. Some steinkerns show a paired series of accessory (pedal?) scars in umbonal region on ventral side of hinge plate (Pl. 1, fig. 12). These small oval scars extend linearly nearly the entire length of the hinge (commonly 5 to 7 pairs). The somewhat larger oval posterior pedal retractor muscle scar is preserved at the posterior end of this accessory series and just dorsal to the posterior adductor. Some shelled specimens show fine concentric growth varices.

Remarks. — *Palaeoconcha ohioensis* has not been reported from the Maquoketa; however, *Palaeoconcha obliqua* (Hall) has been reported by several authors (Table 1). *P. obliqua* is abundant in some Maquoketa samples and rare in others. In the Brassfield, *P. ohioensis* is uncommon and usually composes less than 5 per cent of the total bivalves. Details of the morphology of the types of *P. faberi* Miller, *P. obliqua* (Hall) (Pl. 1, fig. 8) and *P. ohioensis* (Bassler) suggest that each is a distinct species. However, examination of a suite of about 280 specimens (UCGM 19292) *P. obliqua* shows a range in shapes that would encompass all three species. It may be that the three are conspecific. Although given different names in the present state of taxonomy the Maquoketa and Brassfield specimens may also be conspecific. Specimens examined by the author from the Maquoketa at Scales Mound, Illinois, are virtually identical morphologically to some Brassfield specimens.

Figured specimens. — *P. ohioensis* (Bassler) UCGM 42628, 42629, 42631, USNM 88538/15. *P. obliqua* (Hall) AMNH 1360/6.

Superfamily **NUCULANACEA** Adams and Adams

Family **MALLETIIDAE** Adams and Adams

Genus **NUCULITES** Conrad

Nuculites neglectus (Hall) Pl. 1, figs. 14-18; Pl. 2, figs. 1-2

1862. *Clidophorus neglectus* Hall, Rept. Geol. Sur. Wisconsin, vol. 1, p. 55 (figure only).
1894. *Clidophorus neglectus* Hall, Ulrich, Final Rept., Minnesota Geol. Nat. Hist. Sur., vol. 3, pt. 2, p. 607, pl 42, figs 20-25. Reprinted in 1897.
1893[1895]. *Nuculites (Cleidophorus) ferrugineum* Foerste, Ohio Div. Geol. Rept. Inv., vol. 7, pt. 2, p. 564, pl. 37, figs. 2a-b.
1909. *Nuculites neglectus* (Hall), Grabau and Shimer, North American Index Fossils, p. 397.
1970. *Nuculites neglectus* (Hall), Snyder and Bretsky, American Jour. Sci., vol. 271, p. 239, pl. 1, figs. h-j.

Description. — Shell outline oval with anterior and posterior margins attenuated in larger forms (Pl. 1, fig. 14) but blunt in smaller ones (Pl. 1, figs. 16, 18). Posterior region elongate, high pointed beak in the anterior third of the shell. Internal anterior septum well developed, long and narrow with general anterior slant that is markedly curved anteriorly in its ventral half (Pl. 1, fig. 16). Septum at least half shell height. Dentition is on a nearly straight hinge plate with the anterior teeth undulose and larger and fewer (usually less than 7) than the posterior ones which are numerous (up to 16) and chevron-shaped (Pl. 1, fig. 17).

Adductors oval, slightly impressed just below the anterior and posterior ends of the hinge plate. Anterior adductor and pedal protractor and retractor are bounded on their posterior margins by septum. Small, well-impressed pedal scars are just below hinge plate with retractor directly above protractor (Pl. 2, fig. 1). Posterior retractor scar narrow and elongate, impressed on the ventral side of the hinge plate at about mid-length of the posterior dental series (Pl. 2, fig. 2). Umbonal muscles produce two or three pair of elongate scars. Ligamental groove long and narrow situated just posterior to the beak (Pl. 1, fig. 17). Fine, closely spaced growth varices mark external shell surface.

Remarks. — *Nuculites neglectus* is the second most abundant nuculoid in the Maquoketa (Snyder and Bretsky, 1971) and in the Brassfield. However, *Lyrodesma* sp. (not a nuculoid) is the second most abundant bivalve in the Brassfield. *N. neglectus* usually comprises 5 percent or more of the Brassfield bivalve fauna, while this species may be 40 percent or more of the Maquoketa fauna (estimated from Snyder and Bretsky's text-figures 4, 5, 8, 9). This deposit feeding nuculoid is commonly broken in the Brassfield sample and may have a less durable shell than other nuculoids. Foerste (1893[1895]) described *N. ferrugineum* from one broken specimen found in the ferrugenous zone of the Brassfield. This specimen is virtually identical to some collected in this study and is assignable to *N. neglectus*. Although complete valves were rare in the Brassfield, the estimated size (length) of such specimens is similar to those of Snyder and Bretsky (1971), about 1 to 5 mm.

Figured specimens. — *N. neglectus* (Hall) UCGM 42633, 42632, 42634, 42637. AMNH 1362/2.

Genus **PALAEONEILO** Hall and Whitfield

Palaeoneilo fecunda (Hall) Pl. 2, figs. 3-10

1862. *Nucula (Tellinomya) fecunda* Hall, Rept. Geol. Sur. Wisconsin, vol. 1, p. 55 (figure only).
1869 [1870]. [*Non*] *Palaeoneilo fecunda* Hall and Whitfield, Cooper, 1931, Washington Acad. Sci., Jour., vol. 21, No. 18, p. 459.
1894. [*Non*] *Ctenodonta simulatrix* Ulrich, Final Rept. Minnesota Geol. Nat. Hist. Sur., vol. 3, pt. 2, Paleont., p. 595, pl. 42, figs. 67-73. Reprinted in 1897.
1894. *Ctenodonta fecunda* (Hall), Ulrich, Final Rept. Minnesota Geol. Nat. Hist. Sur., vol. 3, pt. 2, Paleont., p. 595, pl. 42, figs. 67-73. Reprinted in 1897.
1894. *Ctenodonta calvini* Ulrich, Final Rept. Minnesota Geol. Nat. Hist. Sur., vol. 3, pt. 2, Paleont., p. 596, pl. 42, figs 61-64. Reprinted in 1897.
1923. *Ctenodonta* cf. *simulatrix* Ulrich, Foerste, Dennison Univ., Sci. Lab., Bull., vol. 20, p. 87.
1971. *Palaeoneilo*? *fecunda* (Hall), Snyder and Bretsky, American Jour. Sci., vol. 271, p. 237.

Description. — Shell outline oval; beak low, rounded, slightly prosogyrous. Umbones are more inflated in smaller shells. Radial sulcus extends from beak to posterior margin but is only faintly if at all developed. Dentition continuous along a dorsally arched hinge plate (Pl. 2, fig. 10). Anterior teeth straight, inclined anteriorly and range from three to eight, depending upon shell size. Posterior teeth similar in size to anterior ones but are chevron-shaped (Pl. 2, fig. 4, 8, 10) ranging from four to twenty, depending upon size. Anterior and posterior length is nearly equal in smallest shells, but become markedly unequal as size increases. Beak in largest shells near the anterior quarter of the valve. Muscle scars are commonly preserved on steinkerns and may be found on shells. Adductors oval, slightly impressed just ventral to ends of hinge plate. Anterior pedal muscle scars (protractor and retractor) elongate and separated from dorsum of adductor; posterior pedal retractor elongate, disjunct from and dorsal to adductor. Umbonal muscles (dorso-median?) produce two or three pairs of small elongate scars beneath the beak. Pallial line preserved in a few specimens and appears to be non-sinuate (Pl. 2, fig. 7). Ligament contained in a long narrow groove posterior to beak on dorsal margin of hinge plate (Pl. 2, fig. 8). Surface marked by fine varices of growth (Pl. 2, figs. 3, 9).

Remarks. — This species is the most abundant bivalve constituent of the Maquoketa fauna, representing 50 percent of the total bivalves. In the Brassfield, *P. fecunda* may represent as much as 75 percent of the bivalve fauna. The dominance of this species in both formations is extraordinary and suggests similar ecological conditions. The morphology of Maquoketa specimens is so similar to that of the Brassfield specimens that their affinity is clear. Size variation reported by Snyder and Bretsky (1971) is nearly identical to that of the Brassfield specimens (about 0.3 to 6.5 mm in length).

In proposing *Nucula levata,* Hall (1847) included several specimens in his type suite; some were from the Trenton (Ordovician) of New York, others from the Maquoketa. Clark and Ruedemann (1903, p. 521) designated one of the New York specimens as the lectotype. It is different from the Maquoketa specimens which can readily be placed in *Palaeoneilo fecunda.* Ulrich described *Ctenodonta calvini* (Ulrich, 1894, p. 595) from Maquoketa equivalent strata in Minnesota. It also can be accommodated within the morphologic variation of the populations of *P. fecunda* from the Brassfield. Specimens also assignable to this species were reported previously from the Brassfield as *Ctenodonta* cf. *simulatrix* Foerste (1923, p. 87).

Figured specimens. — *P. fecunda* UCGM 42642, 42647, 42645, 42644, AMNH 1365/5, 1360/5G, 1360/5E, 1362/3.

Genus A

Genus A aff. **"Ctenodonta" longa** (Ulrich) Pl. 2, figs. 12, 13

1892. *Tellinomya longa* Ulrich, American Geol. vol. 10, p. 103, pl. 7, figs. 17-18.
1894. *Ctenodonta longa* (Ulrich), Ulrich, Final Rept. Minnesota Geol. Nat. Hist. Sur., vol. 3, pt. 2, Paleont., p. 560, pl. 37, figs. 30-31. Reprinted in 1897.

Description. — Hinge plate consists of anterior and posterior dental series, meeting beneath the beak at a variably obtuse angle. Beak small, low, rounded and slightly opisthogyrous, situated in anterior third of shell. Anterior teeth are few (3 to 6), large, straight or slightly undulose vertically. Posterior teeth more numerous (6 to 9) and chevron-shaped. Adductor muscle scars oval and deeply impressed at ends of hinge plate. Other musculature, ligament and ornament unknown.

Remarks. — Brassfield specimens are represented by broken valves only. The hinge plates, however, are often intact and represent the morphologic feature characterizing this species.

This species has not been reported from the Maquoketa and was not observed by this author from several samples collected at Scales Mound, Illinois. This species is uncommon in the Brassfield, comprising about 1 percent of the total bivalve fauna in most samples. Although this species generally resembles some *Nuculites* species, differences in internal features (as shape of dentition and lack of septum) distinctly separate it. It is unlike any genus and species [except *Ctenodonta longa* (Ulrich)] now known. A new name should be proposed; however, given the fragmental nature of the Brassfield specimens, it seems unwarranted to base new taxa upon them.

Figured specimens. — Genus A aff. *"Ctenodonta" longa* (Ulrich) UCGM 42651, 42652.

Subclass HETEROCONCHIA Hertwig

Order TRIGONIOIDA Dall

Superfamily **LYRODESMATACEA** Ulrich

Family **LYRODESMATIDAE** Ulrich

Genus **LYRODESMA** Conrad

Lyrodesma sp. Pl. 2, figs. 11, 14-17

Description. — Shell outline subtrigonal; anterior and posterior margins rounded. Umbonal ridge extends from beak to posterior margin dividing the shell into area and flank. Umbo inflated. Beak blunt, erect and standing just slightly above the dorsal shell margin. Dentition consists of two to four ventrally diverging cardinal teeth in each valve for individuals less than 2 mm in length. (No complete specimens were found greater than 2 mm in length, although a hinge with five teeth, total length of 2.5 mm was recovered.) Typical dental pattern is two teeth in the right valve (Pl. 2, fig. 15), and three teeth in the left valve (Pl. 2, fig. 16).

Adductors small and located near dorsal margin at anterior and posterior edges of shell. Two or three pairs of accessory muscle scars are preserved in the umbonal region of steinkerns. Fine concentric growth varices mark the shell.

Remarks. — No *Lyrodesma* species have been reported from the Maquoketa, and there seems to be no bivalve analogue to this infaunal suspension feeder of the Brassfield. All of the complete shells of this species in the Brassfield are less than 2 mm in length. However, rare hinge plates of much larger specimens (about 15 mm? in length) are found. These larger hinge plates show the typical *Lyrodesma* dentition.

The small *Lyrodesma* range in length from 0.6 mm to 2.0 mm. The separate hinges may be up to 2 mm in length (Pl. 2, fig. 11).

In one sample where 982 valves were recovered, *Lyrodesma* sp. was represented by 146 specimens, or 14.9 percent.

Figured specimens. — *Lyrodesma* sp. UCGM 42660, 42661, 42659, 42666.

Phylum, Class, Order and Family Uncertain

"Plagioglypta" iowaensis (James) Pl. 3, figs. 2-4

1890. *Coleolus?* sp. *iowaensis* James, American Geol. vol. 5, p. 355.
1929. *Coleolus iowensis* James, Ladd, 1925, Ph.D. dissert., Univ. Iowa, p. 384.
1959. *Coleolus iowensis* James, Ojakangas, 1959, M.S. dissert., Univ. Missouri, p. 72, pl. 7, figs. B1-B4.
1970. *Plagioglypta iowaensis* (James), Bretsky and Bermingham, Jour. Paleont. vol. 44, No. 5, p. 911, pl. 131, figs. 3-16.

Remarks. — The Brassfield specimens are comparable to those of the Maquoketa, but are more elongate. The characteristic ornament of *"P." iowaensis* is preserved only as external molds. Specimens range from 3.0 to 10.25 mm in length. We cannot be sure whether this species from examination of our specimens and those from the Maquoketa (studied by Ojakangas and others deposited at the USNM) is a scaphopod or a worm tube.

Figured specimens. — USNM 207421, 207422, 207423.

Class GASTROPODA Cuvier

Subclass PROSOBRANCHIA Milne Edwards

Order ARCHAEOGASTROPODA Thiele

Suborder BELLEROPHONTINA Ulrich and Scofield

Superfamily **BELLEROPHONTACEA** M'Coy

Family **CYRTOLITIDAE** S. A. Miller

Genus **CYRTOLITES** Conrad

Cyrtolites sp. Pl. 3, figs. 5-8

Description. — Small *Cyrtolites* with prominent median carina and two lateral carinae. Umbilici are relatively narrow, occupying one-sixth the greatest diameter. Shell expands rapidly and aperture is moderately flared and quadrate. No apertural sinus was observed. Surface ornament is not known. Most specimens show broad collabral undulations. Two specimens with the same shell shape (Pl. 3, fig. 8) show more numerous, closer undulations. One and one-half whorls are visible. Specimens measure 0.6 to 4.6 mm in greatest diameter.

Remarks. — Species assignment of these steinkerns cannot be made. In the broad transverse undulations, they are like some of the steinkerns of *C. ornatus* Conrad illustrated by Horny (1965, pl. 2, figs. 4, 7, 8). He commented that the morphology of the keel and the collabral undulations is variable in specimens of this genus.

C. carinatus Miller, which is similar to this species, was described from the basal Maquoketa (Ojakangas, 1959, p. 57). One of Ojakangas' specimens (UMMG 14034) is illustrated on Plate 3, figure 9. *C. carinatus* differs from *C.* sp. in possessing more prominent lateral ridges which produce a wider, more angularly quadrate aperture. More numerous, smaller collabral undulations (which are reflected on the steinkerns as well as the exterior of that species) are similar to those found on two of the steinkerns from the Brassfield (Pl. 3, figs. 5-7).

Figured specimens. — USNM 207424, 207425, UMMG 14034.

Family **SINUITIDAE** Dall

Subfamily **BUCANELLINAE** Koken

Genus **BUCANELLA** Meek

Subgenus **PLECTONOTUS** Clarke

Bucanella (Plectonotus) sp. Pl. 3, figs. 10-12

Description. — Small, phaneromphalous bellerophontoid, with prominent median lobe and two lateral lobes which produce a trilobate whorl profile. Median lobe is high and relatively wide with steep lateral slopes. Upper and lateral surfaces of lateral lobes strongly curved. Umbilical shoulders well rounded and umbilici relatively narrow, occupying slightly less than one-fifth of the greatest diameter. Ornament unknown. Trilobate aperture wider than high. Broad U-shaped sinus occurs, but no selenizone was observed. Specimens measure 0.6 to 4.1 mm in greatest diameter.

Remarks. — Without external features these steinkerns cannot be assigned specific names. Somewhat larger trilobed forms from the Brassfield in Montgomery County, Ohio, were referred to *Bellerophon (Bucania) trilobatus* J. de C. Sowerby by Foerste (1893 [1895], p. 550). In the Maquoketa, similar diminutive trilobed gastropods were referred to *Cyrtolites conradi* Hall by Ladd (1925, pl. 29, fig. 21). His specimens were not available for study, but his illustrations are copied on Plate 3, figures 13 and 14. Boucot and Yochelson (1966, p. A7) removed *Plectonotus* from the genus *Bucanella* and erected a new subfamily Plectonotinae for the genus. This removal was prompted by their having found what they thought was an apertural slit on the holotype *Plectonotus derbyi* Clarke. Yochelson (personal communication) now believes this removal was unwarranted and that the holotype does not possess a slit.

Figured specimens. — USNM 207426, 207427.

Family **BELLEROPHONTIDAE** M'Coy

Subfamily **TROPIDODISCINAE** Knight

Genus **TROPIDODISCUS** Meek and Worthen

Tropidodiscus sp. Pl. 3, figs. 15, 16

Description. — Small, compressed lanceolate phaneromphalous bellerophontaceans. Whorl profile lanceolate, deeply angulated at narrow dorsal carina, gently convex from dorsum to lateral rounded ridge above umbilical shoulders, roundedly flaring at shoulders, and rounded but more steeply angulated into moderately deep umbilicus. Umbilici are narrow, occupy one-fifth of the greatest diameter. One and one-half to two whorls visible. Specimens range from 1.2 to 1.9 mm in greatest diameter.

Remarks. — Wanting external shell characteristics, this form cannot be assigned to a species. This form is unlike *T. subacutus* Ulrich described from the basal Maquoketa (Ojakangas, 1959, p. 59) in being much more laterally compressed and whorls increasing much more rapidly in size and in having wider umbilici.

Figured specimens. — USNM 207428, 207429.

Subfamily **BUCANINAE** Ulrich and Scofield

Tribe **BUCANIIDES** Ulrich and Scofield

Bucania? sp. Pl. 4, figs. 2-4

Description. — Small phaneromphalous bellerophontaceans; whorl profile broadly rounded at the dorsum, convex between dorsum and umbilical shoulders and strongly angulated from umbilical shoulders into the umbilici. Umbilical shoulders gently rounded and the strong angulation of whorl profile from them into umbilicus produces deep umbilici which occupy one-fourth of the greatest diameter. Shell increases in size rapidly and produces only a slightly, if at all, expanded aperture. Some specimens have slight median dorsal carina; most do not. Broad, low longitudinal keel is developed on floor of whorls. Aperture is wider than high, with width to height ratio of .85 to .9. One and one-half to two and one-half whorls are visible. Ornament unknown.

Remarks. — These steinkerns have a longitudinal keel which is suggestive of *Bucanopsis* but is not so well developed as in that genus. They do not possess the extended parietal lip of *Bucanopsis* nor the dorsal carina. The deep highly angulated umbilici of these specimens is more suggestive of *Bucania.*

Ladd's (1925, pl. 29, fig. 23) illustration of *Bucania liratus* Hall is similar to this species in shell shape and size and is copied on Plate 4, figure 5.

Figured specimens. — USNM 207430, 207431, 207432.

Suborder PLEUROTOMARIINA Cox and Knight

Superfamily **PLEUROTOMARIACEA** Swainson

Family **RAPHISTOMATIDAE** Koken

Subfamily **LIOSPIRINAE** Knight

Genus **LIOSPIRA** Ulrich and Scofield

Liospira micula (Hall) Pl. 3, figs. 17, 18; Pl. 4, fig. 1

1862. *Pleurotomaria micula* Hall, Geol. Rep. Wisconsin, p. 55, fig. 1.

1897. *Liospira micula* Hall, Ulrich and Scofield, Geol. Minnesota, Final Rept. Geol. Nat. Hist., Sur., vol. 3, pt. 2, p. 994, pl. 68, figs. 24-29.
1959. *Liospira micula* Hall, Ojakangas, M.S. dissert., Univ. Missouri, pp. 53-54, pl. 3, figs. A1-5.

Remarks. — Although specimens from the Brassfield are steinkerns, some still retain portions of the shell. Umbilical plugs are found, isolated from shells, and rarely still in place. No specimens preserved the selenizone and the aperture was invariably broken. Brassfield and basal Maquoketa specimens examined were similar in morphology and size. Ojakangas' (1959) Brassfield specimens were compared with the lectotype of *L. micula* (Hall) (AMNH 1383/1) and found to be identical in morphology. All specimens in the type suite as well as the lectotype (from the Maquoketa) are steinkerns with small fragments of shell. One of Ojakangas' (1959) specimens (UMMG 14029) is figured on Plate 4, figure 1. The diameter of Brassfield specimens ranges from 1.9 to 12.0 mm.

Figured specimens. — USNM 207433, UMMG 14029.

Family **LOPHOSPIRIDAE** Wenz

Subfamily **LOPHOSPIRINAE** Wenz

Genus **LOXOPLOCUS** Fischer

Loxoplocus (Lophospira?) sp. Pl. 4, fig. 6

Description. — Small, turbinate, relatively high-spired with angulated periphery. On steinkerns, whorl profile of all except last whorl is slightly flattened and inclined downward on the upper surface; mid-whorl a slight angulation occurs; below this angulation whorl face continues steeply down to the bottom of the whorl. Body whorl differs in having two angulations, one above the mid-point and the other more prominent angulation below the mid-point of the whorl. On these steinkerns, whorls not in contact. On rare specimens which preserve parts of shell, whorls are in contact and sutures not depressed. Umbilicus anomphalous. Aperture broken so that details of its morphology are unknown. Three to four whorls visible. Specimens range from 1.4 to 4.5 mm in height.

Remarks. — These specimens cannot be certainly assigned to *Lophospira* because they are not gradate. Because only rare specimens preserve portions of the shell, this may be attributed to preservation. Ojakangas (1959) described two new species of *Lopho-*

spira from the Maquoketa — in addition to *L. tropidophora* Meek.

Figured specimen. — USNM 207434.

Subgenus **DONALDIELLA** Cossmann

Loxoplocus (Donaldiella) sp. Pl. 4, fig. 7

Description. — Small, high-spired, loosely coiled with slightly angulated periphery. Upper whorl profile of these steinkerns slightly flattened and inclined downward. Angulation which is only slightly reflected on steinkerns occurs above mid-whorl, from which whorl face proceeds steeply to bottom of whorl. Whorls not in contact, as they are loosely coiled. Umbilicus possibly anomphalous. Characteristics of aperture unknown. Four to five whorls visible. Specimens range from 1.5 to 5.6 mm in height.

Remarks. — Because all these specimens are steinkerns, external characteristics are unknown, preventing their specific identification.

Figured specimen. — USNM 207435.

Suborder TROCHINA Cox and Knight

Superfamily **PLATYCERATACEA** Hall

Family **HOLOPEIDAE** Wenz

Holopea? sp. Pl. 4, figs. 9, 10

1893[1895]. *Cyclora alta* Foerste, Geol. Sur. Ohio Pal. 7, p. 552, pl. 26, figs. 17a,b.

Description. — Steinkerns small, trochiform. Earlier whorls rounded on upper and lower surfaces but more flattened along lateral face. Upper surface of the body whorl profile flattened and slopes downward and outward, forming a slight shoulder; from this slight shoulder, whorl face slopes downward curving outward to a slight angulation at the bottom of whorl, from which it proceeds roundedly into the umbilicus. Aperture is polygonal, probably narrowly phaneromphalous. Ornament not known. Three whorls visible. Specimens range from 0.8 to 1.7 mm in height.

Remarks. — This species is questionably assigned to the genus *Holopea* because, as Foerste (1893[1895], p. 552) commented, it "looks very much like a very small *Holopea*" in general shape. The slight shoulder and lower gentle angulation, as well as the resultant polygonal aperture, are not so characteristic of *Holopea* but are somewhat suggestive of *Cyclonema.* However, as Thompson (1970,

p. 228) pointed out, concerning *"C." alta,* this species is too high-spired for *Cyclonema.*

Figured specimen. — USNM 207437.

Genus **HOLOPEA** Hall

Holopea cf. **H. symmetrica** Hall Pl. 4, fig. 8

Description. — Small, moderately high-spired *Holopea.* Whorl profile strongly rounded and whorls tightly coiled. Probably narrowly phaneromphalous. Aperture slightly oblique, circular to polygonal. Ornament unknown. Three whorls present. Specimens range from 1.1 to 1.9 mm in height.

Remarks. — These steinkerns are similar to steinkerns of *Holopea symmetrica* Hall described from the basal Maquoketa (Ojakangas, 1959), but the spire is higher in the Brassfield forms. The spire is also higher on the holotype of *Holopea symmetrica* Hall (AMNH 751/1) which was compared to the Brassfield specimens. The holotype is also considerably larger than the Maquoketa and Brassfield specimens, measuring 12 mm in height.

Figured specimen. — USNM 207436.

Genus **CYCLONEMA** Hall

Cyclonema (Dyeria?) sp. Pl. 4, figs. 11, 12

Remarks. — This identification of *Dyeria*? sp. is based on one broken steinkern. The earlier whorls are incomplete and fractured. There are one or possibly two rotelliform earlier whorls which were apparently in contact. Although not preserved, the apical whorl was probably globose, because the earliest whorl preserved is globose. These earlier whorls are depressed below the upper whorl surface of the uncoiled body whorl which expands much more rapidly along the lower whorl surface, producing a rounded ellipsoidal whorl profile. Details of the umbilicus, aperture and ornament are unknown. It was probably phaneromphalous. Assignment of this specimen to the genus *Dyeria* is questionable because it may have fewer earlier whorls than *Dyeria,* the shell expands at a somewhat greater rate, and the body whorl is more coiled.

Figured specimen. — 207438.

Suborder MURCHISONIINA Cox and Knight

Superfamily **MURCHISONIACEA** Koken

Family **MURCHISONIIDAE** Koken
Genus **MURCHISONIA** Archiac and Verneuil
Subgenus **MURCHISONIA** Archiac and Verneuil

Murchisonia (Murchisonia) sp. Pl. 4, figs. 13, 14

Description. — Small, high spired with two parallel carinae at mid-whorl. Whorl face slopes sharply downward from upper surface to mid-whorl carinae. Surface between carinae is gently concave and presumably was site of a selenizone. Whorl face between lower carina and lower surface of whorl steeply rounded. Sutures preserved only on one partially shelled specimen relatively shallow, depressed on steinkerns. Umbilicus probably anomphalous. Aperture not preserved. Four to five whorls visible. Height ranges from 2.2 to 9.2 mm.

Remarks. — Similar high-spired gastropods from the basal Maquoketa have been called "*Hormotoma gracilis* (Hall)" by Ladd (1925, p. 185). His illustrations of this species are copied on Plate 5, figures 1 and 2. One of these specimens (Pl. 5, fig. 1) shows a pair of angulations. Specimens identified by Johnson (1939, p. 151, pl. 1, fig. 1) as "*Hormotoma* sp." from the basal Maquoketa of Missouri, are similar in form to the Brassfield specimens.

Figured specimens. — USNM 207439, 207440.

Order ?ARCHEOGASTROPODA

Genera inquirendum
Genus **"CYCLORA"** Hall

"Cyclora" depauperata (Hall) Pl. 5, figs. 8-10

1862. *Pleurotomaria depauperata* Hall, Geol. Rep. Wisconsin, p. 55, fig. 5.
1925. *Pleurotomaria (Lophospira?) depauperata* Hall, Ladd, Ph.D. dissert., Univ. Iowa, p. 183, pl. 29, fig. 25 [partim].

Description. — Small, trochiform. Whorl profile rounded and shell enlarges rapidly. Umbilicus cryptomphalous. Aperture circular. Ornament and other external characteristics unknown. Three to four whorls visible. Specimens range from 1.0 to 2.8 mm in height.

Remarks. — Hall first illustrated this species from the Maquoketa but did not describe it. Ladd (1925) described this species from the basal Maquoketa. His specimens were not available for study, but his illustrations of this species are copied on Plate 5, figures 3-6. Judging from the illustrations, Ladd may have collected two form of "*Cyclora*". Plate 5, figures 3-6 were all labeled *Pleuro-*

tomaria (*Lophospira*?) *depauperata* Hall. However, figures 3 and 4 are apparently higher spired, and the whorls increase less rapidly than figures 5 and 6. The apertural view (figure 5) is apparently of a specimen like figure 6. The Brassfield contains specimens of both morphologies, the higher-spired one being referred to this species; Hall's (1862) original drawing of this species shows approximately the same spire height. Ulrich and Bassler (personal communication with Ladd, 1927) thought that Ladd's specimens (whether they saw both morphologies is not clear) were best referred to *Cyclora pulchella* Miller. The morphology of figures 5 and 6 is closer to the illustration of *C. pulchella* than to that of *C. depauperata*. The lower-spired specimens which increase more rapidly in size found in the Brassfield are called *"Cyclora"* cf. *"C." pulchella* Miller (see that species below).

A form similar in whorl shape and size but with somewhat lower spire was reported by Ojakangas (1959, p. 55) from the basal Maquoketa in Iowa and Illinois. The same form was found in samples collected at Scales Mound, Illinois (Pl. 5, fig. 7). It, along with a smaller, lower-spired form with a greater width to height ratio were referred to *Cyclora minuta* Hall. These specimens were compared to the type suite and lectotype of *"Cyclora" minuta* (AMNH 1387). The smaller form may well be referred to this species, but the larger form probably should not be.

Thompson (1970) discussed the genus *"Cyclora"* and suggested that it is a juvenile of *Cyclonema* or a smaller genus which was sympatric with *Cyclonema*. Species of *"Cyclora"* have previously been reported only from the Upper Ordovician.

Figured specimens. — USNM 207442, 207443, 207444, 207445.

"Cyclora" cf. **"C." pulchella** Miller Pl. 5, figs. 11, 12

Remarks. — This species occurs only sparsely and all specimens are steinkerns. They resemble *"C." pulchella* in their greater rate of shell expansion, having a rounded whorl profile, being wider than high, and in having a circular aperture. The spire of this species is somewhat lower than *"C." depauperata*. Ladd's (1925) illustrations of *C. depauperata* include two forms which are much more like *"C." pulchella* than *"C." depauperata*. They are herein copied on Plate 5, figures 5 and 6 from Ladd's work.

Figured specimens. — USNM 207441.

Class HYOLITHA Marek

Order HYOLITHIDA Sysoev

Family HYOLITHIDAE Nicholson

Elegantilites? sp. Pl. 5, figs. 13-17

Description. — Conch straight to slightly dorsally concave with rounded subtrigonal cross section. Lateral edges sharp but may be rounded at apex, and lie at one-fifth the height of the conch. Ligula short, attaining a length one-seventh of the apertural width. Angle of divergence about 10°-12°.

External ornament consists of extremely fine transverse elements which are not well enough defined to permit measurement. They cover both dorsal and ventral sides. Dorsally, they are arched backward along the median broad crest, forward along the conch face proceeding toward the lateral edges, and just above the lateral edges they arch backward again, forming a lateral sinus. Ventrally, these fine transverse elements are arched forward. Fine longitudinal striations (hairlines) occur only sparsely on both dorsal and ventral surfaces and are not continuous. On the internal surface a different ornament appears (Plate 5, figure 15 shows both types of ornament). The internal transverse elements are much better defined, and there are 50 to 60 per millimeter (Pl. 5, figs. 14, 16, 17). Dorsally, their curvature is like that of the external ornamentaion. Ventrally, they are much less arched, being straight across the median portion of the conch, arched only toward the edges. No longitudinal ornament is present.

The operculum is unknown. This species varies in length from 2.4 to 9.8 mm.

Remarks. — This species is questionably assigned to *Elegantilites* because of its ornamentation and sharp lateral edges. *E. elegans* (Barrande) was described (by Marek, 1967, p. 72) as having a finer transverse ornamentation on the internal shell layer than the outer, although even the inner riblets (20-25 per mm) are much coarser than those found here (the longest conch of *E. elegans* was "more than 120 mm"). Without the operculum, this species cannot be attributed to the genus *Elegantilites* with certainty. The longitudinal sinus is more characteristic of species of *Joachimilites* such as *J. novaki* Marek. These two genera are apparently closely related and are distinguished primarily on features of the operculum. On the basis of external ornament, sharp lateral edges, and conch shape, the basal Maquoketa hyolithid "*Hyolithes*" *parviusculus* might also be questionably assigned to the genus *Elegantilites*. No evidence was found, however, of different internal shell layer ornament.

Figured specimens. — USNM 207446, 207447, 207448, 207449.

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EXPLANATION OF PLATE 1

Figure

1-6. **Deceptrix scofieldi** (Ulrich)

Brassfield Formation, Adams County, Ohio. 1. Left lateral view. UCGM 42619; × 9. 2. Dorsal view of steinkern. Note large anterior teeth and small posterior teeth. UCGM 42620; × 17.5. 3. Right lateral view of steinkern. Note oval scars of anterior and posterior adductors. UCGM 42621; × 26.5. 4. Chip of phosphatic matrix showing external mold of growth lines. UCGM 42626; × 17.5. 5. Dorsal view of steinkern. Note circular posterior pedal retractor scars near hinge and elongate umbonal scars near beak. UCGM 42625; × 17.5. 6. Enlargement of anterior musculature of specimen in figure 3; × 35.

7. **Praenucula albertina** (Ulrich)

Brassfield Formation, Adams County, Ohio. 7. Interior view of right valve. UCGM 42627; × 12.5.

8. **Palaeoconcha obliqua** (Hall)

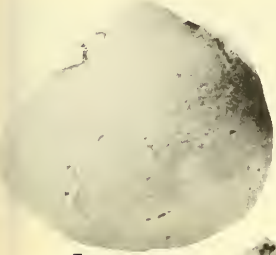
Maquoketa Formation, near Scales Mound, Illinois. 8. Right lateral view of steinkern. This specimen is in the type suite of *Palaeoneilo fecunda* (Hall). AMNH 1360/6; × 6.5.

9-13. **Palaeoconcha ohioensis** (Bassler)

Brassfield Formation, Montgomery County, Ohio. 9. Right lateral view of steinkern of Foerste (1895) syntype. USNM 88538/15; × 14. Brassfield Formation, Adams County, Ohio. 10. Dorsal view of steinkern. Note impression of dentition. UCGM 42628; × 42. 11. Right lateral view of steinkern. UCGM 42629; × 35. 12. Dorsal view of specimen in figure 11. Note series of accessory muscle scars near hinge; × 35. 13. External view of right valve. Note inflated umbo. UCGM 42631; × 35.

14-18. **Nuculites neglectus** (Hall)

Maquoketa Formation, near Scales, Mound, Illinois. 14. Left lateral view of syntype figured by Hall, 1962, p. 55, fig. 3. AMNH 1362/2; × 3. 16. Left lateral view of steinkern. Unfigured syntype. AMNH 1362/2; × 5.5. Brassfield Formation, Adams County, Ohio. 15. Internal cast of right valve. UCGM 42633; × 10.5. 17. Hinge of right valve. Note larger undulose anterior teeth and narrow ligament groove above posterior teeth. UCGM 42637; × 28. 18. Right lateral view of steinkern. UCGM 42632; × 14.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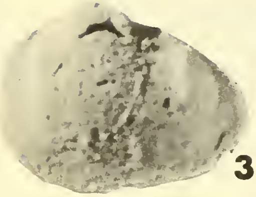
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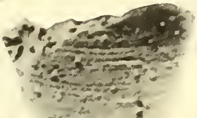
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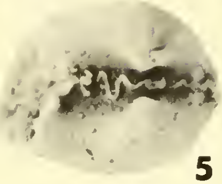
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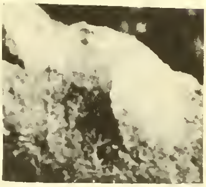
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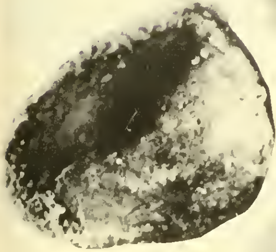
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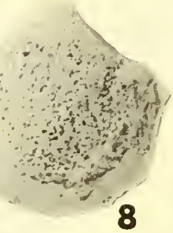
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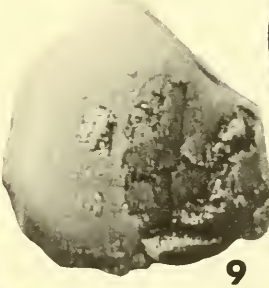
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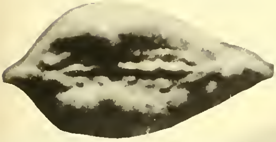
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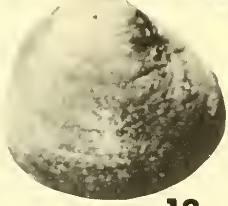
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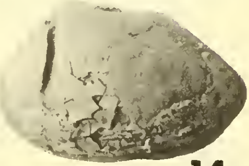
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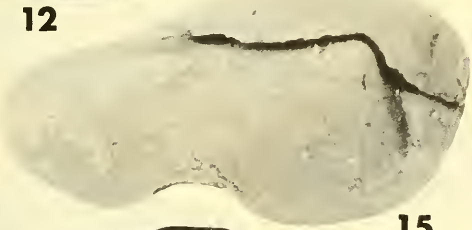
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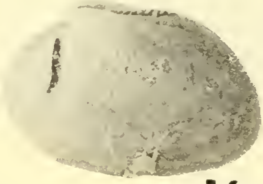
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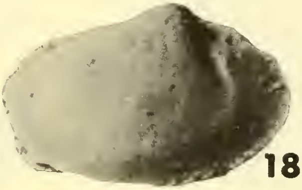
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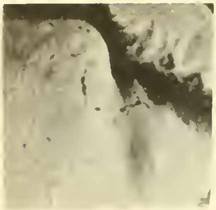
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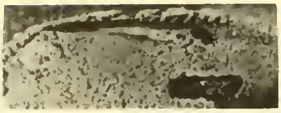
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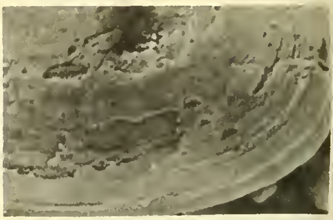
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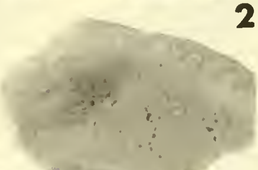
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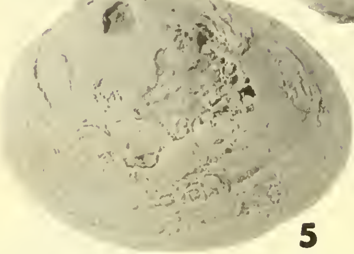
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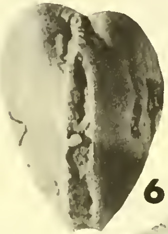
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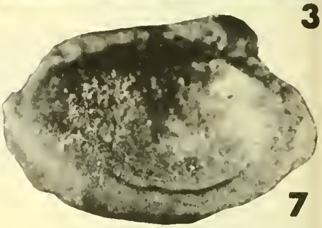
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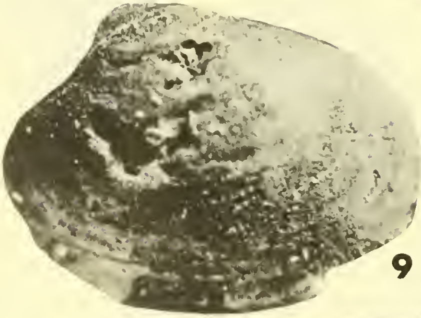
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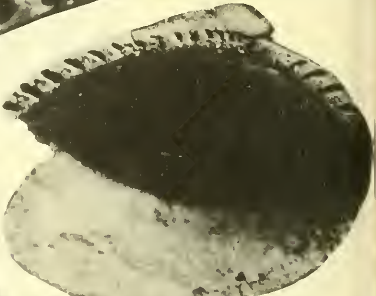
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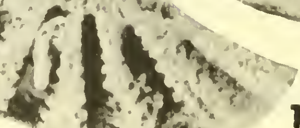
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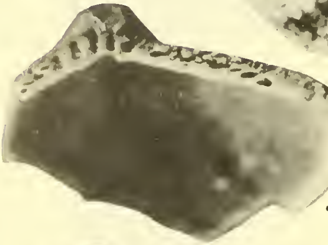
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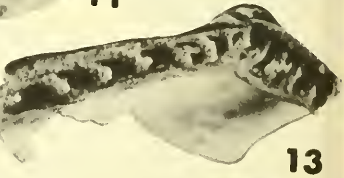
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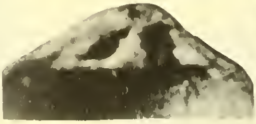
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EXPLANATION OF PLATE 2

Figure

1-2. **Nuculites neglectus** (Hall)

Brassfield Formation, Adams County, Ohio. 1. Enlargement of anterior region of specimen in Pl. 1, fig. 15. Note umbonal muscle scars, anterior septum and pedal muscle scars. UCGM 42633; × 14. 2. Enlargement of posterior hinge of left valve interior cast. Note dentition and elongate scar of posterior pedal retractor. UCGM 42634; × 10.5.

3-10. **Palaeoneilo fecunda** (Hall)

Maquoketa Formation, near Scales Mound, Illinois. 3. Enlargement of surface ornament on left valve of articulated specimen. Unfigured syntype of Hall (1862). AMNH 1360/5G. × 10. 4. Interior of right valve. Unfigured syntype of Hall (1862). AMNH 1360/5E; × 6.5. 5. Left view of articulated specimen. Figured syntype of Hall (1862, p. 55, fig. 1). AMNH 1360/5; × 4.5. 6. Anterior view of steinkern. Originally figured by Hall (1847, pl. 34, fig. h) as syntype of *"Nucula" levata*. Note oval anterior pedal muscle scars near hinge. AMNH 1362/3; × 3.5. Brassfield Formation, Adams County, Ohio. 7. Interior of left valve. Note pallial line. UCGM 42642; × 28. 8. Portion of left valve hinge. Note chevron-shaped teeth and narrow ligament groove. UCGM 42647; × 28. 9. Exterior of left valve. UCGM 42644; × 24.5. 10. Interior of left valve. UCGM 42645; × 24.5.

12-13. Genus A aff. **"Ctenodonta" longa** (Ulrich)

Brassfield Formation, Adams County, Ohio. 12. Interior view of right valve. UCGM 42652; × 28. 13. Interior view of left valve. Note chevron-shaped posterior teeth. UCGM 42651; × 21.

11, 14-17. **Lyrodesma** sp.

Brassfield Formation, Adams County, Ohio. 11. Hinge plate of adult specimen. UCGM 42666; × 26.5. 14. Interior view of right valve. UCGM 42661; × 45.5. 15. Enlargement of cardinal teeth in right valve. UCGM 42659; × 70. 16. Enlargement of cardinal teeth in left valve. Central triangular tooth is "2" tooth. UCGM 42660; × 70. 17. Interior of left valve. Same specimen as figure 16; × 45.5.

Explanation of Plate 3

Figure

1. Orthoconic cephalopod

Brassfield Formation, Adams County, Ohio. USNM 207420; × 17.5.

2-4. **"Plagioglypta" iowaensis** (James)

Brassfield Formation, Adams County, Ohio. 2. Showing ornament preserved on external mold. USNM 207421; × 25. 3. Showing dorso-median groove. USNM 207422; × 13. 4. Side view. USNM 207423; × 9.

5-8. **Cyrtolites** sp.

Brassfield Formation, Adams County, Ohio. 5-7. Respectively, apical, adapertural and apertural view, USNM 207424, showing broad collabral undulations; × 9. 8. Apical view of specimen showing finer collabral undulations, USNM 207425; × 9.

9. **Cyrtolites carinatus** Miller

Maquoketa Formation, Iowa or Illinois. Apical view of one of Ojakangas (1959) specimens UMMG 14034; × 9.

10-12. **Bucanella (Plectonotus)** sp.

Brassfield Formation, Adams County, Ohio. 10-11. Apertural and apical views, respectively, USNM 207426; × 10. 12. Adapertural view, USNM 207427; × 10.

13-14. **Bucanella (Plectonotus)** sp.

Maquoketa Formation, Iowa. Referred to as "*Cyrtolites conradi* Hall" by Ladd (1925). Copied from Ladd (1925) pl. XXIX, fig. 21; × 6.

15-16. **Tropidodiscus** sp.

Brassfield Formation, Adams County, Ohio. 15. Apical view, USNM 207428; × 13. 16. Apertural view, USNM 207429; × 13.

17-18. **Liospira micula** (Hall)

Brassfield Formation, Adams County, Ohio. 17, 18. Apertural and apical views, USNM 207433; × 6.


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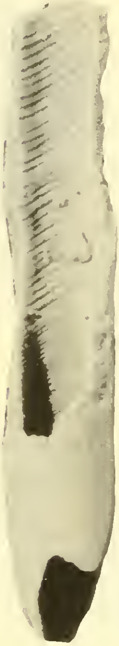
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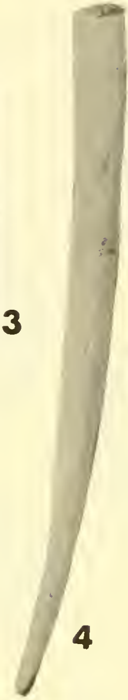
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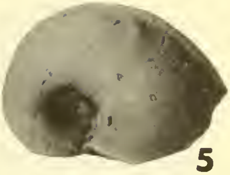
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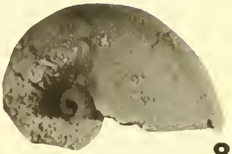
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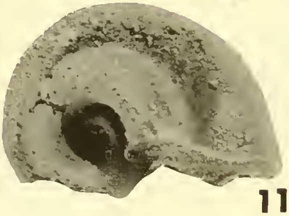
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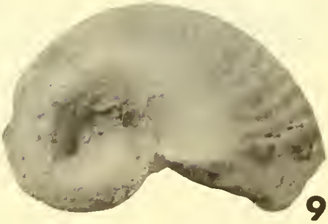
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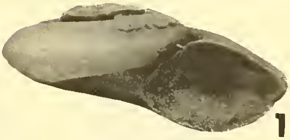
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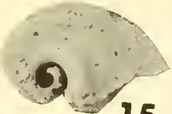
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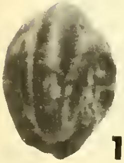
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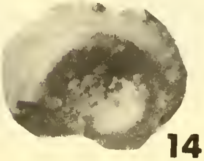
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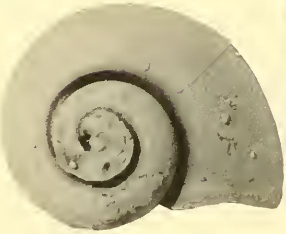
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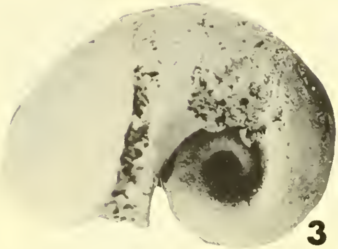
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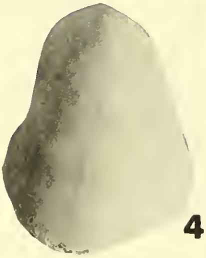
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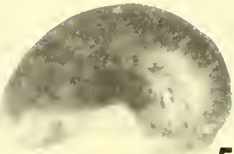
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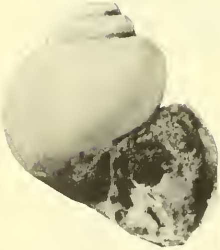
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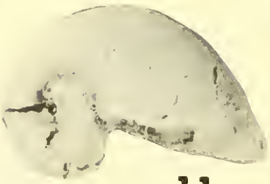
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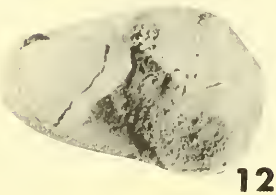
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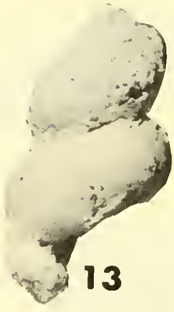
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EXPLANATION OF PLATE 4

Figure

1. **Liospira micula** (Hall)

Maquoketa Formation, Iowa or Illinois. Apical view of one of Ojakangas (1959) specimens numbered UMMG 14029; × 10.

2-4. **Bucania** ? sp.

Brassfield Formation, Adams County, Ohio. 2. Apertural view, USNM 207432; × 6. 3. Apical view, USNM 207430; × 17. 4. Adapical view, USNM 207431; × 7.5.

5. **"Bellerophon patersoni** Hall"

Maquoketa Formation, Iowa. Apical view of specimen referred to as "*Bellerophon patersoni* Hall" by Ladd (1925). Copied from Ladd (1925) pl. XXIX, fig. 24; × 7.5.

6. **Loxoplocus (Lophospira)** sp.

Brassfield Formation, Adams County, Ohio. Apertural view, USNM 207434; × 10.

7. **Loxoplocus (Donaldiella)** sp.

Brassfield Formation, Adams County, Ohio. Apertural view, USNM 207435; × 9.

8. **Holopea** cf. **H. symmetrica** Hall

Brassfield Formation, Adams County, Ohio. Apertural view, USNM 207436; × 23.

9-10. **Holopea** ? sp.

Brassfield Formation, Adams County, Ohio. 9-10. Adapertural and apertural views, respectively, USNM 207437; × 5 and × 6, respectively.

11-12. **Cyclonema (Dyeria** ?) sp.

Brassfield Formation, Adams County, Ohio. 11-12. Apical and apertural views, respectively, USNM 207438; × 10.

13-14. **Murchisonia (Murchisonia)** sp.

Brassfield Formation, Adams County, Ohio. 13. Apertural or side view, USNM 207439; × 6. 14. Apertural view, USNM 207440; × 6.

Explanation of Plate 5

Figure

1-2. **"Hormotoma gracilis** Hall"

Maquoketa Formation, Iowa. Apertural views of specimens referred to as *"Hormotoma gracilis* Hall" by Ladd (1925). Copied from Ladd (1925) pl. XXIX, figs. 30 and 31, respectively; × 17.5 and × 9, respectively.

3-6. **"Pleurotomaria depauperata** Hall"

Maquoketa Formation, Iowa. 3-6. Apical, basal surface, apertural, and apical views, respectively of specimens referred to as *"Pleurotomaria depauperata* Hall" by Ladd (ms). Copied from Ladd (1925) pl. XXIX, figs. 25 and 26; × 5.

7. **"Cyclora"** sp.

Maquoketa Formation, Scales Mound, Illinois. Apical view of specimen, identical in form to those identified as *"Cyclora minuta* Hall" by Ojakangas (1959, p. 55, pl. 4, figs. A1-5), USNM 207442; × 14.

8-10. **"Cyclora" depauperata** (Hall)

Brassfield Formation, Adams County, Ohio. 8. Apical view, USNM 207445; × 14. 9. View of basal surface, USNM 207443; × 14. 10. Apertural view, USNM 207444; × 14.

11-12. **"Cyclora"** cf. **"C." pulchella** Miller

Brassfield Formation, Adams County, Ohio. 11-12. Apical and apertural views, respectively, USNM 207441; × 17.5.

13-17. **Elegantilites** ? sp.

Brassfield Formation, Adams County, Ohio. 13-14. Cross section and lateral edge, respectively, USNM 207449; × 10 and × 11, respectively. 15. Ventral side, USNM 207446; × 25. 16. Dorsal view, USNM 207447; × 15. 17. Lateral edge, USNM 207448; × 28.


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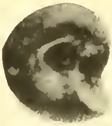
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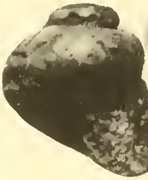
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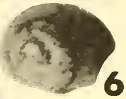
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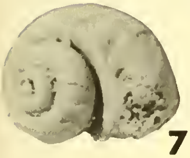
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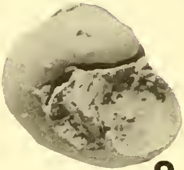
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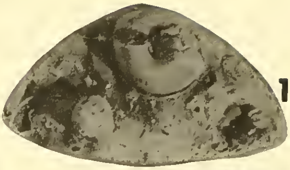
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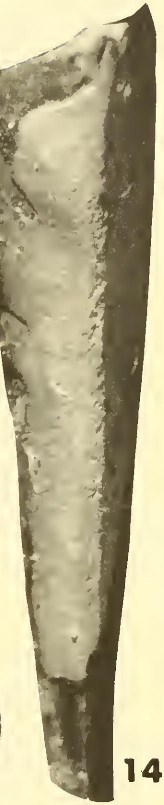
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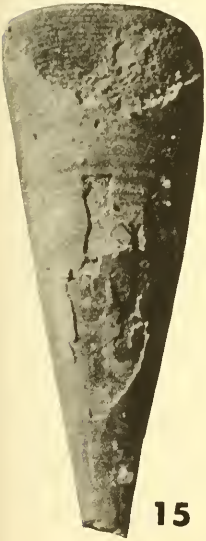
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CASTEROLIMULUS: A NEW LATE CRETACEOUS GENERIC LINK IN LIMULID LINEAGE

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ABSTRACT

An olive gray siltstone near the top of the Fox Hills Formation (Maestrichtian) of North Dakota, has yielded a well-preserved prosoma of a new limulid merostome arthropod. The new genus *Casterolimulus* is interpreted as an advanced Mesozoic representative of the main Tethyan limulid lineage leading to modern genera of the Tachypleinae. Although the limulid was found in strata containing abundant floral remains, known stratigraphic relationships indicate burial in an estuarine environment far from shore. The fundamental marine nature of limulids should be honored rather more than their occurrence with detrital plant remains.

INTRODUCTION

A considerable knowledge of the occurrence of fossil limulids based on ichnology has accumulated due, in no small part, to the work of Caster (1938, 1939, 1940, 1941, 1944, 1957). Yet the only known record of a limulid body fossil from North American Mesozoic strata is *Limulus coffini* Reeside and Harris (1952) from the Pierre Shale of Colorado. Thus a well-preserved specimen of a limulid xiphosuran from an unnamed member of the Fox Hills Formation (Maestrichtian) in North Dakota (Text-figure 1) is described herein even though it is known only from the prosoma. We place this specimen in a new genus, *Casterolimulus,* named in honor of Kenneth E. Caster of the University of Cincinnati.

During the past decade, the Late Cretaceous Fox Hills Formation in North Dakota has been undergoing thorough paleontologic and stratigraphic scrutiny (Feldmann, 1964, 1966, 1967, 1968, 1972; Holland and Feldmann, 1967; Artzner, 1973; Erickson, 1973, 1974; Bailey and Erickson, 1973; Chayes and Erickson, 1973). The formation represents a complex of marginal marine facies which records the waning regressive fluctuations of the late Maestrichtian seaway in the Williston Basin. It was during further detailed stratigraphic and sedimentologic studies conducted by Erickson and his students (Klett and Erickson, 1974) that the discovery here reported was made. Field relationships of Fox Hills lithofacies resulting from these studies are illustrated schematically in Text-figure 2.

SYSTEMATIC PALEONTOLOGY

Phylum ARTHROPODA Siebold and Stannius
Subphylum CHELICERATA Heymons
Class MEROSTOMATA Dana
Subclass XIPHOSURA Latreille
Order XIPHOSURIDA Latreille
Suborder LIMULINA Richter and Richter

Superfamily **LIMULACEA** Zittel

Family **LIMULIDAE** Zittel

Subfamily **TACHYPLEINAE** Pocock

Genus **CASTEROLIMULUS** Holland, Erickson, and O'Brien, n. gen.

Type species: *Casterolimulus kletti* Holland, Erickson, and O'Brien, n. sp.

Generic diagnosis. — Prosoma low, gently vaulted, of medium size; well-developed doublure parallel-sided through most of its arc, widening rapidly past a position anterior to the eyes. Ophthalmic ridges low but well developed, waning in strength forward from the eyes, arcing toward the median crest of the cardiac lobe but not joining it anteriorly. Axial furrows deep, angled obliquely toward the anterior end of the median crest from their origin on the posterior margin of the prosoma. Axis possessing a well-defined ridge lacking spines or protuberances. Margins of genal spines subparallel to central axis and becoming laterally more oblique toward their tips. Ocelli not defined. Opisthosoma, telson, and appendages unknown.

Etymology. — The new genus is named in honor of Kenneth E. Caster, student of the Xiphosura.

Discussion. — The new genus is a conservative limulid and combines characteristics of several fossil and extant genera, in a manner that, from published descriptions, appears to be common to none previously known. The axial furrows are distinct and converging. The ophthalmic ridges extend well toward the anterior of the prosoma and curve toward the axis though they do not meet there. In addition, the genal spines are gently but definitely directed laterally. These are traits which Størmer (1952, p. 638; 1955, p. P22) assigned to the Mesolimulidae. Yet Riek and Gill (1971, p. 207) pointed out that there are indications that the ophthalmic ridges of *Limulitella* Størmer, placed in the Mesolimulidae by Størmer, meet in front of the cardiac lobe; this is a characteristic of the Paleolimulidae, so they transferred *Limulitella* to the Paleolimulidae. They also described *Victalimulus,* a genus from the Lower Cretaceous of Australia, as intermediate in some characters between *Mesolimulus* and modern limulids. Based on this and their judgment that the characters ascribed to the Mesolimulidae are quantitative and not qualitative they denuded Størmer's Mesolimulidae by assignment of *Psammolimulus* Lange and *Mesolimulus* Størmer to the Limulidae. Størmer (written communication, 1973) has tended to agree with this position.

Paleolimulids are characterized by a distinctly annulated opisthosoma on which the ultimate segment is moveable, in addition to the meeting of the ophthalmic ridges anteriorly. Because our specimen lacks the opisthosoma, *Casterolimulus* is assigned to the Limulidae solely on prosomal characters. The anteriorly convergent axial furrows and the low arch of the prosoma suggest that *Casterolimulus* belongs to the subfamily Tachypleinae rather than the highly vaulted Limulinae.

The convergence of the axial furrows of *Casterolimulus* anteriorly toward the median crest or ridge is reminiscent of the Jurassic *Mesolimulus* and Early Cretaceous *Victalimulus* and indicative of relationship with the Holocene *Tachypleus* Leach. However, differences in the genera are definite. *Casterolimulus* lacks the narrow cardiac lobe and sharp, spine-bearing median keel of *Victalimulus* and has the genal angles more laterally directed than in *Mesolimulus* and slightly more so than in *Victalimulus. Casterolimulus* is also larger than Riek and Gill's specimen of *Victalimulus* which they regarded as adult. The anterior convergence of the axial furrows and ophthalmic ridges, lesser backward prolongation of the genal spines, and lesser arch of *Casterolimulus* readily separate it from *Limulus* Müller.

Casterolimulus kletti Holland, Erickson, and O'Brien, n. sp.
Pl. 1, 2; Text-fig. 3

Description. — Having the characters ascribed to the genus; additionally, the broad, smooth, median crest of the cardiac lobe is maintained for two-thirds the length of the prosoma and becomes ill-defined where the axial furrows approach it. The eyes are low and lunate; the posterior of the prosoma is marked by a slightly raised border.

Etymology. — Following well-known, Casterian, pedagogical tactics (described by Caster and Macke, 1952, p. 754) the writers persuaded Mark C. Klett, finder of the specimen, to surrender it. The specific name attests to Mr. Klett's efforts and our appreciation of his diligence.

Dimensions of holotype. — The following measurements were taken from the internal mold of the prosoma:

Length at axis	5.2 cm
Width from tip-to-tip of genal spines (calculated as twice the half-width):	10.6 cm
Distance between ophthalmic ridges posterior margin:	5.0 cm
Distance between axial furrows at posterior margin:	2.2 cm
Minimum length of genal spine:	1.4 cm

Types. — Internal and external molds of the holotype are stored at the U.S. National Museum where they carry catalogue number 206801. Plastotypes of the external mold are housed in the paleontological collections of the Department of Geology and Geography, St. Lawrence University, Canton, New York (SLU 500), and in the paleontological collections of the Geology Department at the University of North Dakota in Grand Forks (UND 13,795).

Contrary to frequent patterns of limulid preservation in which the remains have been compressed by sediment loading so that characters of dorsum and venter appear superimposed in a single plane, out specimen is little compressed and the prosoma has a marked thickness.

One half of the specimen is a mold of the exterior of the prosoma (Pl. 2). The other half, which gives the prosoma in positive relief, is a mold of the interior of the dorsal carapace; when collected this exfoliated, in all but the cardiophthalmic region, revealed a mold of the exterior of the doublure and part of the wrinkled contiguous ventral membrane. (Pl. 1, fig. 2). These very fragile exfoliations were saved (shown restored to position in Pl. 1, fig. 1) but have not been permanently re-assembled because they are largely a mold of the interior of the doublure. Thus our specimen consists of the mold of all four prosomal surfaces. The left genal spine separated along a joint plane in the rock and was not found during excavation.

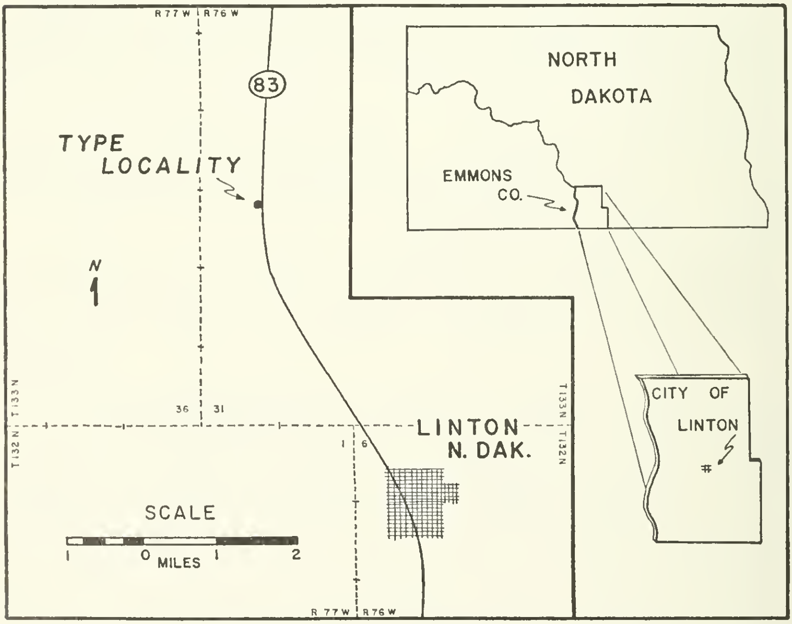
As preserved, the prosoma is gently vaulted. Although there are some depressed regions and slight wrinkling on the dorsal side, the arch of the prosoma seems to be much as it was in life. Preservation at the perimeter of the prosoma indicates that there was little space between the mold surfaces. This and the slight wrinkling indicates that the cuticle was thin, delicate, and flexible compared with that of modern limulids. This flexibility is easily attained by many living marine Crustacea by withdrawing calcium from their sclerotized exoskeleton prior to ecdysis. Although we do not know of any analogous process in living Xiphosura, we see no reason why some skeletal softening, at least in the ventral region, should not occur. The cephalothorax seems to have been in this pliable state when filled and encased in sediment in such a way that crushing was largely avoided.

It is also possible that we have the unhardened prosoma of a newly molted individual which died of unknown causes. It might well have been dismembered by scavengers; if this occurred, they left no trace, and we feel the specimen is the disarticulated result of normal ecdysis.

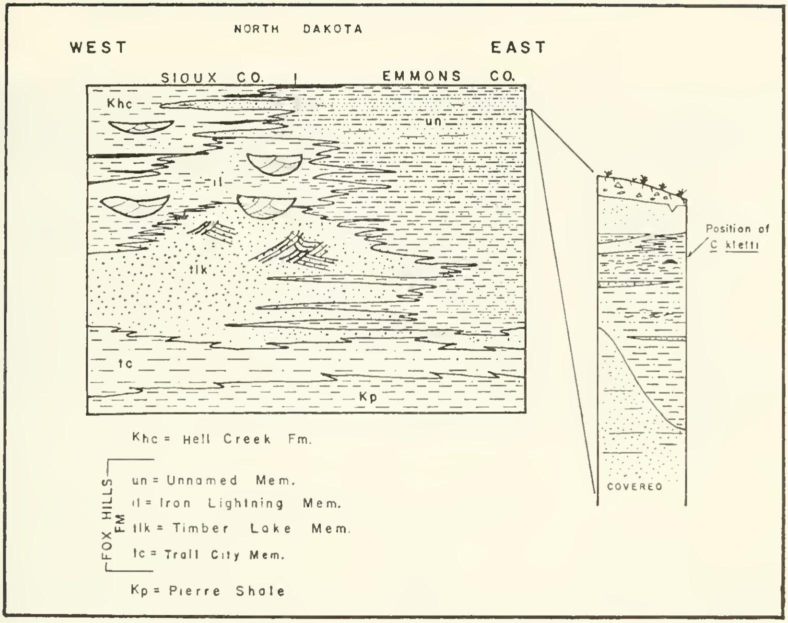
Type locality. — The specimen was collected from a roadcut on the west side of North Dakota Highway 83 about 7 kilometers north of Linton; SE¼, NE¼, NE¼, sec. 19, T. 133 N., R. 76 W., Emmons County, North Dakota (Text-fig. 1).

Lithologic relationships in the roadcut are intricate and difficult to determine due to vegetational overgrowth and slope creep. The new limulid was excavated from a moderate olive brown (5Y 4/4, wet) to light olive gray (5Y 6/2, dry) siltstone which apparently fills a channel cut in an olive gray, fine-grained sandstone of unknown thickness. Upward the siltstone grades abruptly into another fine-grained sandstone truncated by weathering and by glacial erosion at the top of the roadcut. This channel in an unnamed member of the Fox Hills Formation occurs within 10 meters of the top of the formation.

The siltstone channel contains plant material; this fact led Fisher (1952) to suggest that the siltstone was the basal unit of the overlying Hell Creek Formation. But it is not. The manner of occurrence and preservation of the plants indicates that they were wafted to the depositional site by gentle currents but under conditions of rapid silt deposition relatively far from the estuarine shore. The channel is well within the unnamed member which is marine at its base and is overlain by the widespread Linton Member of the Fox Hills (Klett and Erickson, 1974, and in press) that is responsible for the butte caps in the vicinity. The fine-grained sandstone lithofacies of the unnamed member intertongues with units in both the Fox Hills Formation and Hell Creek Formation to the west and this makes location of the contact between the formations difficult where visible sections are short and incomplete. We are defining the contact at the lowest indications of truly terrestrial or fresh-water depositional facies — for example, paleo-soil zones, presence of abundant lignite or presence of non-transported fresh-water fauna. We do not regard the presence of plant fossils in the siltstone associated with the limulid as diagnostic of the Hell Creek



Text-figure 1. — Location of the type locality of *Casterolimulus kletti,* n. gen., n. sp., Fox Hills Formation, Upper Cretaceous.



Text-figure 2. — Generalized stratigraphic relationships of unnamed member of the Fox Hills Formation (Upper Cretaceous) in North Dakota, which has yielded *Casterolimulus kletti,* n. gen., n. sp. Diagrammatic stratigraphic column at the type locality (see Text-figure 1) of *C. kletti* indicates the approximate position of occurrence of the holotype.

Text-figure 3. — Reconstruction of prosoma of *Casterolimulus kletti,* n. gen., n. sp., from the Fox Hills Formation, Upper Maestrichtian, of North Dakota. Bar is 1 cm long.

for plant remains are common throughout much of the Fox Hills sequence; this is analogous to a situation which Caster (1938, p. 51) pointed out with regard to depositional environments of *"Paramphibius"* as follows:

> Plant remains occur everywhere in the Upper Devonian of the [Penn-York] embayment and, in the absence of a soil zone, cannot by themselves be used to judge conditions of sedimentation.

The stratigraphy has been diagrammed as well as is currently practicable in Text-figure 2. Further details are now in preparation and will be the subject of later publication.

Geologic age. — Maestrichtian, Late Cretaceous.

LIMULID PHYLOGENY

Conservatism in limulid form through time (Størmer, 1944, p. 73) combined with a sparse fossil record makes phylogenetic reconstruction difficult. The rare, discrete glimpses we get of this lineage indicate that it is, indeed, a modest, conservative one in which major morphologic modification is the exception. Størmer (1952, pp. 632, 637) outlined certain trends in general phylogenetic development of the dorsal skeleton of limulaceans: gradual increase in size, gradual reduction in depth of the axial furrows, backward extension and prolongation of the genal angles, increasing sharpness of an axial keel, and backward migration of the movable lateral spines of the abdomen.

Extant limulid genera are three in number: *Limulus* Müller, *Tachypleus* Leach, and *Carcinoscorpius* Pocock. *Limulus* is the limulid inhabitant of the Atlantic Ocean and Gulf of Mexico today; the other genera are southwestern Pacific Ocean forms. The Pacific forms belong to the Tachypleinae Pocock, whereas *Limulus* stands by itself in a monogeneric subfamily, the Limulinae Zittel. Most of the Mesozoic occurrences of limulids are in rocks bordering the Tethys seaway or near seas with access to Tethys. Because of similarities in their morphology *Mesolimulus, Victalimulus,* and *Casterolimulus* are probably all on the main line of limulid evolution leading to *Tachypleus.* Modern *Limulus* seems an isolate from this main lineage. In terms of the prosoma, it alone possesses axial furrows which are nearly parallel to the median crest rather than being uniformly converging toward the anterior as in all other Mesozoic and

Cenozoic forms. The cephalothorax is highly vaulted as well. It remains to explain this isolation and the inland North American occurrence of the tachyplein genus *Casterolimulus.*

Casterolimulus kletti was taken from rocks deposited at the end of the Late Cretaceous seaway in the Western Interior of the United States. Recent paleogeographic studies (Sohl, 1971; Jeletzky, 1971; Erickson, 1973; Kauffman, 1973) have documented biogeographic units in the Upper Cretaceous of the Western Interior. This seaway joined the Atlantic, *via* the Gulf Coast, with the northeast Pacific allowing mixing of their faunas on a large scale, perhaps for the last time. Although these dual faunal sources were present during the time of the Fox Hills deposition in North Dakota, the major source contributing to the molluscan fauna of North Dakota was Tethyan from the Gulf Coast (Erickson, 1973). For these reasons, we believe it likely that *Casterolimulus* immigrated to North Dakota *via* the Gulf Coast seaway rather than by a route from the Pacific. In like manner, *Limulus* probably originated in Tethyan (Gulf Coast) waters prior to the Campanian following the opening of the Atlantic (Dietz and Holden, 1970; Smith, Briden, and Drewry, 1973), and *Limulus coffini* Reeside and Harris appears in Upper Campanian marine strata in Colorado. Thus, only in the Cenozoic, as Tethys closed and the Atlantic opened further, did the Tachypleinae become confined to the Eurasian side of the Atlantic, and eventually to the Pacific. *Casterolimulus* was likely the last of the Tethyan Tachypleinae in North America.

LIMULID PALEOECOLOGY

We believe that the stratigraphic relationships indicate that the final resting place of *Casterolimulus kletti* was in the brackish-water or marine portion of a Late Cretaceous estuary. We think that Størmer (1955, p. P9) implied over-simplification of the limulid habitat when he said:

> Inasmuch as most older-than-Recent merostomes are nonmarine forms, fossil remains of these arthropods are chiefly confined to the less common fresh-water and brackish-water sediments and are not common.

Caster (1938) expressed apprehension regarding use of floral evidence in assigning a fresh-water origin to rocks containing limulids.

He further said (1957, p. 1026):

> There is equally sound logic in the assumption that the habits of the present day [xiphosuran] descendants are very ancient, and that a remarkable vitality made them tolerant of considerable freshening of the water, perhaps even making occasional or seasonal incursions into estuaries or coastal plain swamps feasible, while they nevertheless remained fundamentally marine.

It seems only an application of Occam's razor that in most cases limulid remains should be taken as an indication of marine deposition or of proximity to the marine environment. The consideration of so many species as "freshwater", in a conservative group with such persistence in the rock record and with such global distribution of similar forms, raises many phylogenetic questions. To such consideration logical answers are most readily provided (not by suggestions of numerous evolutionary experiments with the freshwater environments, which in turn would mean paleontologists are seeing remains of many endemic forms) by simply honoring the fact that these animals have always exhibited a wide tolerance of salinities and that they have always roamed the nearshore zones of the seas. Our view of limulid evolution would be far more punctuated and far more inconsistent, due to all the fresh-water "dead ends", were this not the case. Caster's (1957, p. 1025) repeated warning might well bear remembering in the future: "The Xiphosura, as well as merostomes in general, bespeak the sea."

ACKNOWLEDGMENTS

We are indebted to a number of people and institutions for support of this research. Klett was conducting his study while an NSF Undergraduate Research Participant under Grant GY-10713 to the Geology and Geography Department of St. Lawrence University when he discovered the specimen. O'Brien's initial research on the Fox Hills Formation was carried out as an Undergraduate Research Participant as part of an earlier NSF grant (GY-9761) to St. Lawrence. He and Erickson were continuing their study of the Fox Hills under a grant from "Involvement," a student organization which aids faculty research at St. Lawrence. Photography was done in the paleontology laboratory at the University of North Dakota. We appreciate the support of these institutions.

At various times Alice Quackenbush, Mark C. Klett, Cynthia

J. Munsell, Marguerite Walsh, and Margine M. Holland helped in preparation of the manuscript. Henry Roberts and W. J. Kennedy made many helpful suggestions. Each has our thanks for his or her contribution to the final product.

This is contribution No. 6 from the Department of Geology and Geography of St. Lawrence University.

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EXPLANATION OF PLATE 1

Both figures approximately natural size.

Figure

1-2. **Casterolimulus kletti** Holland, Erickson, and O'Brien, n. gen., n. sp.
Holotype (USNM 206801). 1. Mold of the interior of prosoma with exfoliated portions (note cracks) restored to their natural positions. Note, on impression of the slightly wrinkled carapace, the deep converging axial furrows, the moderately developed ophthalmic ridges, and the mold of the exterior of the right genal spine extending from below a broken exfoliation. 2. Exfoliated portions removed to expose the mold of the exterior of the doublure and part of the wrinkled ventral integument. The internal boundary of the doublure on the right side is difficult to trace because its impression blends with that of the thin, wrinkled, ventral membrane. Neither this wrinkling nor the plant fossil near the left limb of the doublure should be construed as the remains of an appendage.

1

2

1

EXPLANATION OF PLATE 2

Figure

1. **Casterolimulus kletti** Holland, Erickson, and O'Brien, n. gen., n. sp. Holotype (USNM 206801). × 1. Mold of the exterior.

ONTOGENIES OF THREE LATE CAMBRIAN TRILOBITES FROM THE DEADWOOD FORMATION, NORTHERN BLACK HILLS, SOUTH DAKOTA

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Cheng Kung University, Taiwan
Republic of China

ABSTRACT

Ontogenies of three Late Cambrian trilobites are described. They are *Coosia albertensis* Resser, *Blountia nixonensis* Lochman, and *Plethopeltis arbucklensis* Stitt. *Plethopeltis arbucklensis* is represented by two morphologically distinct groups. Differences are interpreted as sexual dimorphism within one species. The phylogenetic relationships of each species are discussed.

INTRODUCTION

In the summer of 1962, Christina Lochman-Balk, the author, and a few students from the New Mexico Institute of Mining and Technology, held a geologic field camp in the Black Hills of South Dakota and east-central Wyoming. During the field season several tons of research material were collected, including some limestones which contained well-preserved early ontogenic stages of trilobites. The present report deals with a part of these collections.

Three ontogenic growth sequences of Late Cambrian trilobites are described. They are assigned to *Coosia albertensis* Resser, collected from Lead, about 2.5 miles southwest of Deadwood City; *Blountia nixonensis* Lochman from about 6 miles southeast of Deadwood City, and *Plethopeltis arbucklensis* Stitt from the south slope of Sheep Mountain, near Bearlodge Ranch, east-central Wyoming. The result of these ontogenic studies suggest that *Coosia albertensis* is phylogenetically related to *Crepicephalus deadwoodensis* Hu, *Syspacheilus dunoirensis* (Miller), *Meteoraspis globosa* (Miller), and *Coosella convexa* Tasch. Their earlier protaspid shields possess faint longitudinal central furrows and slender axial lobes, the meraspid cranidia are coarsely granulated and the glabellae are cylindrical. *Blountia nixonensis* Lochman is related to *Kingstonia ara* (Walcott) and *Komaspidella laevis* Rasetti. Their protaspid shields are all marked by distinct longitudinal furrows, forwardly expanded axial lobes and well-defined glabellar segments. The meraspid cranidia are smooth trapezoidal, glabellae subquadrate, without defined glabellar furrows. *Plethopeltis arbucklensis* is related to *Acerocare ecorne* Angelin, *Ptychaspis bullasus* Lochman and Hu, *Leptoplastus crassicornis* (Westergård), and *Peltura scarabaeoides* (Wahlenberg). Their protaspid shields have fusiform axial lobes, distinct glabellar segments, and densely granulated exoskeletal surface. In the meraspid stages, the cranidia are trapezoidal, and the slender conical glabellae are deeply demarked by paired glabellar furrows. The ontogenetic resemblances of each group possibly show the closeness of their phylogenetical relationships.

It is also noted that the late ontogenetic developmental stages of *Plethopeltis arbucklensis* are morphologically closely similar to those of *Ponumia obscura* (Lochman), and *Housia canadensis* (Walcott) (Hu, 1970b). This phenomenon probably results from convergent evolution.

The author thanks Kenneth E. Caster, University of Cincinnati, for his supervision and encouragement. Christina Lochman-Balk, New Mexico Institute of Mining and Technology, is thanked for guidance in the field during 1962 and for permission to describe part of her collections. M. E. Taylor, U.S. Geological Survey, is thanked for kindly reading over the manuscript and offering suggestions for its improvement. All described specimens are stored in the Geology Museum, University of Cincinnati, Cincinnati, Ohio (UCGM).

SYSTEMATIC PALEONTOLOGY

Family **COOSELLIDAE** Palmer, 1954

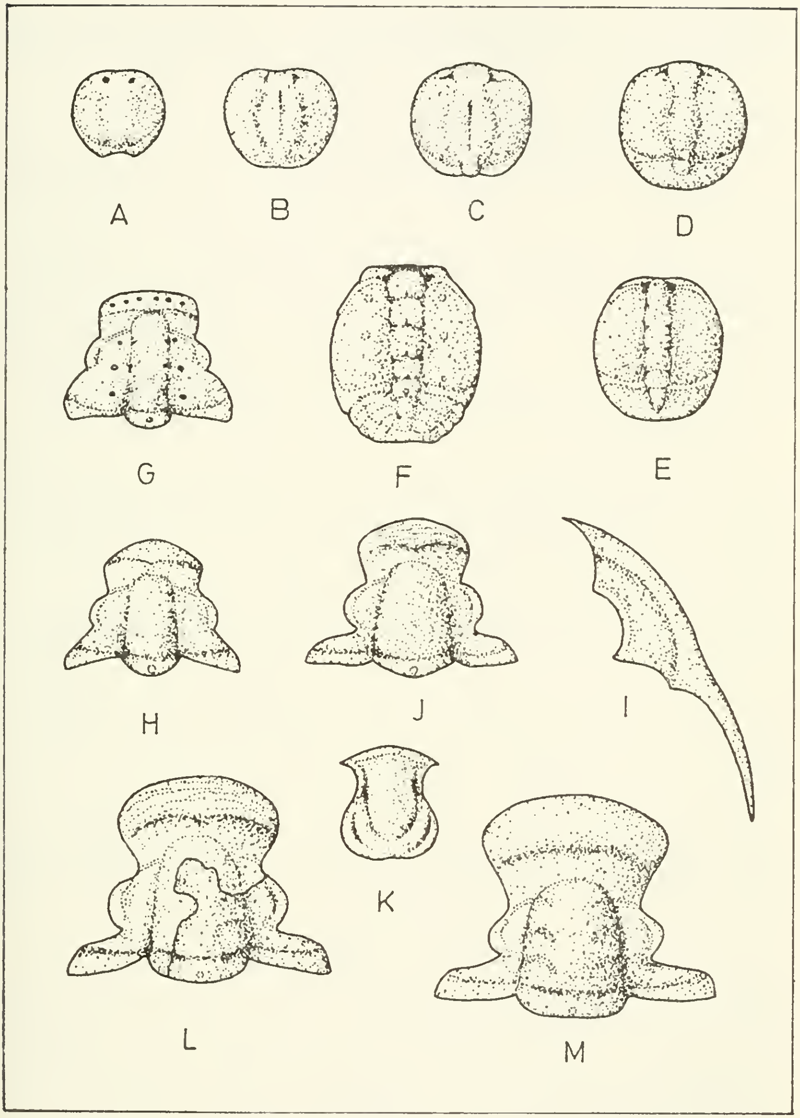
Genus **COOSIA** Walcott, 1911

Coosia albertensis Resser Pl. 1, figs. 1-29; text-fig. 1A-M

Coosia albertensis Resser, 1942, p. 73, pl. 13, figs. 25-28; Lochman, 1950, p. 335, pl. 49, figs. 13-21.
Coosia modesta Lochman, (Lochman and Duncan, 1944), p. 48, pl. 6, figs. 1-6.

Remarks. — The material studied is in a brownish gray medium crystalline limestone, that contains both large and small pebbles. The species commonly occurs in the *Crepicephalus* Zone. The largest cranidium is about 20 mm, and the pygidium 15 mm in sagittal length. *Cossia albertensis* Resser and *C. modesta* Lochman were reported by Lochman from the Little Rocky Mountains of Montana. The former species is distinguished by its smaller size, narrow and longer glabella, and broader preglabellar field. *C. modesta* is shorter and broader, and the preglabellar field is narrower. The forms are considered to represent different growth stages of a single species.

C. albertensis is similar to *C. dakotensis* Resser (1942) which was reported from the same general area at Galena, near Deadwood City, but *C. albertensis* has a shorter glabella, narrower anterior brim, and the librigena lacks a genal spine.



Text-figure 1. A growth series of *Coosia albertensis* Resser. A. Anaprotaspis, × 50; B, C. Two metaprotaspides, × 50, × 48; D, E. Small and large paraprotaspides, × 40, × 38; F. Small early meraspis, × 13; G. Large early meraspid cranidium, × 8; H. J. Two late meraspid cranidia, × 13, × 19; I. Immature librigena, × 6; K. Hypostoma, × 10; L, M. Small and large holaspid cranidia, × 2.4, × 1.7. (All drawings were made from photographs.)

Horizon and Locality. — East side of Iron quarry, near Lead, about 2.5 miles southwest of Deadwood City, South Dakota, Deadwood Formation, *Crepicephalus* Zone, Upper Cambrian.

Coosia albertensis Resser, ontogeny

Anaprotaspid stage (Pl. 1, fig. 1; Text-fig. 1A). — The shield is round in outline, convex, about 0.25-0.30 mm in length (sag.), and lacks distinct dorsal or axial and pleural lobes. The anterior margin of the shield is distinctly differentiated by a pair of round pits. The posterior margin shows a small elevated terminal node which suggests the posterior end of the axial lobe. No marginal border is observed except for a narrow flat band surrounding the posterior margin beside the terminal node. The surface of the shield is smooth or minutely granulated.

Metaprotaspid stage (Pl. 1, figs. 2-4; Text-fig. 1B, C). — The shield is round, moderately convex, and about 0.32-0.38 mm in sagittal length. The axis is fusiform, narrowing posteriorly and anteriorly from the mid-line of the shield (tr.), and ends in a terminal node. The dorsal furrow is rather faint and suggested only by the concave position, which lies between the pleural and the dorsal lobes. The triangular anterior pits are distinctly demarked at the sides of the frontal lobe between the eye-brow ridges and the palpebral ridges. The posterior margin is narrow, flat, and shows a pair of projections at the sides of the terminal node. The surface of the shield is faintly granulated.

The metaprotaspid stage is differentiated from the anaprotaspid stage by the faintly demarked axis with a longitudinal furrow, the distance between the anterior pits is reduced, and the posterior shield margin has a pair of broad projections.

Paraprotaspid stage (Pl. 1, figs. 5-9; Text-fig. 1D, E). — The shield is round to subround in outline, convex, about 0.40-0.85 mm in length (sag.), and has the pleural and axial lobes well separated by a dorsal furrow. The axis is narrowly fusiform, tapering both anteriorly and posteriorly from the mid-line (tr.) of the shield. No distinct axial segments are seen. The frontal pits are triangular to subtriangular, distinct and well delimited by eye-brow ridges and the faint palpebral ridges. The eye-brow ridge curves posterolaterally from the sides of the small frontal lobe and ends in front of the narrow elevated palpebral ridge. The occipital ring is small, elevated, and shows no median tubercle. The fixigena is convex, and well surrounded by a narrow marginal border. The marginal border is narrow and flat, broadening posteriorly from the midline (tr.) of the shield. The transverse protopygidium slopes downward from the posterior fixigenal border, and consists of possibly one or two indistinguishable segments. The skeletal surface shows fine granules and scarce coarse granules.

The paraprotaspis differs from the previous stage in having the axis and pleural lobes well differentiated, the posterior pygidium is present, and the earliest librigena is probably present along the anterolateral margin of the shield.

Early meraspid stage (Pl. 1, figs. 10-13; Text-fig. 1F, G).— The cranidium is subtrapezoidal in outline, convex, and about 0.60-0.75 mm in sagittal length. Axial and pleural lobes are well differentiated by deep dorsal furrows. The slender glabella consists of a medium-sized frontal lobe, two pairs of glabellar lobes, and a small fourth segment. The occipital ring is round to transversely oval, convex, and well differentiated by the occipital furrow. The narrow anterior border arches forward and is separated from the first glabellar segment by a furrow. The fixigena is convex, about the same width as the glabella between the palpebral lobe and the dorsal furrow. The palpebral lobe is narrow, well defined by the palpebral furrow, elevated, continuously running convergently to the side of the first glabellar lobe and is located on the same level as the first segmental furrow (tr.). The posterior fixigena is broad, convex, and the posterolateral border curving posterolaterally into a short broad fixigenal spine. The short anterior facial suture is convergently convex, and the posterior one is long, and divergently convex.

The early meraspid pygidium is transversely subround, convex, and consists of more than two loosely articulated segments. The axial lobe is cylindrical, tapering slightly posteriorly, with both dorsal and the segmental furrows well defined. The pleural lobe is gently convex, narrow, and flat along the margin. No marginal border is known. The surface of the exoskeleton is covered by minute granules. Three or four pairs of coarse nodes are present on the fixigenae and anterior border.

The early meraspid shield is differentiated from the paraprotaspis by the presence of the anterior border, well-defined facial sutures, cylindrical glabella, and the loosely articulated pygidial segments.

Late meraspid stage (Pl. 1, figs. 14, 15, 17, 18; Text-fig. 1H, J). — The cranidium is trapezoidal in outline, has the dorsal furrows deeply demarked, and is about 0.9-1.8 mm long (sag.). The glabella is slenderly conical or cylindrical, without distinct glabellar furrows. The occipital ring is distinctly separated by a narrow occipital furrow, crescentic, arching posteriorly, convex, and marked by a minute median tubercle. The narrow preglabellar field is convex, except for the median depression. The convex anterior border curves anteriorly, and is well differentiated by the broad anterior furrow. The anterior furrow has a median embayment toward the anterior glabellar margin. The fixigena is narrower than one-half the width of the glabella, upturned from the dorsal furrow, and the palpebral lobe is horizontal. The medium-sized palpebral lobe is located on the mid-line (tr.) of the glabella, narrow, and well differentiated by palpebral furrows. The posterior fixigena is narrow, shorter (tr.) than the occipital ring, with the convex border deeply separated by a border furrow. The anterior facial suture is convergently convex, the posterior one laterally divergent, and concave to convex.

Growth of the pygidium. — The supposedly early meraspid pygidium (Pl. 1, figs. 21, 22) is about 0.70-1.50 mm in sagittal length, convex, has either loosely articulated segments or ankylosed pygidium associated with a few thoracic segments. The pygidium is convex, roundly triangular in outline, and has the conical axial ring tapering posteriorly and divided into seven to eight convex rings by distinct ring furrows. The pleural lobe is twice as wide as the axis, distinctly demarked by pleural furrows and interpleural grooves, and each segment is ended with a pair of short spines. The narrow flat margin of the ankylosed pygidium is indistinctly separated by a marginal furrow (Pl. 1, fig. 26). The late meraspid pygidium (Pl. 1, figs. 27, 28) is semicircular in outline, moderately convex, and has well-recognizable axial and pleural furrows. The conical axial lobe is extended less than the full length of the pygidium, and divided into four or five axial rings and a triangular-shaped terminal piece. The dorsal furrows deepen along the sides of the axis and shallow posteriorly. The pleural lobe is convex, about

1.5 times the width of the axis. The pygidial margin is broad, and faintly demarked by a broad marginal furrow. The late meraspid pygidium differs from the holaspid by its numerous pygidial segments and the deeper segmental furrows.

Growth of the librigena (Pl. 1, figs. 19, 20; Text-fig. 1I) — The distinct morphologic characters of the librigena are the reduction in length and final disappearence of genal spines, with the genal angles becoming rounded. The lateral border increases in width and the lateral furrow is shallower. These features are similar to those reported by Hu (1970b) for *Housia canadensis* (Walcott).

Remarks. — The ontogenic development of the present species is similar to those described for *Coosella convexa* Tasch (Hu, 1968), *Crepicephalus deadwoodensis* Hu (1971), and *Syspacheilus dunoirensis* (Miller) (Hu, 1972). All of their early protaspides have no distinct axial and pleural lobes. The late protaspid glabellae are slender, fusiform, and without distinct glabellar segments. The meraspid shields are marked by paired coarse granules on the fixigenae, the anterior borders, and the pygidial pleura; the glabellae are slender conical. The librigenal spines are reduced in length. Thus, these genera certainly belong to the same superageneric group and are closely related phylogenetically.

Figured specimens. — Cranidium, UCGM 42616; Cranidia, UCGM 42616r,x; Librigenae, UCGM 42616s,t; Pygidia, UCGM 42616u, v,y,a′-c′; Hypostomata, UCGM 42616p,w; Anaprotaspis, UCGM 42616a; Metaprotaspides, UCGM 42616b-d; Paraprotaspides, UCGM 42616e-i; Early meraspides, UCGM 42616j-m; Late meraspides, UCGM 42616n-q.

Family **ASAPHISCIDAE** Raymond, 1924

Genus **BLOUNTIA** Walcott, 1916

Blountia nixonensis Lochman Pl. 2, figs. 1-35; Text-fig. 2A-J

Blountia nixonensis Lochman, (Lochman and Duncan, 1944), p. 42, pl. 4, figs. 7-12. (Not Palmer, 1954, p. 722, pl. 79, fig. 4.)

Remarks. — A small piece of medium crystalline, platy, gray limestone was collected from the northern Black Hills, near Deadwood City, which contains abundant *Blountia nixonensis* Lochman, a few *Cheilocephalus* sp. and *Glaphyraspis* sp. No. exoskeletons belonging to *Aphelaspis* were found. The material is most similar to specimens from Montana reported by Lochman (Lochman and Duncan, 1944), and less similar to material from Utah described by Palmer (1962). However, the present species was synonymized with *B. bristolensis* Resser by Palmer (1962). In comparison, the type specimens of *B. bristolensis* have narrower and longer glabellae, and subtriangular pygidia, whereas those of *B. nixonensis* are shorter and broader, and the pygidium is semicircular in outline. The cranidium reported from Utah has an anterior border strongly arching forward, and the genal spine is broader. These differences suggest that *B. nixonensis* is an independent species that is not synonymous with *B. bristolensis*.

B. nixonensis differs from species from the *Cedaria* Zone and *Crepicephalus* Zone in having forwardly located palpebral lobes semicircular pygidia.

Horizon and Locality. — Deadwood Formation, Upper Cambrian, *Aphelaspis* Zone; Bear Butte section, about six miles southeast of Deadwood City, South Dakota.

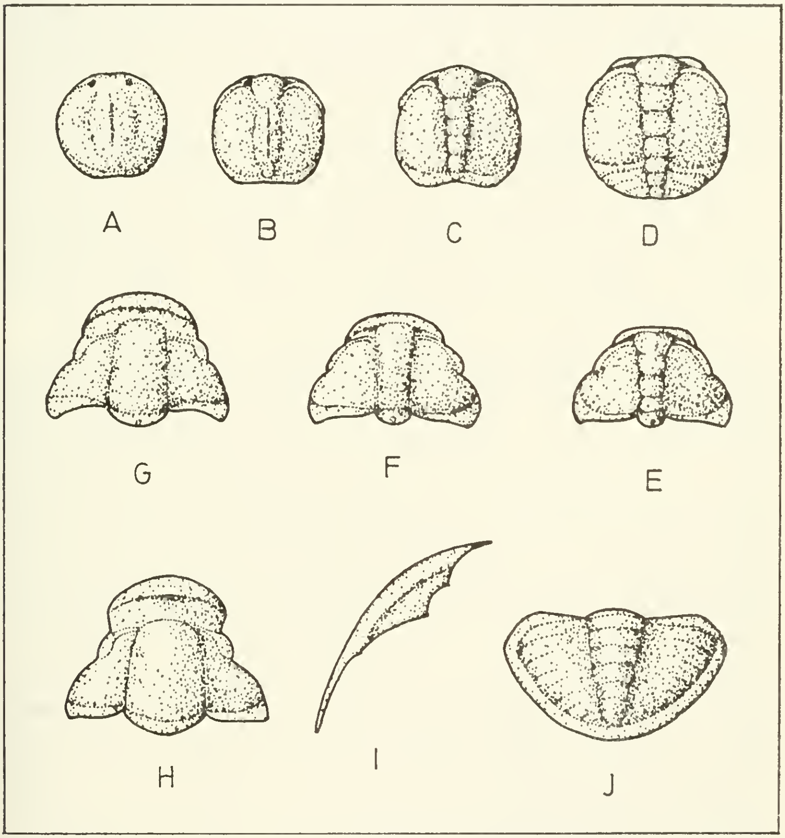
Blountia nixonensis Lochman, ontogeny

Anaprotaspid stage (Pl. 2, fig. 1; Text-fig. 2A). — The shield is round, moderately convex, with a central well-differentiated axial furrow, and is about 0.30-0.40 mm in sagittal length. The central furrow is extended nearly the full length of the shield and ends both anteriorly and posteriorly before reaching the margin. A pair of minute pits is present at the sides of the frontal lobe. The axial lobe, axial segments, and dorsal furrows are not recognizable. The exoskeletal surface is faintly granulated or roughened.

Metaprotaspid stage (Pl. 2, figs. 2-6; Text-fig. 2B, C). — The shield is round or subround, convex, and about 0.40-0.55 mm in length (sag.). The axial lobe is faintly delimited by a dorsal furrow. The central axis is distinctly differentiated by longitudinal furrows. The axial lobe is composed of five segments, a large triangular frontal lobe, two pairs of central nodes, a rounded fourth axial ring, and a rounded triangular terminal piece. The round-or oval-shaped frontal pits are impressed at the sides of the frontal lobe. A pair of faint eye-brow ridges extend posterolaterally from the anterolateral corners of the frontal lobe. The fixigena is convex, twice as wide as the axis, and surrounded by a narrow and faintly defined marginal border. Exoskeletal surfaces are minutely granulated.

The metaprotaspid stage differs from the anaprotaspid in having the axial lobe well delimited by a dorsal furrow and the presence of five glabellar segments. The frontal pits are elongate, and the shield becomes roundly subquadrate.

Paraprotaspid stage (Pl. 2, figs. 7-15; Text-fig. 2D). — The shield is roundly quadrate to oval in outline, convex, and about 0.45-0.70 mm in length (sag.). The axial lobe is cylindrical, ex-



Text-figure 2. Growth series of *Blountia nixonensis* Lochman. A. Anaprotaspis, × 36; B, C. Metaprotaspides, × 30, × 28; D. Paraprotaspis, × 28; E, F. Small and large-sized early meraspid cranidia, × 20, × 15; G. Late meraspid cranidium, × 12; H. Holaspid cranidium, × 6; I. Holaspid librigena, × 30; J. Holaspid pygidium, × 5 (all drawings were made from photographs.)

panded forward, and well defined by dorsal and segmental furrows. The first glabellar segment is largest and those that follow posteriorly are reduced in size. The occipital ring is smaller than the fourth glabellar segment and convex. The fixigena is about twice as wide as the glabella at mid-line (tr.) of the shield. The eye-brow ridges are short and extend laterally from the sides of the frontal lobe. The round or triangular frontal pits are distinctly demarked on the sides of the frontal lobe. The narrow elevated palpebral ridges are extended posterolaterally from the sides of the frontal pits and may be the earliest indication of the librigenal locality. The fixigenal border is narrow, and curves laterally to form a short fixigenal spine. The protopygidium is transversely lenticular, turned downward from the posterior cephalic margin, and composed of one to three segments. The surface of the shield is faintly granulated.

The paraprotaspid stage is differentiated from the earlier one by the presence of the protopygidium, a forward expanding axis, glabellar segments that are complete, eye-brow ridges that are shorter, and well differentiated palpebral ridges.

Early meraspid stage (Pl. 2, figs. 16-21; Text-fig. 2E, F).— The cranidium is trapezoidal in outline, convex, and about 0.60-1.20 mm in length (sag.). The cylindrical glabella is deeply impressed by dorsal furrows, slightly expanded forward, and divided into four convex glabellar segments by furrows. The glabellar furrows deepen laterally near the axial furrow and shallow across the central axis. The anterior glabellar segment is the largest, transversely oval, while those following it posteriorly are rounded and small. The occipital ring is smaller than the glabellar segments, transversely oval, and without an occipital spine or node. The convex fixigena slopes gently toward the anterior margin, and is about equal to or slightly narrower than the glabella between the dorsal furrows and the posterior end of the palpebral lobes. The narrow crescentic palpebral lobes are located in front of the mid-line (tr.) of the cranidium, elevated, arching anterolateral, and distinctly demarked by the occipital furrow. The palpebral ridge is elevated, running continuously from the anterior palpebral lobe and terminating at the side of the first glabellar segment. The narrow anterior border is convex, arches gently anteriorly, and is well defined by the frontal furrow. The posterior fixigena is broad, triangular, convex, has the narrow rear border running slightly posteriorly at the extreme end, and shows an obtuse projection.

The early meraspid pygidium (Pl. 2, figs. 28-32) is semicircular in outline, moderately convex, and divided into six segments by furrows. These segments are loosely articulated and show no ankylosed terminal plate. The lateral end of each segment is flat and terminated by a pair of short broad spines. The broad pleural furrows are deep and the interpleural grooves are faint. The convex axial lobe is slender, conical, tapers posteriorly, is well defined by dorsal furrows, and is about one-half the width of the pleural lobe.

The supposedly early meraspid hypostoma (Pl. 2, fig. 26) is subquadrate in outline, moderately convex, and has the narrow triangular median body deeply delimited by lateral furrows. The pleural lobe is narrow, lenticular, convex, and distinctly defined by a marginal furrow. The posterior marginal border is narrow, elevated, and has two pairs of short lateral spines. The anterior wing is triangular, slopes downward, and the anterior free margin curves upward.

The exoskeletal surface of the early meraspid stage is faintly granulated, the cranidium is differentiated from the paraprotaspid by the presence of the anterior border, the clearly defined palpebral lobe and the facial sutures. The glabellar furrows are nearly complete, and the pygidium increases the number of segments.

Late meraspid stage (Pl. 2, figs. 22, 24; Text-fig. 2G). — The cranidium is trapezoidal in outline, moderately convex, and about 1.20-1.60 mm in sagittal length. The glabella is subquadrate, well defined by dorsal furrows, and the glabellar furrows are faint. The narrow-ridged occipital ring arches posteriorly and is convex below the glabella. No occipital spine or tubercle is seen. The narrow preglabellar field slopes downward, is well delimited by the broad frontal furrow, and has a median depression. The anterior border is narrow, crescentic, convex, and arches anteriorly. The fixigena is less than one-half the width of the glabella, convex, slopes downward from the dorsal furrow, and has the small palpebral lobe located in front of the mid-line (tr.) of the cranidium. The palpebral lobe and ridges are faintly defined. The posterior fixigena is triangular and convex. The posterior border is well delimited by a furrow that is directed posterolaterally. The anterior facial suture is convergently convex, and the posterior one is divergently convex.

The attributed librigena of the late meraspid stage (Pl. 2, fig. 27) is crescentic with a broad marginal border, and medium-sized genal spine. The lateral furrow is well defined, and concave. The ocular platform is of medium width, convex, and has the ocular ring located anteriorly at the inner free margin.

The late meraspid stage differs from the early meraspid stage in the presence of the preglabellar field, subquadrate glabella, narrower occipital ring, smaller and posteriorly located palpebral lobes. The pygidial segments are well ankylosed.

The late meraspides are differentiated from holaspides by the narrower, longer glabellae, pygidia that are triangular with well-depressed segmental furrows; whereas holaspides are shorter, and broader, and the pygidia are nearly semicircular with incomplete segmental furrows.

Remarks. — The ontogenic development of *Blountia nixonensis* is similar to that of *Kingstonia ara* (Walcott) (Hu, 1968), *Nixonella montanensis* Lochman (Hu, 1972), and *Komaspidella laevis* Rasetti (Hu, 1970a). The protaspid shields are all marked by distinct frontal pits, deeply impressed dorsal furrows, forwardly expanded glabellae, and well-defined glabellar segments. The meraspid cranidia are trapezoidal, having cylindrical or subquadrate glabellae tapering slightly posteriorly, and the faintly demarked glabellar furrows. Their immature librigenae are narrow, crescentic, and the pygidia are semicircular. Therefore, these similarities are possibly the indication of close phylogenetic relationship, and they belong to the same suprageneric group.

Figured specimens. — Cranidium, UCGM 42617; Pygidia, UCGM 42617a′,b′,d′,e′,f′-h′; Librigena, UCGM 42617z; Thoracic segment UCGM 42617c′; Hypostoma, UCGM 42617y; Anaprotaspis, UCGM 42617a; Metaprotaspides, UCGM 42617b-f; Paraprotaspides, UCGM 42617g-o; Early meraspides, UCGM 42617p-u; Late meraspides, UCGM 42617v-x.

Family **PLETHOPELTIDAE** Raymond, 1925

Genus **PLETHOPELTIS** Raymond, 1913

Plethopletis arbucklensis Stitt Pl. 3, figs. 1-35; Text-fig. 3A-O

Plethopeltis arbucklensis Stitt, 1971, p. 35, pl. 8, figs. 10-15.

Remarks. — The species is represented by abundant specimens of both adult and immature exoskeletons showing a continuous growth sequence. The adult forms are represented by two different morphologic groups. The first group (Pl. 3, figs. 22, 25, 27, 29, 30, 34, 35) has cranidia with broader glabellae, narrower preglabellar fields, and pygidia that are roundly subtriangular in outline and marked by well-differentiated axial rings. The second group (Pl. 3, figs. 26, 28, 31, 32, 33) has narrower and longer glabellae, preglabellar fields are broader, pygidia are triangular in outline, the pygidial marginal borders are broader and deeply concave, and only three axial rings are present. These differences are interpreted as sexual dimorphism. The first group is postulated as "male" and the later the "female" form. The male individuals are more numerous than the females.

The material studied is a single piece of light gray, medium crystalline, platy limestone. *Homagnostus* sp. skeletal fragments are also recovered beside those of *P. arbucklensis,* but no *Missisquoia* or *Symphysurina* are known as reported from the Arbuckle Mountains, Oklahoma, by Stitt (1971). *P. arbucklensis* is certainly close to *"Plethometopus albertensis"* Resser (not Resser, 1942) reported from Little Rocky Mountains, Montana, by Lochman (1950); both possess similar shaped cranidia, deep dorsal furrows, short occipital spines, and semicircular to roundly triangular pygidia. They are possibly synonymous and occur in the same stratigraphic horizon.

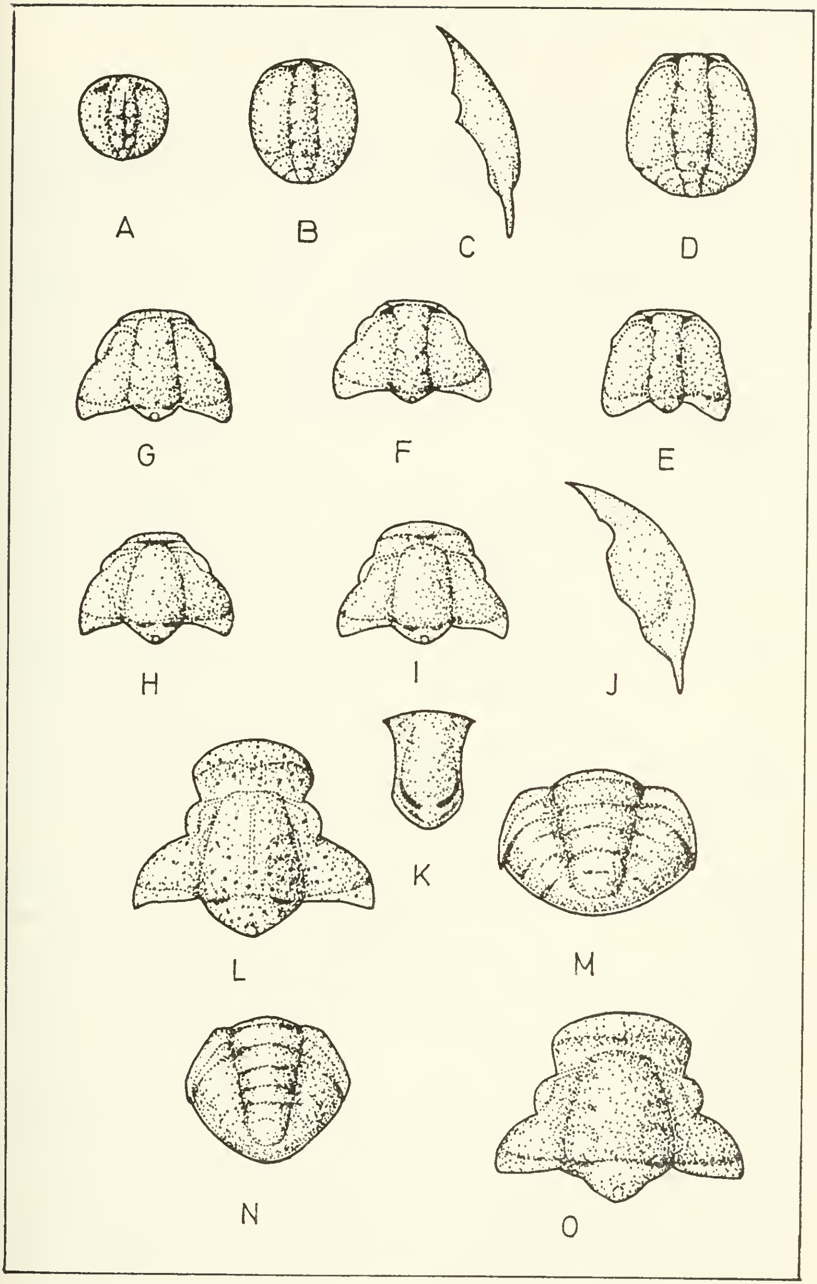
For the geologic age, Lochman (1950) stated that "it (*Plethometopus albertensis* Resser) should be considered somewhat later in age — the lower *Dikelocephalus* Zone". Stitt (1971) placed *P. arbucklensis* at the lowest *Missisquoia* Zone, the lowest Ordovician. Taylor (1971) recognized four trilobite zones in the upper member of the Notch Peak Formation, *i.e., Saukiella junia, Saukiella serotina, Corbinia apopsis,* and *Missisquoia,* in the central Great Basin, Nevada, and Utah regions. He regarded the *Missisquoia* Zone as Ordovician, and the *Corbinia apopsis* Zone as the latest Cambrian (from Hintze, 1973, p. 5). Hu (1973) also reported *Missisquoia, Symphysurina, Euloma, Highgatella* and some other trilobites from the same section — Sheep Mountain, Wyoming, and he placed this fauna in the *Missisquoia* Zone. Unfortunately, this faunal assemblage contains no *P. arbucklensis*. The specimens of *P. arbucklensis* were collected immediately below the *Missisquoia-Symphysurina* Zone. Therefore, *P. arbucklensis* may lie between *Missisquoia* Zone and *Corbinia apopsis* Zone in Black Hills region, and belongs to lowest Tremadocian.

Horizon and locality. — Deadwood Formation, Lowest Tremadocian, possibly in *Corbinia apopsis-Missisquoia* Zones. Southern slope of Sheep Mountain, near Bearlodge Ranch, east-central Wyoming and northwestern South Dakota.

Plethopeltis arbucklensis Stitt, ontogeny

Metaprotaspid stage (Pl. 3, fig. 1; Text-fig. 3A). — The shield is moderately convex, with well-differentiated axis and pleuron, and is about 0.30 mm in sagittal length. The axis is slender, tapering both anteriorly and posteriorly from the mid-line (tr.), and has a triangular frontal lobe, two pairs of central nodes, a third lenticular axial ring, and a small terminal tubercle. The dorsal furrow is shallow but well defined. A pair of anterior pits is distinctly demarked at the side of the frontal lobe. The pleural lobe is moderately convex, narrower than the axis, and slopes downward along the outer margin. No marginal border is visible. The exoskeletal surface is minutely granulated.

Paraprotaspid stage (Pl. 3, figs. 2-6; Text-fig. 3B, D). — The shield is elongate-oval in outline, moderately convex, and composed of a well-defined cranidium and small protopygidium that together vary from 0.40-0.60 mm in length (sag.). The cranidium occupies about two-thirds the length of the total shield, and is convex with well-differentiated axial and pleural lobes. The axis is deeply demarked by a dorsal furrow, fusiform, tapering both anteriorly and posteriorly from the mid-line (tr.) of the glabella, and divided into four axial rings by indistinct furrows. The occipital ring is convex, lenticular, and deeply separated by the occipital furrow. The paired frontal pits are distinct. A pair of eye-brow ridges extend from the sides of the frontal lobe, and terminate in front of the small palpebral lobes. The convex pleuron is about the same width as the axis. The posterior fixigenal border arches posterolaterally from the occipital ring, and ends in a broad-based projection.



Text-figure 3. Growth sequence of *Plethopeltis arbucklensis* Stitt. A. Metaprotaspis, × 37; B, D. Small and large-sized paraprotaspides, × 34, × 36; C. Immature librigena, × 8; E-G. Three different sized early meraspid cranidia, × 20; × 21, × 20; H, I. Two different sized late meraspid cranidia, × 16, × 15; J. Holaspid librigena, × 5; K. Small hypostoma, × 3; L, N. "Female" cranidium and pygidium, × 8, × 5; M, O. "Male" pygidium and cranidium, × 4, × 7. (All drawings were made from photographs.)

The protopygidium contains one or more segments, which are semicircular in outline, convex, and without any recognizable marginal spines. The axial rings are convex and delimited by dorsal furrows. The pleural lobe is convex, and faintly impressed by two shallow, broad pleural furrows.

Early meraspid stage (Pl. 3, figs. 7-10, 13-15; Text-fig. 3E, G). — The cranidium is trapezoidal in outline, moderately convex, with deeply impressed dorsal furrows and varies in length from about 0.50-0.80 mm (sag.). The glabella is slender conical, tapering forward and divided into four rings by indistinct furrows. The convex lenticular occipital ring is convex, bears a minute median node, and is deeply separated by the occipital furrow. The fixigena is convex, about the same width as the axis between the palpebral and the dorsal furrows. The small palpebral lobes are located at one-fourth the length of the cranidium, and are elevated, shallowly delimited by the palpebral furrows. The posterior fixigena is convex, and slopes downward along the anterior free margin. The posterior fixigenal border is elevated, arches posterolaterally from the occipital ring, and ends in a broad-based spine. The anterior facial suture line is short and convergent; the posterior one is strongly divergent convex. The anterior border is narrow, elevated, and arches slightly anteriorly. The cranidial surface is covered by minute granules.

During the early meraspid stage, the glabella changes from narrow to broad, and from slender conical to cylindrical; the glabellar furrows from incomplete to complete. The anterior border increases in width, the palpebral lobe moves backward from near the side of the anterior border and shows well-recognizable anterior facial sutures. The anterior facial suture is long and the posterior facial suture is short.

Late meraspid stage (Pl. 3, figs. 11, 12, 16-19, 23, 24; Text-figs. 3H, I). — The cranidium is trapezoidal in outline, moderately convex, and about 1.0-1.6 mm in length (sag.). The glabella is conical, tapering forward. The occipital ring is transverse, convex, drawn out to a posteriorly directed occipital median tubercle, and delimited by a narrow occipital furrow. The anterior border is convex, arching anteriorly, and well delimited by the frontal furrow. The preglabellar field is narrow and has a median depression. The fixigena is subtriangular, convex, and has medium-sized palpebral lobes located at one-third the length of the glabella (tr.). The palpebral lobes are narrow, elevated, and defined by the palpebral furrow. The posterior fixigenal border is about the same width as the occipital ring (tr.), convex, and delimited by a border furrow. The meraspid librigena (Pl. 3, fig. 12; Text-fig. 3C) is narrow and crescentic. The convex ocular platform is indistinctly differentiated by a lateral furrow. The lateral and the posterior furrows are not connected at the genal angle. A short stout genal spine is directed posterolaterally. The exoskeletal surface is covered by coarse and minute granules.

During the late meraspid stage, the distinct morphologic changes are: the glabella increases in width, the fixigena becomes narrower, and the preglabellar field becomes broader.

The meraspid pygidium is triangular to semicircular in outline, convex, and composed of five to six loosely articulated segments (Pl. 3, figs. 23, 24). The conical axis tapers posteriorly and is convex. The pleural lobe is gently convex. Four to five pairs of marginal spines are recognizable which form the lateral end of each pygidial segment.

Remarks. — The early ontogenic development (*i.e.*, protaspid period) of *P. arbucklensis* closely resembles that of *Acerocare ecorne* Angelin (Hu, 1971), *Ptychaspis bullasus* Lochman and Hu (Hu, 1971), *Leptoplastus crassicornis* (Westergård) (Whitworth, 1970), *Peltura scarabaeoides* (Wahlenberg) (Hu, 1964, Whittington, 1958), and *Paranumia triangularia* Hu (Hu, 1973). All possess the fusiformed axial lobe and transverse oval axial rings. But during the late stages, *i.e.*, meraspid period, the axial lobe becomes cylindrical or conical and the ring furrows are separated. Those characteristics are most similar to the same growth period of *Ponumia obscura* (Lochman) (Hu, 1970b), and *Housia canadensis* (Walcott) (Hu, 1970b). These phenomena might indicate that the phylogenetic development of *P. arbucklensis* is closely related to *A. ecorne*, *P. bullasus*, *L. crassicornis*, *P. scarabaeoides*, and *P. triangularia*.

The late ontogenic similarities among the present species and *P. obscura*, and *Housia candensis* are possibly due to convergent evolution. They are apparently developed from different ancestors.

Figured specimens. — Cranidium, UCGM 42618; Cranidia, UCGM 42618a′,d′-c′; Librigenae, UCGM 42618 l, u; Pygidia, UCGM 42618v-z,b′,f′,g′; Hypostoma, UCGM 42618t; Metaprotaspides, UCGM 42618a; Paraprotaspides, UCGM 42618b-f; Early meraspides, UCGM 42618g-j,m-o; Late meraspides, UCGM 42618k,p-s.

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EXPLANATION OF PLATE 1

Figure

1-29. **Coosia albertensis** Resser.

1. Anaprotaspis; notice the pair of distinct pits marked on the anterior shield margin. × 50, UCGM 42616a.

2-4. Metaprotaspides, showing the presence of the longitudinal furrow along the central axis, and the rather faintly impressed dorsal furrows. 2. × 50, UCGM 42616b; 3. × 48, UCGM 42616c; 4. × 48, UCGM 42616d.

5-9. Paraprotaspides, showing the differentiations of the axial and pleural lobes. 5. × 40, UCGM 42616e; 6. × 40, UCGM 42616f; 7. × 38, UCGM 42616g; 8. × 40, UCGM 42616h; 9. × 42, UCGM 42616i.

10-13. Four early meraspides, showing the presence of the anterior border and the glabellar lobes. 10. × 38, UCGM 42616j; 11. × 30, UCGM 42616k; 12. × 24, UCGM 42616l; 13. × 30, UCGM 42616m.

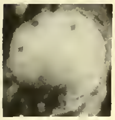
14, 15, 17, 18. Several late meraspid cranidia; notice the presence of the preglabellar field. 14. × 13, UCGM 42616n; 15. × 14, UCGM 42616o; 17. × 19, UCGM 42616q; 18. × 8, UCGM 42616r.

16, 23. Two nearly complete hypostomata. 16. × 15, UCGM 42616p; 23. × 10, UCGM 42616w.

19, 20. A small and a large-sized librigena. 19. × 6.5, UCGM 42616s; 20. × 1.8, UCGM 42616t.

24, 25. Two large-sized cranidia, showing the morphologic varieties of the glabella and the anterior border. 24. × 2.4, UCGM 42616x; 25. × 1.7, UCGM 42616.

21, 22, 26-29. A growth series of pygidia. 21. × 19, UCGM 42616u; 22. × 10, UCGM 42616v; 26. × 7, UCGM 42616y; 27. × 7, UCGM 42616a′; 28. × 6, UCGM 42616b′; 29. × 10, UCGM 42616c′.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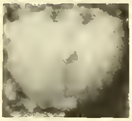
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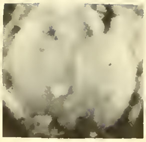
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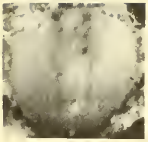
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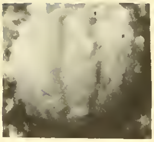
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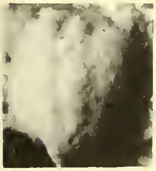
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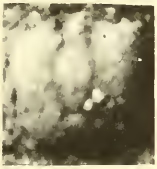
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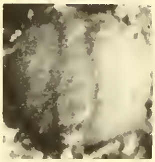
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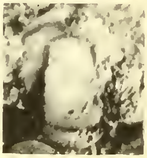
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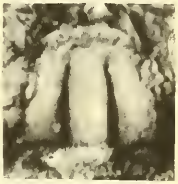
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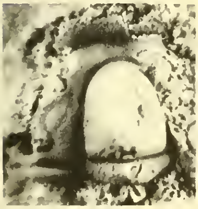
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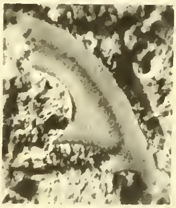
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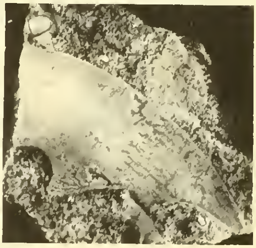
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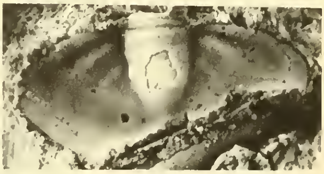
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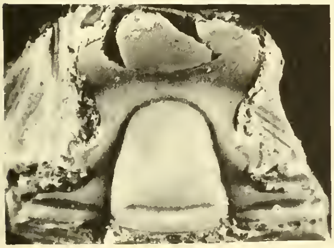
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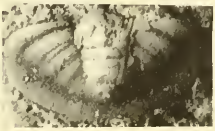
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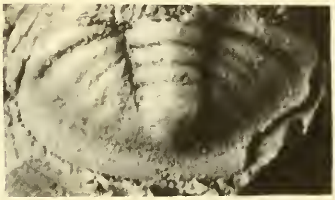
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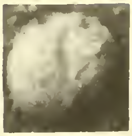
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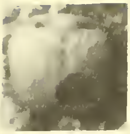
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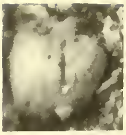
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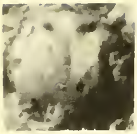
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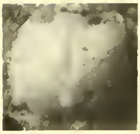
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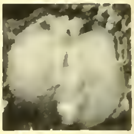
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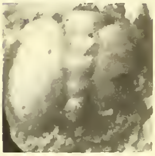
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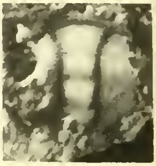
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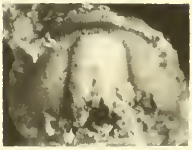
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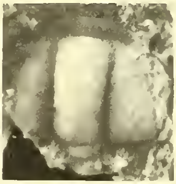
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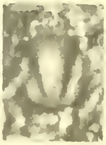
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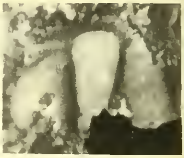
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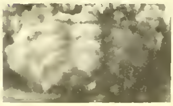
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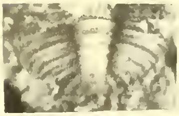
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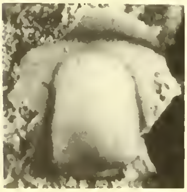
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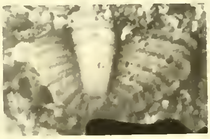
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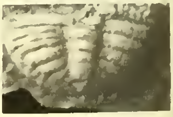
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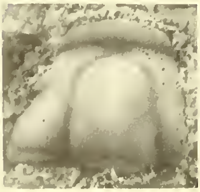
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EXPLANATION OF PLATE 2

Figure

1-35. **Blountia nixonensis** Lochman.

1. Anaprotaspis; notice the median furrow along the central axis. × 36, UCGM 42617a.

2-6. A few metaprotaspides, showing the presence of the glabellar nodes. 2. × 30, UCGM 42617b; 3. × 30, UCGM 42617c; 4. × 30, UCGM 42617d; 5. × 28, UCGM 42617e; 6. × 28, UCGM 42617f.

7-15. Several paraprotaspides, showing the completion of the axial rings and the presence of the protopygidium. 7. × 28, UCGM 42617g; 8. × 28, UCGM 42617h; 9. × 28, UCGM 42617i; 10. × 28, UCGM 42617j; 11. × 28, UCGM 42617k; 12. × 30, UCGM 42617l; 13. × 30, UCGM 42617m; 14. × 25, UCGM 42617n; 15. × 30, UCGM 42617o.

16-21. A growth series of early meraspid cranidia, showing the forwardly expanded glabella, and the presence of the anterior border. 16. × 25; UCGM 42617p; 17. × 25, UCGM 42617q; 18. × 20, UCGM 42617r; 19. × 14, UCGM 42617s; 20. × 21, UCGM 42617t; 21. × 24, UCGM 42617u.

22-24. A few late meraspid cranidia, showing the presence of the preglabellar field and subquadrate glabella. 22. × 12, UCGM 42617v; 23. × 11, UCGM 42617w; 24. × 9, UCGM 42617x.

25. A nearly complete cranidium. × 6, UCGM 42617.

26. An immature hypostoma. × 40, UCGM 42617y.

27. A nearly complete librigena. × 30, UCGM 42617z.

30. A thoracic segment. × 6, UCGM 42617c′.

28, 29, 31-35. A growth sequence of pygidia; notice the progressive ankylosis of the pygidial segments. 28. × 30, UCGM 42617a′; 29. × 30, UCGM 42617b′; 31. × 26, UCGM 42617d′; 32. × 20, UCGM 42617e′; 33. × 8, UCGM 42617f′; 34. × 8, UCGM 42617g′; 35. × 5, UCGM 42617h′.

Explanation of Plate 3

Figure

1-35. **Plethopeltis arbucklensis** Stitt.

1. A metaprotaspid shield, showing the well differentiated axial nodes. × 37, UCGM 42618a.

2-6. A few paraprotaspides, showing the well-defined axis and the protopygidium. 2. × 34, UCGM 42618b; 3. × 34, UCGM 42618c; 4. × 34, UCGM 42618d; 5. × 28, UCGM 42618e; 6. × 36, UCGM 42618f.

7-10, 13-15. Several early meraspid cranidia, showing the development of the anterior borders. 7. × 24, UCGM 42618g; 8. × 24, UCGM 42618h; 9. × 31, UCGM 42618i; 10. × 15, UCGM 42618j; 13. × 20, UCGM 42618m; 14. × 21, UCGM 42618n; 15. × 20, UCGM 42618o.

12. An immature librigena, showing the narrow ocular platform. × 8, UCGM 42618l.

11, 16-19. A few late meraspid cranidia, showing the development of the preglabellar field. 11. × 16, UCGM 42618k; 16. × 11, UCGM 42618p; 17. × 20, UCGM 42618q; 18. × 15, UCGM 42618r; 19. × 12, UCGM 42618s.

20. A nearly complete hypostoma. × 3.3, UCGM 42618t.

22. A broken librigena. × 5, UCGM 42618u.

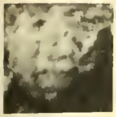
23, 24. Two immature pygidia, showing the loosely articulated thoracic segments. 23. × 14, UCGM 42618v; 24. × 24, UCGM 42618w.

26, 33. Two "female" pygidia. 26. × 7, UCGM 42618y; 33. × 5, UCGM 42618f′.

28, 31, 32. Three "female" cranidia; notice the conical glabella and the broad preglabellar field. 28. × 12, UCGM 42618a′; 31. × 8, UCGM 42618d′; 32. × 10, UCGM 42618e′.

25, 27, 29, 34. Four "male" pygidia; notice the narrow and low concave marginal border. 25. × 7, UCGM 42618x; 27. × 10, UCGM 42618z; 29. × 5, UCGM 42618b′; 34. × 4.5, UCGM 42618g′.

21, 30, 35. Two "male" cranidia, showing the subquadrate glabella and the narrow preglabellar field. 30. × 4, UCGM 42618c′; 21, 35. Side and dorsal views of a nearly complete cranidium, × 7, UCGM 42618.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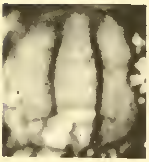
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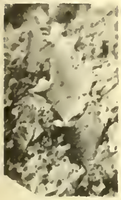
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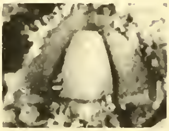
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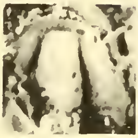
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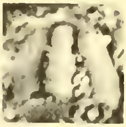
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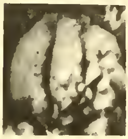
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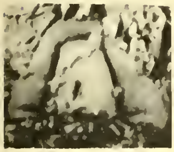
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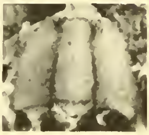
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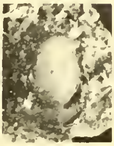
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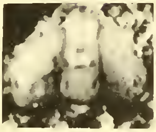
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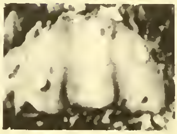
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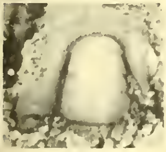
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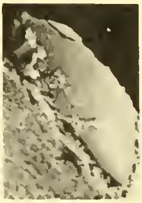
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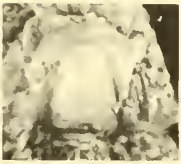
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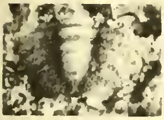
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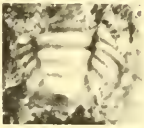
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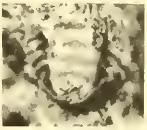
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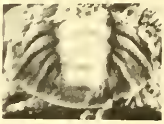
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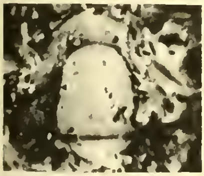
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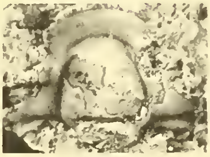
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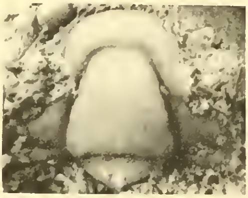
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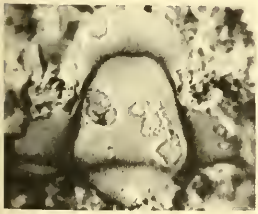
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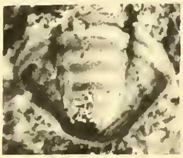
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THE ANCESTRY, GEOGRAPHICAL EXTENT, AND FATE OF THE BRASSFIELD CORAL FAUNA (MIDDLE LLANDOVERY, NORTH AMERICA)*

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ABSTRACT

To date, 53 coral species have been identified from the Brassfield Formation (here considered to include the Noland Formation) of Middle Llandovery age, in the Cincinnati Arch area (southwest Ohio, southeast Indiana, and north-central Kentucky). This fauna was restricted to a relatively small area; only eight of the species are known to have occurred outside of the region during Middle Llandovery time. There is no single ancestral homeland from which this fauna migrated. Rather, about 12 of the species appear to have existed in various parts of the world before Brassfield time, and the rest presumably originated in or near the Cincinnati Arch area. Between 27 and 32 of the species survived the termination of Brassfield sedimentation and became important elements of the later Silurian world-wide coral faunas.

INTRODUCTION

A study of the coral fauna of the Middle Llandovery Brassfield Formation (here considered to include the Noland Formation) of southwest Ohio, southeast Indiana and north-central Kentucky (the Cincinnati Arch), led to questions about its origin, the area it occupied, and its ultimate fate. To gain insight into these problems, an extensive search was made of the literature on Late Ordovician through Wenlockian (and some Ludlovian) corals throughout the world. In all, some 200 references were consulted, with the object of gaining information from as many parts of the world as possible (Text-fig. 1).

Studies by Berry and Boucot (1970, 1972), Hamada (1958), Gignoux (1950), and Manten (1971) made it possible to define the ages of almost all occurrences sufficiently to give meaningful information on the history of these species before, during, and after Brassfield sedimentation (Table I). These results are presented here, using the most up-to-date map currently available to me (Briden, *et al.*, 1973). Space limitation precludes a presentation herein of species descriptions and figures, and of an itemization of the references used in this search, but these will be included in a later work on the Brassfield coral fauna.

It should be noted that all references consisted of descriptions and figures (or, in the absence of figures, of descriptions sufficiently detailed to give reasonable confidence of identification). Where pos-

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* Scientific contribution of the Geology Department of the University of Cincinnati, and the Geology Department of the Buffalo Museum of Science.

Text-figure 1.—Map showing continental distribution during the Silurian and Early Devonian. Localities for which coral data were obtained in this study are marked by numbers which represent the approximate number of references covering that spot. Numerous other references did not apply to one specific locality and are not included in this count. Longitudinal scale in 30° intervals. Base map after Briden, *et al.* (1973, p. 127).

sible, the specimens themselves were examined, but these represent a small number of the species considered. In no instance was a faunal list, or the mere mention of an occurrence used as data in this compilation.

The Brassfield Coral Fauna. — The 53 coral species so far recognized in this fauna (Table II) constitute the earliest-known major Silurian coral fauna in North America. This fact, together with the sparse data available on Llandovery corals, makes the Brassfield fauna a critical link between the corals of the Ordovician, and those that populated the vast cnidarian empire that followed, giving to the Silurian the cognomen "Age of Corals".

The intermediate position occupied by the Brassfield corals between these two faunas is strikingly shown by its elements. Here we find an intimate association of *Catenipora* with *Halysites,* of *Paleo-*

Table I

Table I. — Lists of Brassfield corals arranged geographically and chronologically. Generic names are written out in Table II. Ed.

PRE-BRASSFIELD	COEVAL WITH BRASSFIELD	POST-BRASSFIELD
	EASTERN UNITED STATES	
P. conferta		*A. mamillare*
Cladochonus sp. C.		*C. spongiosa*
A. labechii ?		*S. benedicti*
		S. ipomaea
		D. linguliferum ?
		T. radicula ?
		H. nitidus
		H. meandrinus (?) ?
		F. forbesi
		F. hisingeri
		Favosites sp. A. n. sp.
		A. labrosus
		S. flexuosa
		H. spongodes

	NORTHERN GREAT LAKES	
P. conferta	*S. socialis*	*T. radicula*
P. prolificus	*F. favosus* ?	*A. mamillare*
		D. stokesi
		F. favosus ?
		F. hisingeri
		P. prolificus
		A. labrosus ?
		A. labechii ?
		S. reteformis
		P. eminula?
	CANADIAN MARITIMES	
P. conferta	*P. pelagicum*	*A. mamillare*
P. exigua	*F. favosus* ?	*D. stokesi*
P. prolificus	*F. forbesi*	*F. favosus* ?
F. forbesi	*F. hisingeri*	*F. forbesi*
	P. prolificus	*F. hisingeri*
	P. conferta	*P. prolificus*
		H. nitidus
		A. labechii
		S. flexuosa
		P. conferta
		P. exigua
		P. eminula ?
	BALTIC	
P. conferta	*P. pelagicum*	*T. cylindrica*
C. gotlandica	*R. daytonensis* ?	*S. patellatum*
P. suecicum		*R. daytonensis* ?
D. linguliferum ?		*F. forbesi*
		F. hisingeri
		P. prolificus
		H. catenularius
		C. gotlandica
		P. exigua
		H. spongodes
		H. spongiosa ?
	BRITAIN	
		S. benedicti
		C. lindstroemi
		D. linguliferum ?
		F. forbesi
		F. hisingeri
		A. labrosus
		A. labechii
	SIBERIAN PLATFORM	
P. primarium		*S. socialis*
P. cf. *P. cybaeus* (an ancestral species)		*C. typus*

SW SIBERIA AND IRAN

S. patellatum
S. socialis
H. catenularius
C. gotlandica

FAR EAST

P. prolificus
  Japan
H. catenularius
  Japan
P. conferta
  Japan
H. spongodes
  Kansu Prov., China

MISCELLANEOUS LOCALITIES

P. conferta
  NE Canadian Arctic
P. prolificus
  Manitoba
R. daytonensis ?
  Venezuela

P. conferta
  Manitoba

T. radicula
  Oklahoma
A. mamillare
  Iowa
S. socialis
  Lake Timiskaming, in Canada
F. favosus
  Iowa, Brit. Columbia
F. hisingeri
  Bohemia
H. nitidus ?
  Brit. Columbia, Venezuela
H. spongodes
  Bohemia

H. catenularius of undetermined age in Australia
P. conferta Silurian of Korea, and in Silurian of Siberian Platform
F. forbesi Silurian of Korea
T. radicula Silurian of Great Basin (western U.S.)
Favosites sp. A. n. sp. Silurian of Baffin Island
F. hisingeri Llandovery of Southampton Island (Canadian Arctic)
A. labrosus Silurian of Canadian Maritimes

TABLE II

Table II. — The corals of the Brassfield fauna, arranged systematically, and with their ranges shown. Column *A* corresponds to pre-Brassfield time (*O* indicates a Late Ordovician date, *S* an Early Llandovery date). Column *B* corresponds to Brassfield time, and includes only those Brassfield species also found outside of the Cincinnati Arch area. Column *C* corresponds to post-Brassfield time, up to and including the Early Ludlovian. An *X* in a column indicates the occurrence of that species in that time period. Family assignments for the rugose genera are based upon those of Moore (1956). The assignments for the tabulates and heliolitids are based on Sokolov (1962).

TABLE II

RUGOSA	A	B	C
Streptelasmatidae			
Streptelasma, n. sp.			
Dinophyllum stokesi (Milne-Edwards and Haime), 1851			X
Dinophyllum hoskinsoni (Foerste), 1890			
Dinophyllum, n. sp.			
Dalmanophyllum linguliferum (Foerste), 1906	X? (O)?		X?
Dalmanophyllum obliquior (Foerste), 1890			
Rhegmaphyllum daytonensis (Foerste), 1890	X? (S)	X?	X?
Schlotheimophyllum patellatum (Schlotheim), 1820			X
Schlotheimophyllum benedicti (Greene), 1900			X
Schlotheimophyllum ipomaea (Davis), 1887			X
Paliphyllidae			
Paliphyllum primarium Soshkina, 1955	X (O)		
Paliphyllum succicum Neuman, 1968 "var." new	X (O)		
Paliphyllum, n. sp.			
Cyathactis typus Soshkina, 1955			X
Cyathactis sedentarius (Foerste), 1906			
Protocyathactis cf. *P. cybaeus* Ivanovskiĭ, 1961	X? (O)		
Tryplasmatidae			
Tryplasma radicula (Rominger), 1876			X
Tryplasma cylindrica (Wedekind), 1927			X
Tryplasma sp.			
Calostylidae			
Calostylis spongiosa Foerste, 1906			X
Calostylis lindstroemi Nicholson and Etheridge, 1878			X
Chonophyllidae			
Strombodes socialis (Soshkina), 1955		X	X
Arachnophyllidae			
Arachnophyllum mamillare (Owen), 1844			X
Arachnophyllum granulosum Foerste, 1906			
Petrozium pelagicum (Billings), 1865a		X	
Craterophyllum(?) *solitarium* (Foerste), 1906			
Halliidae			
Pycnactis(?), n. sp.			
Genus new			

TABULATA	A	B	C
Favositidae			
Favosites favosus (Goldfuss), 1826		X?	X
Favosites forbesi Milne-Edwards and Haime, 1851, "var." new	X (S)	X	X
Favosites hisingeri Milne-Edwards and Haime, 1851		X	X
Favosites sp. A, n. sp.			X
Favosites sp. B, n. sp.			
Paleofavosites prolificus (Billings), 1865b	X (O)	X	X
Halysitidae			
Halysites catenularius (Linnaeus), 1767			X
Halysites nitidus Lambe, 1899			X
Halysites meandrinus (?) (Troost), 1840			X (?)
Catenipora gotlandica (Yabe), 1915	X (S)		X
Catenipora, n. sp.			
Moniloporidae			
Cladochonus sp. A			
Cladochonus sp. B			
Cladochonus sp. C	X (O)		
Syringoporidae			
Syringopora reteformis Billings, 1858			X
Syringolitidae			
Syringolites, n. sp.			
Alveolitidae			
Alveolites labrosus (Milne-Edwards and Haime), 1851			X
Alveolites labechii Milne-Edwards and Haime, 1851	X? (O)		X
Pachyporidae			
Striatopora flexuosa Hall, 1852			X
HELIOLITIDS			
Proporidae			
Propora conferta Milne-Edwards and Haime, 1851	X (O)	X	X
Propora exigua (Billings), 1865b	X (S)		X
Propora eminula (Foerste), 1906			X?
Heliolitidae			
Heliolites spongodes Lindström, 1899			X
Heliolites spongiosus Foerste, 1906			X?

favosites with *Favosites,* of *Propora* with *Heliolites,* of rugose corals lacking a dissepimentarium with dissepimentariate corals. Here we find species stemming from the Late Ordovician living beside exclusive Silurian forms, and here we find the typical Ordovician genus *Streptelasma* in Silurian beds.

Pre-Brassfield distribution (Text-figure 2). — Eight species of this fauna have been recognized as having existed prior to Brassfield time, and three more were possibly in existence. Yet another, *Protocyathactis* cf. *P. cybaeus* Ivanovskii, has what appears to be a closely-related ancestor, *P. cybaeus,* in pre-Brassfield time. Of this total of 12 species, eight extended back to the Late Ordovician, while the remainder are found in the Early Llandovery.

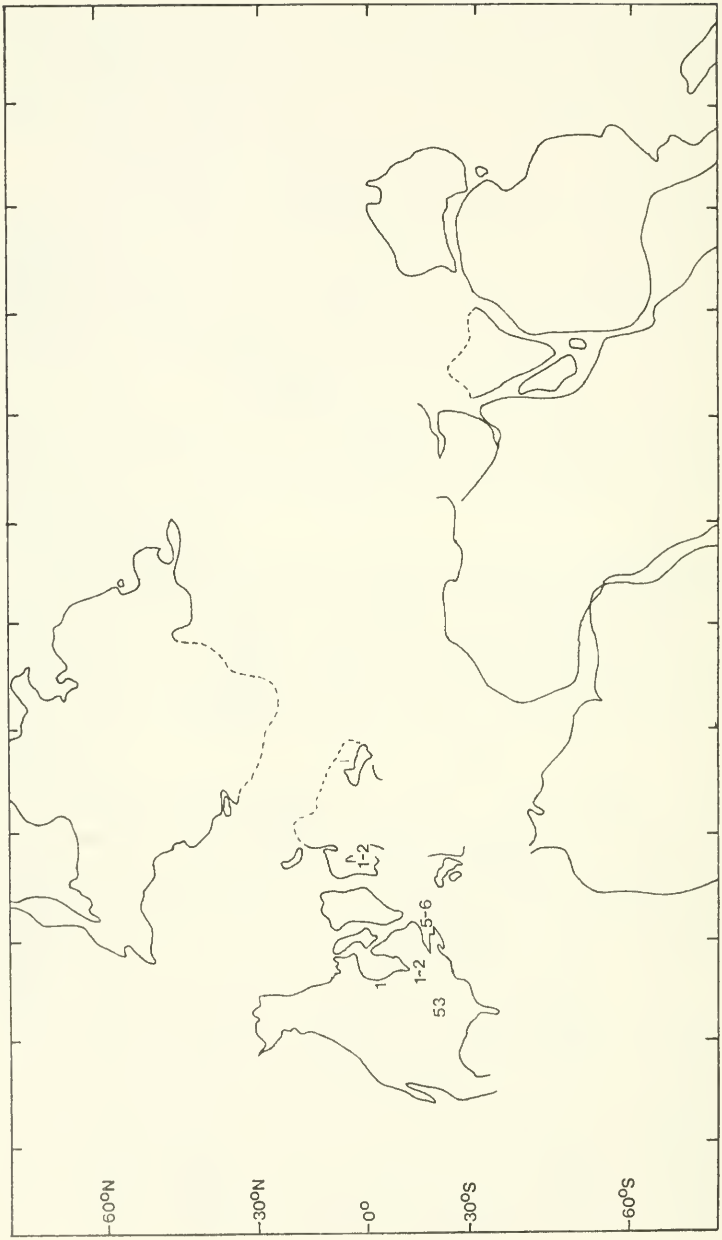
No single region appears to have been the homeland of these earliest Brassfield species. Rather, they occurred on the North American continent, Europe, Asia, and possibly South America, with the Canadian Maritime Provinces and the Baltic area containing the largest numbers.

Of interest is the fact that none of the rugose species have been found in the pre-Brassfield rocks of North America. Instead, they occur in the Baltic area and the Siberian Platform, with a possible occurrence in Venezuela. On the other hand, except for occurrences in the Baltic region, the tabulates and heliolitids that later helped populate the Brassfield Sea were found only on the North American continent.

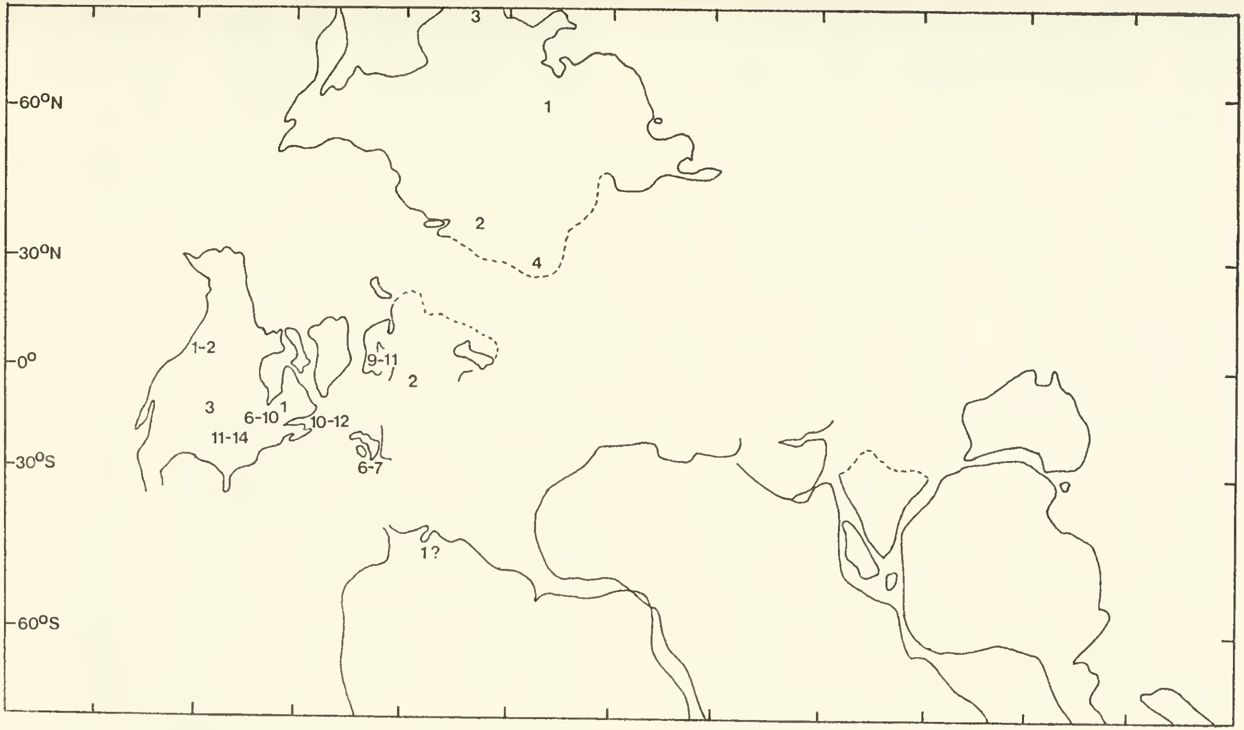
Distribution during Brassfield time (Text-figure 3). — The current data indicate that about 40 of the 53 Brassfield coral species first appear in the fossil record during Brassfield time. The fauna appears to have been rather restricted geographically, only six to eight of its species living in other parts of the world during this time. These were found in four general areas: the northern Great Lakes, Manitoba, the Canadian Maritime Provinces, and the Baltic area. Of these, the fauna of the Maritimes unquestionably shows the greatest similarity to the Brassfield fauna on the species level.

Post-Brassfield distribution (Text-figure 4). — Some 27, and possibly as many as 32 coral species survived the termination of Brassfield conditions in the Cincinnati Arch region. These went on to populate a large portion of the epicontinental sea area in later

Text-figure 2.—Areas where Brassfield species have been identified in pre-Brassfield beds (Late Ordovician and Early Llandovery). The numbers here, and in the remaining Text-figures indicate the number of such coral species found at each locality. Same base-map as that shown in Text-figure 1.



Text-figure 3.—The distribution of Brassfield coral species in beds contemporaneous with the Brassfield Formation. Map and symbols as in Text-figure 2.



Text-figure 4. — The distribution of Brassfield species after Brassfield deposition terminated in the Cincinnati Arch area. This map covers the distribution up to and including Early Ludlovian time. Map and symbols as in Text-figure 2.

Silurian time, uniting with other species to form the well-known post-Brassfield coral faunas of Gotland, Britain, Bohemia, the Siberian Platform, the Far East, and eastern North America.

Several species reappeared in the general vicinity of what had been the Brassfield Sea. When the Louisville Limestone (Late Wenlock and Early Ludlow) was being deposited at Louisville, Kentucky, seven or eight Brassfield species were present (*S. benedicti, H. nitidus, A. mamillare, H. spongodes, F. forbesi, F. hisingeri, S. ipomaea,* and possibly *D. linguliferum*). Later in the Early Ludlow, the Brownsport Formation was deposited in western Tennessee, again with Brassfield corals in attendance (*H. spongodes, F. forbesi, Favosites sp. A, H. meandrinus,* and possibly *T. radicula.*

The current knowledge of the Ordovician and Silurian corals of western North America and South America is spotty. The presence of Brassfield species in the former, and possibly the latter areas marks them as promising regions for future investigations into the history of this fauna.

ACKNOWLEDGMENTS

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HITCHHIKING CLAMS IN THE MARCELLUS SEA

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ABSTRACT

Many examples of Recent epiplanktonic assemblages are known but few such occurrences are documented in the fossil record. Herein is described an association between the Devonian bivalve, *Lunulacardium curtum* Hall and a log. The bivalves presumably attached to the log while it was floating. After drifting, the log sank into the euxinic bottom environment of the Marcellus Shale (Middle Devonian).

INTRODUCTION

There are numerous examples of Recent epiplanktonic assemblages. The classic case is the floating substrates provided by the Sargassum seaweeds. Examples of many major taxa, such as hydroids, bryozoans, worms, snails, sea slugs, crabs, shrimps, fishes, forams, and many others which exploit an attached or vagrant mode of life have been observed on the Sargassum weed (Ruedemann, 1934, pp. 17-22). Barnacles and shipworms obviously belong to this category. According to Por (1971, p. 153), several species of bryozoans and perhaps the byssally attached bivalve clam *Pteria occa* Reeve have been passively transported through the Suez Canal area by means of ancient or modern ships. Examples of extant epiplanktonic bivalves are less well known.

Brower has seen numerous extant specimens of *Mytilus* Linné attached to plants, logs, pilings, and various types of driftwood on beaches in the vicinity of Edinburgh, Scotland. T. J. F. Schopf and Steven Stanley (personal communication) reported that *Mytilus* is commonly found on pilings along the New England Coast. *Dreissena* Beneden often cements the byssus to the roots of trees, sunken logs, and submerged bushes (Lyakhov and Mikheev, 1964, pp. 3, 4). *Brachidontes recurvus* Rafinesque, and other mussels are often found dwelling on mangrove roots (Warmke and Abbott, 1961, p. 162) and *Anomia simplex* d'Orbigny also sometimes occurs on logs (Warmke and Abbott, 1961, p. 172). The flat tree oyster *Isognomon alatus*

(Gmelin) is a common byssally attached inhabitant of mangrove roots and wharf pilings throughout south Florida (Stanley, 1970, p. 135; Abbott, 1968, p. 202). This tabulation clearly shows that there are a large number of examples known in which byssus bearing clams are found attached to fixed wooden substrates. In addition, there are at least two examples known to us where mussels have been collected from floating or semifloating woody objects. According to Jacobson and Emerson (1971, p. 83), a large colony of the small mussel *Congeria leucophaeata* Conrad was living in the Hudson River on submerged buoys, logs, and diving floats. Rogers (1920, p. 338) cited an unspecified locality, probably along the New England Coast where *Mytilus edulis* Linné was seen attached to sunken and floating logs, planks, and even the hulls of wooden boats.

The mangrove oysters, such as *Crassostrea* Sacco, *Lopha* Röding, and *Saccostrea* Dollfus and Dautzenberg, often cement their valves to mangrove roots, wharf pilings, and other woody substrates along many tropical coastlines (*e.g.* Stenzel, 1971, pp. N1043-N1045). According to Stenzel (1971, p. N1035), oyster larvae sometimes settle on floating driftwood and in some instances survive to sexual maturity. Stenzel (1971, p. N1035) believed that this method of driftwood dispersal is important wherever mangrove swamps and tropical rain forests line the shores.

Well-documented occurrences of epiplanktonic faunal assemblages are relatively rare in the fossil record. The best known example in crinoids is the Jurassic *Seirocrinus subangularis* (Miller). This form attached the distal part of the stem and holdfast to a floating log so that the crown hung down in the water (Seilacher, *et al.*, 1968). Several Devonian melocrinitids were reported attached to logs (Wells, 1947). Various authors have suggested epiplanktonic habits for other groups. Some chonetid, rhynchonellid, and various inarticulate brachiopods are possibly epiplanktonic (*e.g.*, Ruedemann, 1934, pp. 33-34; Bulman, 1964, pp. 468, 469; Bergström, 1968, Havlíček and Vanek, 1966, pp. 39, 40; Rudwick, 1965, p. H201). Some large leptostraceans (arthropods) of the Ordovician might have been epipelagic (Stormer, 1937). The Triassic oyster *Placunopsis* Morris and Lycett is believed to have attached to shells of the pelagic ammonite *Ceratites* de Haan while the shell was still floating (*e.g.*, Meischner, 1968; Seilacher, 1960, p. 189). Kriz (1965, p.

113) suggested that *Butovicella migrans* (Barrande), a bivalve from the Silurian of Bohemia, may have attached to algae by byssal fibers and was transported by sea currents.

The purpose of this paper is to describe an association between a Middle Devonian Marcellus Shale (Cardiff Member) bivalve (*Lunulacardium curtum* Hall) and a presumably terrestrial log (Pl. 1, fig. 1). As will be shown later, the bivalves were epiplanktonic having been attached to a floating log which became waterlogged and sank, thus entombing the log with its attendant bivalves in foul muck of the Marcellus sea.

DESCRIPTION OF THE SPECIMENS

The specimens were collected on a joint field trip for Wayne State University and Syracuse University students held in the fall of 1973. The log and bivalves were found on a loose block of Marcellus (Cardiff Member) black shale (approximately 50 cm on each side). The exact locality is the upper part of the Alpha Portland Cement Company quarry on the east side of Gates Road, 0.3 miles south of the junction of Gates Road and State Route 173, and about 1.4 miles southeast of Jamesville, Onondaga County, New York. Inasmuch as the block was not found in place and definitive sedimentary structures are conspicuously absent, the top cannot be ascertained. The log is roughly 40 cm long by 2 cm wide; thickness is unknown. Thirty-seven specimens of *L. curtum* are associated with the log, a single specimen of *L. curtum* was found on another loose block about 30 meters from the log-bearing block (Pl. 1, fig. 3). Most of the bivalves that can be seen are found on the upper side and in the sediment immediately adjacent to the log. However, at least several individuals were apparently buried under the log; outlines of shells clearly show through the carbonized remains of the log (Pl. 1, fig. 4). The association between the specimens of *Lunulacardium* Münster and the log is significant. Of the bivalves on the log-bearing block, 26 are in contact with the log surface while only 11 were found free in the sediment, all within 3.0 cm of the log. These figures were tested against the hypothesis that there is no association between the log and bivalves. If there is no association between the log and the clams, a first order estimate of the expected probability of observing a specimen in the sediment would be proportional to the (area of the sediment)/(total area of the block, including both sediment and the log) while the expected probability of recovering a specimen from the log would be estimated by (area of log)/(total area of the block). The total area of the bedding plane with the log on the block of shale is 2500 cm^2 of which the log comprises 80 cm^2 while 2420 cm^2 is represented by sediment. Assuming no association between the clams and the log, the expected probability of finding a bivalve on the log is 0.032 or 3.2%. The observed probabilities are as follows. A total of 37 clams were counted of which 26 are on the log and 11 in the sediment. The observed probability of finding a specimen on the log is 26/37 or 0.70. These binomial probabilities were tested by the methods discussed by Snedecor and Cochran (1967, pp. 202-223). The 99% confidence limits for the observed 0.70 probability of a bivalve occurring on the log range from 0.91 to 0.50. Comparing the observed probability of 0.70 with the corresponding expected probability of 0.032 by means of Z and x^2 tests shows that the null hypothesis can be rejected with a minimal risk of less than 0.1%. The observed and the expected probabilities do not derive from the same binomial population. Clearly the association between the bivalves and the log is statistically significant. In the next step, the spatial distribution of clams on the log was examined. The log was divided into two halves by a plane through the medial axis of the log and perpendicular to the bedding plane. The distribution of clams was counted relative to the two halves. Bivalves counted include impressions made by specimens underneath the log as well as specimens located on the upper surface of the log. Of the 26 bivalves observed on the log, 19 were on the right side of the log while seven lie on the left half (Pl. 1, fig. 1). The observed distribution was tested against the hypothesis that the specimens were distributed equally on both sides of the log, using the 50% binomial test of Langley (1971, pp. 254-268). The null hypothesis, *i.e.,* that the specimens are equally distributed on both sides of the log, is rejected subject to a risk of about 5%. It is clear that the bivalves are concentrated on the right side of the log. If, however, the bivalves had attached to the log while it was resting on the bottom, we would expect a more equal distribution over the upper surface of the log.

Lengths could be determined for six internal and five external molds. The pertinent data are listed in Table 1. Although few data are available, the narrow range of lengths is notable. This is consistent with the possibility that all the bivalves represent a single spatfall.

DEPOSITIONAL ENVIRONMENT OF CARDIFF MEMBER, MARCELLUS SHALE

The Cardiff Member of the Marcellus Shale in Onondaga County is the seaward equivalent of the Solsville Shale of the Chenango Valley. Regional stratigraphic relationships suggest that the Cardiff is an offshore black shale facies. Unpublished calculations by Bryce Hand of Syracuse University indicate that the unit was deposited at a depth of about 100 to 150 feet. These depths are roughly similar to those calculated by Hand (1973) and Bowen, *et. al.,* (1970) for similar Upper Devonian black shales.

Lithologically the Cardiff is a finely laminated black shale with an appreciable amount of organic matter and finely disseminated pyrite.

The most conspicuous faunal elements are goniatites, pelagic orthocones, and occasional fish scales. Some beds contain abundant *Styliolina fissurella* (Hall), a pelagic organism of unknown affinities. Wood fragments of terrestrial plants are common. Some large bivalves and brachiopods of unknown affinities are also found. The brachiopods include occasional specimens of linguloids which were probably bottom dwellers. Thin beds composed mainly of the brachiopod *Leiorhynchus limitare* (Vanuxem) have also been observed. These last are commonly interpreted as bottom dwellers. *L. limitare* is thin-shelled and may have floated with a gas bubble in the mantle chamber. Nye has observed numerous floating bivalves in Lake St. Clair, Michigan, during the summer of 1973. The dead bivalves were floated by gases trapped within the mantle. The interpreted environment of the Cardiff Member follows (Cooper, 1957, pp. 259-261). The offshore occurrence of the unit and the presence of nektonic and planktonic fossils indicate normal marine conditions in the surface waters. As previously mentioned the sedi-

Table 1. — Measurements of length of *Lunulacardium curtum* in millimeters.

	Mean	Range	Standard Deviation	Coefficient of Variation
Internal Molds	12.4	12.0-13.0	0.49	3.9
External Molds	13.9	13.5-14.0	0.22	1.6

ment was probably deposited in waters of moderate depth. The fine-grained terrigenous sediment, fine laminations, high concentration of organic matter and pyrite content indicate quiet water conditions. The abundance of organic matter and pyrite, general absence of bottom dwelling epifaunal and burrowing organisms, presence of carbonized and pyritized plant debris, are indicative of a reducing environment at and for some distance above, the sediment-water interface. Beds containing bottom dwelling brachiopods, *Leiorhynchus limitare,* and most likely the linguloids, probably accumulated under conditions of oxygen content of bottom waters marginal to their life requirements. We cannot however discount the possibility that both linguloids and specimens of *L. limitare* were transported to the site of burial.

The intimate association of the bivalves and log indicates that the bivalves utilized the log as substrate. There are no traces of boring in the log and all bivalves observed lie external to the carbonized exterior of the log. Furthermore the shell morphology is not consistent with known rock and wood borers (*e.g.*, Stanley, 1970). We therefore infer that the bivalves lived attached by a byssus to the log surface. As indicated in the systematic description, shell morphology is consistent with the byssally attached mode of life. It is known that attached benthos may colonize exotic substrates when available. For example, photographs of the sea floor taken far from shore show sunken logs, ships, glacially rafted boulders which apparently were colonized by deep-water benthos. If the spat had settled on the log after the log had sunk, we would anticipate that the bivalves would be equally distributed over the exposed surface of the log. The bivalves are, in fact, concentrated on about one half of the log's available surface but the colonized surface is rotated with respect to the bedding plane so that part of the bivalve bearing surface must have lain below the sediment-water interface. From this we infer that the spat attached to the submerged surface of the log while it was floating, and that the preserved orientation reflects partial rotation of the log and its attached residents while sinking. One might postulate that the bivalves attached to the log while it was on the substrate and that subsequent wave and current or current action overturned the log to its present orientation. This possibility is discounted for two reasons. First the environment of deposition was quiet water where the necessary wave and current or current action was conspicuously absent. Second, there is no evidence in the sediment that the log was overturned after it had settled on the seafloor. The size distribution suggests that this population originated from a single spatfall which colonized the log prior to sinking and burial in the euxinic bottom sediments of the Marcellus sea. Presumably the spat were produced by bivalves living in bottom waters with higher oxygen content than that of the Marcellus sea floor. The site of burial was greatly different and perhaps, far removed from the habitat in which *L. curtum* normally lived.

SYSTEMATIC PALEONTOLOGY

Class BIVALVIA

Order PTERIOIDEA Newell

Suborder PTERIINA Newell

Family **LUNULACARDIIDAE** Fischer

Genus **LUNULACARDIUM** Münster

Type species: *Lunulacardium semistriatum* Münster by subsequent designation, Stoliczka.

Remarks.—The marked radial ornamentation and subtrigonal outline serve to differentiate *Lunulacardium* from other Devonian bivalve genera.

Lunulacardium curtum Hall, 1870

Lunulacardium curtum Hall, 1870, p. 97; 1883, pl. 71, figs. 18-23; 1885, p. 439; pl. 71, figs. 18-23.

Material studied.—Three syntypes housed in the New York State Museum at Albany, New York, and figured by Hall, 1883

(NYSM No. 2675, "Hamilton beds", Tully, N.Y., pl. 71, figs. 18, 19, 23; NYSM No. 2676, "Hamilton beds", Cayuga Lake, N.Y., pl. 71, fig. 22). In addition 37 specimens located on or about a woody plant fragment collected from black shale quarry on Gates Road, 0.3 miles south of Route 173, 1.4 miles southeast of Jamesville, Onondaga County, New York (NYSM No. 13291) and a single free specimen (NYSM No. 13292) collected at the same locality.

Description. — Shell small to medium size (length 1.2 to 2.5 cm), equivalved, inequilateral, convex to gibbose, subtriagonal in outline. Umbos small, anterior to middle, above hinge line, directed forward. Posterior and anterior margins less rounded than ventral margin. Commissure non-serrate. Surface sculpture of 18-25 pronounced, rounded, somewhat plicate, simple, radial costae with equally concave interspaces of equal width. Valves also with fine concentric imbricated fillia superimposed on plications without deflection. Hinge line, dentition and internal detail unknown.

Comparison. — *L. curtum* is differentiated from other species of *Lunulacardium* on the basis of its smaller size, more pronounced trigonal outline; and the number, simplicity, configuration, and spacing of the costae.

Discussion. — Hall described and figured (1883, pl. 71, fig. 23) pustulose ornamentation on the ventral margin of *L. curtum*. Pustules can be seen on specimens NYSM 2675 and NYSM 2676. Shells are commonly preserved as molds; rarely are traces of carbonate preserved. The pustules are small (approximately 0.1 mm) framboids of pyrite, identical in appearance to small pyrite inclusions scattered in the shale matrix. The inclusions are centers of reduction probably representing local concentrations of decaying organic matter. We infer that the pustules on the shells had the same origin as those observed in the matrix and are not, therefore, indicative of original shell ornament.

Byssate attachment was the probable life habit of *L. curtum*. Newell's (1969, p. 285) diagnosis of the suborder Pteriina (to which *Lunulacardium* is assigned) included, "Adults fixed by byssus through notch in right valve for part or all of ontogeny". Although a notch has not been observed in specimens of *L. curtum*, Kauffman (1969) noted that a short byssus observed in some members of this order reduces or eliminates the formation of a byssal notch. Furthermore, the morphology of this species is consistent with characteristics of byssate bivalves as cited by Kauffman (1969, pp. 146-148) and Stanley (1970, pp. 21-26).

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Steven Stanley of Johns Hopkins University, T. J. M. Schopf of University of Chicago, Egbert Driscoll of Wayne State University, and R. M. Linsley of Colgate University provided useful information about extant mytilids and mangrove oysters. Bruce M. Bell of the New York State Museum provided specimens and enthusiastic help. Bryce Hand of Syracuse University estimated the depth of deposition of the Cardiff Member of the Marcellus Formation and commented on other aspects of environmental reconstruction. The photographs were taken by Richard Freimark of Syracuse University. Last but by no means least, we thank the participants of the Wayne State University Geology field trip, especially Norman Holst, Kevin Osmun, and Patricia Brady for finding and collecting the specimens.

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EXPLANATION OF PLATE 1

Figure

1-4. Lunulacardium curtum Hall

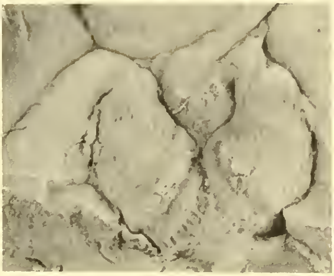
Associated with woody plant fragment (log). Figs. 1, 2, 4. NYSM 13291, Fig. 3. NYSM 13292, from Cardiff Member, Marcellus Shale, collected near Jamesville, N.Y. Fig. 1 uncoated, figs. 2-4 coated with ammonium chloride.

1. Log with bivales located on or close to log. Most bivalves occur on right side of log; × .910.

2-3. External molds of articulated valves, showing radial ribs; × 1.82.

4. Impressions of valves located underneath log and impressions of bivalves attached to right side of log; × 1.82.

1



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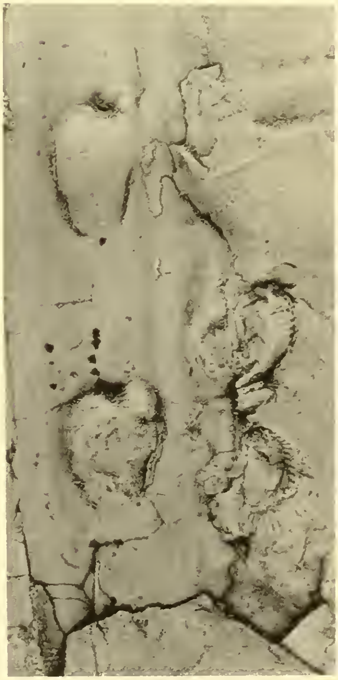

4

TRILOBITE TRACE FOSSILS FROM THE CLINTON GROUP (SILURIAN) OF EAST-CENTRAL NEW YORK STATE

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ABSTRACT

Specimens of *Rusophycus,* as well as trackways of "crustacea or fish" described by Hall (1852), form the basis for a restudy of what we conclude are trilobite traces. Collections were made from 17 Clinton localities, New York State. Two species of the trilobite burrow cast, *Rusophycus, R. pudicum* and *R. bilobatum,* are recognized. The former is attributed to calymenid trilobites, the latter, and more common species, was made by *Trimerus delphinocephalus* and *Dalmanites limulurus. Rusophycus* is interpreted primarily as a hiding trace, although there is evidence to indicate that some specimens represent hunting activity. The long, bilobed furrow-cast, *Cruziana,* common in some Paleozoic localities, is rare in the study area. The significance of this is not clearly understood. Trilobite trackways are abundant at some lower Clinton localities and are assigned to *Diplichnites* sp. Groups A, B, and C. *D.* sp. Group C is the most intriguing and shows that the tracemaker (trilobite-genus unknown) was pentadactylous.

The occurrence of trilobite trackways at three localities in the Otsquago Formation conflicts to some extent with Muskatt's (1972) interpretation of the depositional environment for this unit — brackish or fluviatile conditions. The Otsquago should be remapped using trilobite trace fossils as indicators of a marine environment.

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REPOSITORIES

The specimens collected by the authors which are figured in this paper have been deposited with the New York State Museum in Albany. Hall's (1852) type specimens are at The New York State Museum (NYSM), the United States National Museum (USNM), and the American Museum of Natural History (AMNH). Unfigured material is in the possession of the senior author at the College of Wooster.

INTRODUCTION

This paper is a portion of a larger study in preparation, the goal of which is to restudy the "fucoids" or supposed fossil algae, as well as several varieties of trails, described by James Hall (1850, 1852) from the Clinton beds of east-central New York State. Altogether Hall (1852) proposed over a dozen "fucoid" species and discussed several trails. His work was significant as his genera and species formed the basis for further studies of "fucoids" in North America. One such example is the work conducted by Miller and Dyer in 1878 on the Ordovician "fucoids" of the Cincinnati area. We now know that many fucoid species proposed during the last century are either trace fossils or sedimentary structures. However, to date this knowledge has not been applied in any detail to the Silurian of New York.

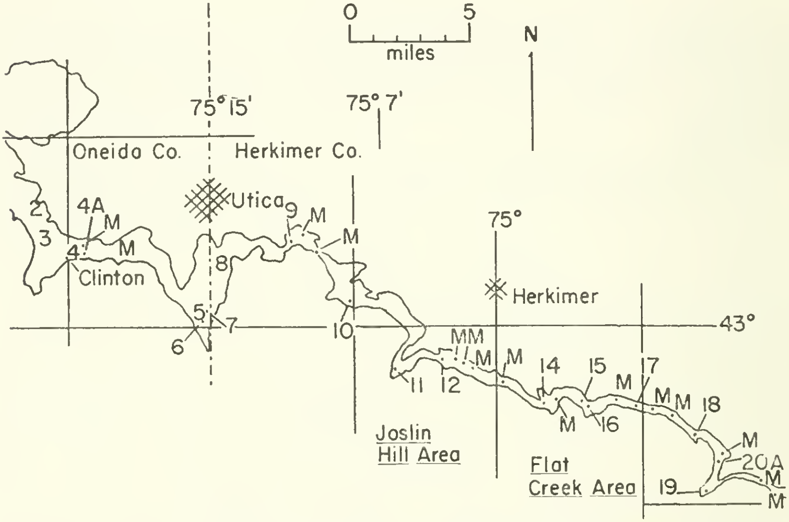
Hall (1852) established four species of *Rusophycus* from the Clinton, believing them to be fucoids. Two of the species, *R. pudicum* and *R. bilobatum,* are discussed herein under *Rusophycus,* whereas the others (Hall's *R. subangulatus* and *R. clavatus*) are assigned to *Cruziana. R. bilobatum* is informally subdivided into Types 1, 2, 3. In addition, Hall (1852, pp. 26-37, pls. 11-16) included a section entitled "Tracks of Gasteropoda, Crustacea, or Other Marine Animals," where he discussed but did not formally name several trails. As a reading of Hall (1850, 1852) vividly demonstrates, the enigmatic nature of these trails fascinated him. With the advantage of an additional century of paleontological knowledge to draw upon, we now see that the forms which he figured on his plates 15-16 are of arthropod origin. We suggest that they were made by trilobites and have assigned them to *Diplichnites* sp., Groups A, B, C.

Most of Hall's figured specimens were obtained by us from the collections of the United States National Museum, the New York State Museum, and the American Museum of Natural History. In addition, the senior author spent the spring of 1972 collecting trace fossils from 17 Clinton localities in Oneida and Herkimer Counties, New York.

Arthropod trace fossils, especially the burrow cast *Rusophycus,* formed the basis for the junior author's Senior Independent Study at The College of Wooster. We hoped to recollect from Hall's original localities, many of which were quarries, because a considerable degree of artistic license was employed in the preparation of his lithographs. Unfortunately, the study area has a great many quarries, some dating back to the late eighteenth century. The Herkimer Formation is widely used as a building stone, and both the Westmoreland and Kirkland Hematites have been mined for their iron content. A search of nineteenth-century land plats and maps proved fruitless. Fortunately Vanuxem (1842, pp. 82-87) gave enough information so that Chadwick (1918, fig. 2) was able to provide stratigraphic if not precise geographic control for the quarries. We were somewhat more successful in locating "Tisdale's Mill," in the stream below which most of the forms described by Hall (1852, pls. 11-16) were collected. As Hartnagel and Newland (1908) pointed out, the "Tisdale's Mill" locality is Flat Creek (herein locality 14).

Following a study of Chadwick's work showing the stratigraphic horizons of Hall's quarries, and based on discussions with geologists who had mapped various sections of the Clinton Group (Muskatt, Rickard, and Zenger), it became apparent that the Herkimer and Sauquoit-Otsquago Formations held the greatest potential for trace fossil collecting. Therefore, we confined our efforts to these units.

Three recent works provide excellent locality data for collecting in the Clinton. Zenger's study (1971) is concerned with the facies relationships within the Herkimer while Muskatt's work (1969, 1972) deals with the entire Clinton Group. To provide uniformity of reference, the locality numbers used in this paper are the same as those listed by Zenger (1971, pp. 55-58; see Appendix herein). Localities important to this work but not appearing in Zenger are also listed in the appendix.



Text-figure 1. Outcrop pattern of the Clinton Group. Numbers refer to localities cited in the text. The letter "M" indicates localities included by Muskatt (after Muskatt, 1972, fig. 2).

STRATIGRAPHY

In Oneida County and Herkimer County the Middle Silurian Clinton Group (see Text-figure 1) crops out in a narrow band some 45 miles in length, parallel to and just south of the Mohawk River. Most outcrops occur in streams, and there is no single locality where the entire Clinton is exposed. Although the original stratigraphic work is over 125 years old, most formations and members now in use were proposed by Chadwick (1918) and Gillette (1947). As we do not propose to deal extensively with the stratigraphy, the reader is referred to the general works of Gillette (1947), Muskatt (1969, 1972), and Zenger (1971), and the quadrangle reports of Dale (1953), Grossman *in* Kay (1953), and Rickard and Zenger (1964). As there are several measured sections in these works, especially in Gillette (1947), we give only a brief synopsis of each unit.

The aggregate thickness of the Clinton ranges from about 50 meters at Verona in western Oneida County (Gillette 1947, pp. 164-167), to 110 meters at the south branch of Moyer Creek (locality 10) near the center of the study area, to approximately 22 meters near Wiltse Four Corners in extreme eastern Herkimer County (Rickard and Zenger 1964). This apparent thinning from Utica eastward is due to post-Clinton beveling. East of Herkimer County the Clinton is usually absent. Tectonic instability to the east also produced at least two lateral changes in facies within the Clinton (see Text-figure 2).

1) Oneida Formation

The Oneida attains a maximum thickness of some 22 meters (Gillette, 1947, p. 33) and disconformably overlies the Upper Ordovician Frankfort Shale. The abundance of milk-white quartz pebbles makes the Oneida an excellent marker bed west of Clinton Village. Farther east, in central and eastern Herkimer County, Rickard and Zenger (1964) reported a gradational contact of 1.5-5 meters with the overlying unit. Although predominately a conglomerate, the Oneida contains some sandy beds which yield a sparse marine fauna. No trace fossils were collected from the Oneida by us.

2) Sauquoit Formation

The Sauquoit was proposed by Chadwick (1918) for beds between the Oneida and the overlying Westmoreland iron ore. The formation attains a thickness of 31 meters in the vicinity of locality 5 (Gillette, 1947, p. 76). Gillette (1947, p. 72) pointed out that the dominant lithology is shale, but there is considerable interbedding of siltstones and fine-grained, slightly dolomitic sandstones. According to Muskatt (1972, p. A-6) the percentage of clastics increases to the east. Shale clasts and phosphate nodules are common in some of the sandstone. Current, oscillation, and truncated ripplemarks have been reported at several localities by the same author. Both Muskatt (1972)and Gillette (1947) observed mud cracks within the Sauquoit, although they were not seen by the present authors. An impressive faunal list can be found in Gillette (1947). Because of the interbedding of clastics and shale, trace fossils also are abundant.

3) Otsquago Formation

To the east of locality 10 (South Moyer Creek) the Sauquoit undergoes a pronounced lateral facies change. Chadwick (1918) called these the Otsquago beds and Muskatt (1972) recognized the unit as a formation coeval with the Sauquoit. As Text-figure 2 shows there is considerable interfingering of the two units. The maximum thickness is about 30 meters. Muskatt (1972, p. A-10) stated that "[The] Typical Otsquago is [a] poorly sorted, to moderately sorted, medium-grained, hematitic and chloritic orthoquartzite." The beds vary in thickness and the formation is noted for its conspicuous planar cross-bedding (Muskatt, 1972, p. A-10). Some clay partings and siltstone are present. Shale clasts, phosphate nodules, symmetrical, asymmetrical and interference ripple marks are common. Although body fossils are rarely found (Muskatt, 1972, p. A-12), trace fossils are relatively common in the finer sandstones.

4) Westmoreland Formation

The Westmoreland is an oolitic iron ore with some thin- to medium-bedded shale partings. The thickness ranges from one meter near Clinton Village to only 1 cm near Van Hornesville (Rickard and Zenger, 1964). This ore, and the stratigraphically higher Kirkland, have been the subject of considerable study and both have been extensively mined in the past. Gillette (1947, p. 94) listed the marine fauna found within the unit. It was not sampled for trace fossils.

5) Willowvale Formation

The Willowvale is a 5-7 meters thick shale which separates the Westmoreland and Kirkland iron ores. Some sandy dolomites are found in the upper part. Fossils are abundant (Gillette, 1947). In the Clinton area, a local unit termed the Dawes Member (Gillette, 1947) wedges in between the Willowvale and the overlying Kirkland. According to Muskatt (1972) both contacts are gradational and the aggregate thickness is less than three meters. The lithology consists of interbedded shale and thick- to thin-bedded sandy dolomites.

6) Kirkland Formation

The Kirkland was proposed by Chadwick (1918) to replace what had formerly been termed the "red flux iron ore." According to Zenger (1971) the matrix is largely dolomitic, where hematite has replaced the abundant marine fossils. Like the Westmoreland, its maximum thickness of some two meters is attained near Clinton. It thins to less than 20 cm in eastern Herkimer County.

7) Herkimer Formation

The Herkimer was restudied by Zenger (1971), who recognized an abrupt lateral facies change, unlike the extensive intertonguing of the Sauquoit-Otsquago transition. The area of change is in Ilion Gorge (locality 11), but nowhere in the gorge is there a single section which clearly illustrates the change. Zenger named the western facies the Joslin Hill Member, whereas the eastern facies is termed the Jordanville Member. The thickness of the Herkimer averages 18-22 meters. In eastern Herkimer County the formation thins rapidly due to subsequent erosion.

a) Joslin Hill Member

This member is composed of interbedded shale and fine- to medium-grained dolomitic sandstones. In outcrops west of Clinton Village some layers of hematitic dolomite are found. As Zenger (1971, p. 15) pointed out, the shale and sandstone/dolomite ratio is 1:1 near the western margin of the study area while it is 1:3 at the South Moyer Creek (loc. 10). Primary sedimentary structures, numerous in the Joslin Hill area consist primarily of tool marks (*e.g.* groove casts) and symmetrical pararipples. Examples of the latter with wave lengths of one meter are present at Dawes Creek (loc. 4). Zenger noted that small scale ripple marks and planar cross-bedding are also common throughout the unit. Fossils, although fragmentary and abraded, are relatively abundant. See Zenger (1971, table II) for a faunal list.

b) Jordanville Member

The Jordanville contrasts strongly with the Joslin Hill. It is a thick-bedded, medium- to coarse-grained orthoquartzite with a few shale stringers. Unlike the Joslin Hill, primary sedimentary structures and fossils are rare. The first definite organic remains were reported by Zenger (1971, p. 23) from Van Hornesville (loc. 20). They are the pelecypods *Modiolopsis* Hall, *Mytilarca* Hall and Whitfield, and a rhynchonellid brachiopod. Despite an intensive search, no trace fossils were found in the Jordanville.

DEPOSITIONAL ENVIRONMENT OF THE CLINTON

The depositional environment of the Clinton was covered in some detail by Gillette (1947), Zenger (1971), and Muskatt (1972). A brief summary is presented here although the Sauquoit-Otsquago is treated in greater detail later in this paper.

The Oneida is regarded by both Gillette (1947) and Muskatt (1972) as the basal marine unit of the Clinton sea which was transgressing to the east. A marine fauna has been found in the finer clastics. The overlying Sauquoit Formation is also considered to be of marine origin. The abundance of mudcracks and ripple marks which occur in the unit in eastern Oneida County led Gillette to postulate that this area was near the strand line. Muskatt (1972) also recognized an eastern shallowing of the Sauquoit sea, thereby suggesting a near-shore or tidal flat environment for eastern outcrops. A variety of evidence led Muskatt (1972, p. A-28) to conclude that the Otsquago ". . . formed under fluviatile and estuarine conditions." Muskatt's cross-section (see Text-figure 2), implies considerable fluctuation of the Sauquoit-Otsquago sea. The Westmoreland iron ore, because of its oolitic nature, is thought to represent a return to marine conditions which continued during deposition of the Willowvale. Muskatt considered the Willowvale to be a clastic wedge which was transgressive in the lower part and regressive (yet still marine) in the upper. Like the Westmoreland, the Kirkland iron ore is thought to be of marine origin as it is composed primarily of fragments of a marine fauna which were replaced by hematite. The fauna and lithology of the Joslin Hill Member of the Herkimer points to ". . . [a] high-energy, nearshore, relatively shallow-water environment" according to Zenger (1971, p. 45). Although Hunter (1960) had considered the Jordanville Member to be of fluviatile origin, Zenger (1971, p. 45) in interpreting the sparse marine fauna that he found, suggested ". . . that the Jordanville represents a beach (intertidal) environment with possible infraneritic or supratidal portions."

ARTHROPOD TRACES AND CLINTON ARTHROPODS

Arthropod, especially trilobite, traces have received considerable study over the past 20 years because they are one of the few groups of trace fossils where the tracemaker can be identified, at least to the class level, with a high degree of confidence. Seilacher (1955) provided the impetus with a method of study which has been adopted by later authors. Since his original work, we have learned a great deal about trilobite life habits, particularly modes of locomotion. For a detailed review of trilobite traces the reader may consult Bergström (1973), Birkenmajer and Bruton (1971), Crimes (1970, a, b), Orłowski, *et al.* (1970), Osgood (1970), and Seilacher (1970).

Generally speaking, trilobite traces fall into three broad categories: 1) trackways where the organism was walking upon the depositional interface; 2) bilobed furrows of varying length where the animal was ploughing horizontally, partially or sometimes completely submerged in the sediment; 3) short, bilobed buckle-like burrows where the movement was predominately directed vertically downward into the sediment. There is considerable divergence of opinion as to which generic names should be applied to trace fossils reflecting these three types of locomotion.

Because we believe that the structures which we describe in this paper are of trilobite origin, we feel it is necessary that we attempt to establish the identity of the tracemaker wherever possible. The most complete faunal list for the Clinton is found in Gillette (1947); additional listings were taken from Dale (1953) and Zenger (1971). Trilobites and ostracodes are the only arthropods known from Clinton age rocks in east-central New York. While synxiphosurids and eurypterids occur in the Upper Silurian of New York, they have not yet been reported in the Clinton. A synopsis of trilobites from the study area is given below. Those more commonly encountered are marked *.

1. Herkimer Formation: *Dalmanites limulurus** (Green); *Trimerus delphinocephalus** (Green); *Calymene niagarensis** Hall; *Arctinurus nereus* (Hall); *Cheirurus niagarensis* (Hall).
2. Westmoreland Formation: *Dalmanites limulurus lunatus** Lambert; *Liocalymene clintoni* (Vanuxem).

3. Willowvale Formation: *Dalmanites limulurus** (Green); *Liocalymene clintoni** (Vanuxem); *Calymene niagarensis* Hall.
4. Kirkland Formation: *Trimerus delphinocephalus** (Green); *Liocalymene clintoni* (Vanuxem).
5. Sauquoit Formation: *Dalmanites limulurus* (?)* (Green); *Liocalymene clintoni** (Vanuxem); *Dalmanites limulurus lunatus* Lambert.

To the west of the study area the Clinton fauna, as a whole, is more diverse (Gillette, 1947). Species of the following genera, not given above, are listed by Gillette: *Bumastus* Murchison, *Proetus* Steininger, *Encrinurus* Emmrich, and *Phacops* Emmrich. We do not know whether the absence of these forms in the study area is due to preservational or environmental conditions; it may be a combination of both. We cannot dismiss the possibility that some of these trilobites left trace fossils in the Clinton while body fossils themselves were not preserved. Indeed, this is a relatively common phenomenon in arthropod trace fossil studies. In addition, it is also possible that eurypterids and synxiphosurids were present within the Clinton but not preserved. However, we feel that it is best to work within a known framework of data, and that organisms not known to occur in a section should not be invoked as tracemakers unless there is some compelling reason to do so. The most convincing evidence would normally be a well-defined trace fossil whose dimensions or morphology cannot be explained within the context of the known body fossils.

Accordingly the trilobite species listed are most critical to this study. The following discussion of the morphological features (size, genal or pygidial spines, nature of dactyls) might key them to a given trace fossil. The material was gathered from original descriptions, subsequent works such as Delo (1940), Whittington (1971), Harrington, *et al. in* Moore, (1959) and written communications with Niles Eldredge of The American Museum of Natural History and Bruce Bell of The New York State Museum who provided measurements of specimens.

A) *Common Clinton Trilobites Within The Study Area*

1) *Trimerus delphinocephalus* (Green) — The key features for this species are its size, length/width ratio, lack of genal or thoracic

spines and a triangular pygidium. As Hall (1843) pointed out, specimens commonly attain a length of 20 cm and, in rare cases, 30 cm. The length/width ratio is 2.5:1. It is by far the largest known Clinton trilobite. See Dale (1953, fig. 18a) for an illustration.

2) *Dalmanites limulurus* (Green) — According to Hall (1843) the normal length is 6.5 cm although none of the specimens in The New York State Museum collections attains this length. Eldredge (personal communication, 1973) reports that dalmanitids are rarely longer than 10 cm. The length/width ratio is 1.6:1. Morphological features which could be important are the fairly long genal spines, and a pronounced single pygidial spine. A figured specimen can be found in Delo (1940, pl. 3, fig. 1).

3) *Liocalymene clintoni* (Vanuxem) and *Calymene niagarensis* Hall — Neither of these species possesses features as distinctive as those for *T. delphinocephalus* and *D. limulurus*. Both are similar in size, ranging from 3-6 cm in length, thus they tend to be slightly smaller than *D. limulurus*. The length/width ratio is 1.4:1. The bodies are without spines. The species are figured by Dale (1953, figs. 18 c, e).

B) *Less Common Clinton Trilobites Within the Study Area*

1. *Arctinurus nereus* (Hall) — Hall (1852, p. 313, pl. 70, figs. 1 h-i) stated that individuals may approach 18 cm in length and rarely are less than 12.5 cm long. This species is easily distinguished by its size, length/width ratio of 1.6:1 and spinose thoracic pleurae.

2. *Cheirurus niagarensis* (Hall) — The species averages 5 cm in length and has a length/width ratio of 1.6:1. It is characterized by moderately long straight thoracic spines and a multispinose pygidium. See Hall (1852, pl. 66A, fig. 4; pl. 67, figs. 9, 10).

To summarize briefly, it is fairly easy to distinguish large *Rusophycus* (short buckle-like burrows; see Pl. 1, fig. 1) by their shape which is reflected in the length/width ratio. Smaller *Rusophycus,* those less than 5 cm, are more difficult to identify unless some hard parts (*e.g.* pygidial spine) made contact with the substrate. Based solely on the given characteristics (long bilobate furrows; see Pl. 4, fig. 1), *Cruziana* in theory should be more difficult to assign to a particular trilobite species, as the length/width ratio is useless — only the width is a valid measurement. Small cruzianids could have been made by any of the species named. Trilobite tracks are difficult to work with if nothing is known of the nature of the terminal dactyls of the trilobite from preserved body fossil material. Unfortunately, this is the case with all the Clinton trilobites. Thus all one can rely on is the *maximum* track width. It may be possible to assign only the larger tracks by a process of elimination.

TRILOBITE BURROWS AND FURROWS

The taxonomic history of the two genera most commonly employed for trilobite burrowing and furrowing activity, *Rusophycus* and *Cruziana,* is extremely involved (see Osgood, 1970, pp. 302-304). Both Osgood (1970) and Crimes (1970, a, b) chose to restrict the genus *Rusophycus* to the short buckle-like imprints, while *Cruziana* was retained for bandlike furrows several centimeters in length. That approach is followed in this paper because we feel that the two genera demonstrate basically different behavior. *Rusophycus* is the result of vertical burrowing either for protection, nourishment or, simply, rest. On the other hand, *Cruziana* is caused by horizontal furrowing with little vertical digging. *Cruziana* may reflect simple movement or it may be a feeding trace.

Seilacher (1970) considered *Rusophycus* as the junior synonym of *Cruziana* because the two forms intergrade. While this is true in some cases (Pl. 2, fig. 4 and Osgood, 1970, pl. 66, fig. 3), we conclude that the two should remain as separate genera. Nevertheless Seilacher's work is invaluable as it represents one of the few monographic studies of a large group of trace fossils carried to the species level. In addition, he proposed that "Tentative subgroups that might technically range as subgenera are labelled 'semiplicata group,' 'almadensis group,' etc. Just as 'resting track' or 'deep undertrack' stand for a particular ecological or preservational situation, these open terms serve their purpose without nomenclatural complication and commitment" (Seilacher, 1970, p. 455). Nine subgroups were proposed and will be used in this report.

Generally, *Rusophycus* and *Cruziana* reveal that the digging movement of the legs was directed posteriorly toward the median line, usually resulting in a series of V-shaped ridges on the lobes of the casts which we term striae. As is the case with trilobite trackways the open end of the V is directed anteriorly. This is confirmed by several specimens from different areas where the imprints of hard parts are preserved. Seilacher (1970) documented several variations in the digging mechanism which in turn alter the morphology of the trace fossil. In general, the *Cruziana* and *Rusophycus* in the Clinton tend to have simple morphology.

CLINTON TRILOBITE TRACE FOSSILS

RUSOPHYCUS Hall,1852

Plates 1; 2; 3, figures 1, 3, 4; Plate 4, figure 2

Non Fucoides Brongniart, 1823, p. 308, pl. 19, fig. 2; *partim* Vanuxem, 1842, p. 79, figs. 11-1.

Non Bilobites Rafinesque, 1831, p. 2; *non* d'Orbigny, 1839, pl. 1.

Non Cruziana d'Orbigny, 1842, p. 30; James, 1885, pp. 153-157, pl. 8, fig. 1; Abel, 1935, pp. 253-255, fig. 224; Seilacher, 1953, pp. 107-115, figs. 4-5; *partim* Seilacher, 1970, pp. 447-476, 11 figs.

Rusophycus Hall, 1852, p. 23, pl. 8, figs. 6a, b; pl. 9, figs. 1-3; Seilacher *in* Schindewolf and Seilacher, p. 368, pl. 16, fig. 2; pl. 19, fig. 1; pl. 20, figs. 1, 3, 4; Seilacher, 1959, pp. 292-293, fig. 4; Häntzschel *in* Moore, 1962, p. W212, figs. 131-3, 5; Radwanski and Roniewicz, 1963, pp. 265-267, pl. II; Bergström, 1970, pp. 37-40, pl. 1; Crimes, 1970a, pp. 53-55, pl. 11; Crimes, 1970b, pp. 114-116, pl. 4; Osgood, 1970, pp. 301-308, pls. 57-60, 66, 71, 82; Orłowski, *et al.*, 1970, p. 352, pl. 3; *partim* Selley, 1970, pl. 2c; Birkenmajer and Bruton, 1971, pp. 303-319, figs. 1-9; Orłowski, *et al.*, 1971, pp. 341-348, 6 pls.; *partim* Bergström, 1973, pp. 53-58, text fig. 16, pl. 5, figs. 10-14.

Rusichnites Dawson, 1864, p. 367.

Rhysophycus Schimper *in* Zittel, 1879, p. 54; Lessertisseur, 1955, pp. 44-47, figs. 25-27, 39, pl. 6, fig. 4.

Trilobite burrows were first recognized in the Clinton by Vanuxem (1842, p. 79) who established the species *Fucoides biloba*. The species was figured but no description given. The reported that the "bilobed fucoid" was abundant at Blackstone's and Davis' quarries. Hall's work in 1852 was much more comprehensive. He proposed the genus *Rusophycus* and, in addition to a discourse on *R. bilobatum,* erected three new species for the genus. Aside from *R. bilobatum,* only one of the three, *R. pudicum,* falls within the confines of our definition of *Rusophycus*. We place Hall's *R. subangulatus* and *R. clavatus* within *Cruziana*. *Rusophycus* is abundant in the Joslin Hill Member of the Herkimer, especially at Dawes Creek Quarry (loc. 4). It is somewhat rarer in the Sauquoit-Otsquago. Our study suggests that retention of two species is justified and that no additional species are necessary. However, as we feel that we can assign certain specimens of *R. bilobatum* to trilobite species within the Clinton, we have elected to subdivide the species into *R. bilobatum* Types 1, 2, and 3. Establishment of new ichnospecies cannot, however, be justified on these grounds alone because the morphological differences are slight and do not reflect changes in behavior.

Rusophycus pudicum Hall, 1852 Pl. 1, fig. 5; Pl. 4, fig. 2

Rusophycus pudicus Hall, 1852, p. 24, pl. 8, figs. 6 a, b.
?*Cruziana pudica* (Hall), James, 1885, pp. 154-157; Seilacher, 1970, p. 471, fig. 11a.
Rusophycus pudicum Hall, Osgood, 1970, pp. 305-307, pl. 57, fig. 6; pl. 58, figs. 3-5, 7, 9, 10; pl. 59, fig. 5; pl. 60, fig. 2; pl. 66, fig. 3; pl. 81, fig. 9.

The two syntypes for this species were figured by Osgood (1970, pl. 58, fig. 6 = Hall, 1852, pl. 8, fig. 6a; Osgood, 1970, pl. 59, fig. 5 = Hall, 1852, pl. 8, fig. 6b) and are not refigured in this paper. Both specimens were taken from Blackstone's quarry and, like Vanuxem's, are Upper Sauquoit in age. Hall (1852, p. 23) gave the locality as "New Hartford, Oneida County." This probably places the quarries between localities 5 and 8. Both syntypes are preserved as convex hyporeliefs. A convex hyporelief may be defined as an elevated mass on the bottom of a slab as viewed from the side. A groove cast is an example. See Osgood (1970, text-figure 4) for a more lengthy treatment of trace fossil preservation.

One specimen measures 3.2 cm in length, the other 4.5 cm. The lobes are moderately well developed and striae are evident but weak. Neither specimen possesses markings which could be attributed to imprints made by hard parts of the body. This species was used by Osgood (1970) for trilobite burrow-casts formed by *Flexicalymene* in the Upper Ordovician of Ohio. Seilacher (1970, p. 471) included forms from the Caradocian (Ordovician) of Jordan.

Our field work revealed that *R. pudicum* is rare in Oneida County and Herkimer County. Only five specimens were collected; three from the Herkimer at locality 4, one from the Sauquoit at Ohisa Creek (loc. 18), and one from the Otsquago at locality 14, Flat Creek. A typical *R. pudicum* is represented by the form from Ohisa Creek (Pl. 4, fig. 2). The length is 3.5 cm and the length/width ratio is 1.6:1. Striae are not evident on the lobes and the specimen gradually tapers posteriorly. None of the five specimens possesses any characteristics which would differentiate it from the syntypes described above.

The species is sufficiently small that it could have been made by any Clinton trilobite with the proper length/width ratio. The most likely tracemakers were *Liocalymene clintoni* and *Calymene niagarensis;* the former is common in the Sauquoit, the latter in the Herkimer.

Seilacher (1970, p. 471) referred to his ninth subdivision of *Cruziana* as the "Pudica Group". He defined the group as "Mainly resting tracks with sharp and multiple endopodal scratches that run mainly transverse. Probably made by calymenid trilobites." In order to include *R. pudicum* in the group whose name it bears, some modification is needed because the scratches are not sharp. This emendation is provided following our discussion of *R. bilobatum.* Seilacher's (1970) diagnosis of *R. pudicum* itself is sufficiently broad that it need not be altered.

Rusophycus bilobatum (Vanuxem), 1842
Pl. 1, figs. 1-4; Pl. 2; Pl. 3, figs. 1, 2, 4

Fucoides biloba Vanuxem, 1842, p. 79, fig. 11-1 no description; Hall, 1843, p. 77, fig. 1; Owen, 1845, p. 307, fig. 1; Lincklaen, 1861, pl. 6, fig. 13.
Cruziana bilobata James, 1885, pp. 156-157.
Rusophycus bilobatus Hall, 1852, p. 24, pl. 9, figs. 1a-c; Rogers, 1858, p. 822, fig. 626; Emmons, 1860, p. 107, fig. 1; Dana, 1863, p. 235, fig. 365; Nicholson, 1875, p. 37, fig. 14; Miller, 1889, p. 914; Seilacher *in* Seilacher and Schindewolf, 1955, pp. 363-364, fig. 5-3.
Rhysophycus bilobatus Hall, Lessertisseur, 1955, fig. 25-c.

Fully developed specimens of *R. bilobatum* differ significantly from *R. pudicum.* Distinguishing features are length, often in excess of 10 cm, and well-developed striae on the lobes. Admittedly, smaller individuals may intergrade somewhat with *R. pudicum.* Hall (1852) figured three specimens from Gaylord and Nelson's quarries which he stated were near New Hartford. This means that the figured specimens are from the Lower Herkimer. The quarries were probably one or two miles west of locality 8.

The form figured by Hall (1852, pl. 9, fig. 3; herein Pl. 2, fig. 3) is large with a maximum width of 6.2 cm and a length of 12 cm. The lobes are moderately well developed but the striae are not as numerous as Hall's lithograph would infer. The best preserved striae are on the posterior half of the specimen and are directed nearly transversely. We cannot determine the number of dactyls of the tracemaker. This is due primarily to the type of preservation, a problem commonly encountered with Clinton *Rusophycus*. Most of the host rock is a fine- to medium-grained sandstone, while the surface bearing the striae is a mixture of sand and shale which tends to mute the details of finer markings. Experience has shown that optimum conditions for preservation of detail occur when the burrow is excavated in mud and later filled with sand. The second specimen illustrated by Hall (1852, pl. 9, fig. 1; herein Pl. 1, fig. 1) is somewhat smaller than the first. The width is 4.5 cm while the length is 8.5 cm. Neither the lobes nor the striae are clearly defined. A hemicylindrical burrow cast, apparently made by a vermiform organism, can be traced from the anterior portion of the *Rusophycus* posteriorly to where it is terminated by the edge of the slab some 5 cm away from the trace. This association may have some ethological significance and is discussed later. Hall's final syntype (Hall, 1852, pl. 9, fig. 2; herein Pl. 2, fig. 2) is an incipient *Rusophycus*. Because it is the cast of a shallow burrow, the dimensions (width 3.5 cm; length 6.5 cm), do not reflect the true size of the tracemaker. In contrast to Hall's other specimens, the striae are abundant and sharp. They are directed transversely and appear to be unbranched. A cylindrical burrow cast 8 mm in diameter passes vertically through the specimen.

As Zenger showed (1971, Table II), *R. bilobatum* is present at nearly every Joslin Hall outcrop of the Herkimer. We can add that it is also present at localities 2 and 4A. In contrast it is quite rare in the Sauquoit, we found it only at localities 5 and 18.

Crimes (1970a) pointed out that in both *Rusophycus* and *Cruziana*, evidence of the digging activity of the legs is never found beyond the lateral margins of the bilobate structure. The senior author confirms this, based on his work with both Cincinnatian and Clinton *Rusophycus*. Therefore the width of *Rusophycus* can provide us with at least a minimum width for the tracemaker. In addition, in many cases, the burrow was sufficiently deep to give a reasonably accurate index of the shape of the burrower, even where imprints of hard parts (genal and pygidial spines) are lacking. Thus, it is apparent that length/width ratios of *Rusophycus* can be useful, especially in the Clinton where three of the four most common trilobite species have quite different outlines. For this reason we have elected to subdivide *R. bilobatum* into three groups.

Rusophycus bilobatum, Type 1 Pl. 2, fig. 1; Pl. 3, fig. 2

At least two specimens, both from Herkimer at locality 4 are assigned with confidence to *Trimerus delphinocephalus.* The specimen illustrated on Plate 2, figure 1 has a length of 15 cm and a length/width ratio of 2.3:1. The striae are conspicuous but the lobes are not. Most striae are unbranched although the presence of some bifid striae indicate that *T. dephinocephalus* possessed a minimum of two dactyls per walking leg. The anterior portion of the burrow was more deeply excavated and it is likely that the pygidium was never completely buried. This accounts for the somewhat rounded posterior margin. The form seen on Plate 3, figure 2 is 13.5 cm long and also possesses a length/width ratio of 2.3:1. Neither lobes nor striae are well preserved, possibly due to the fine grained nature of the rock. Nevertheless, the outline closely approximates that of *T. dephinocephalus* which has a length/width ratio of 2.5:1.

Rusophycus bilobatum, Type 2 Pl. 1, figs. 3, 4; Pl. 2, fig. 4

Four specimens, again all from the Herkimer at locality 4, are attributed to *Dalmanites limulurus.* They differ from Type 1 in overall shape and by the appearance in some specimens of what we interpret as casts of genal and pygidial spines. The form figured on Plate 1, figure 4 is one of two small specimens; both have a length of 3.5 cm and a width of 2.3 cm. The posterior half has two lateral ridges and a pronounced median ridge which probably represents casts of the genal and pygidial spines respectively. Another *Rusophycus* attributed to *D. limulurus* (Pl. 1, fig. 3) has coarse striae and a marked median ridge. Lateral ridges are present but not pronounced. The only reservation regarding the assignment of this trace fossil to *D. limulurus* is its large size. The length is 13.5 cm, the width 6 cm, somewhat in excess of the median size for the trilobite. Nevertheless, it is otherwise difficult to explain the median ridge. The final form (Pl. 2, fig. 4) differs from those above in lacking any trace of the pygidial spine. However, it displays two well-defined lateral ridges. The specimen also shows what Seilacher (1953) termed "horizontal repetition." The organism excavated the burrow, then partially resurfaced and burrowed again. The width of the burrow cast is 4.0 cm. The lack of a median ridge might indicate that this particular specimen was made by *D. limulurus lunatus,* which according to Delo (1940, pp. 44-45, pl. 3, fig. 2), has a somewhat shorter pygidial spine than *D. limulurus.*

Unfortunately, the grain size of the rocks bearing the specimens with striae is too coarse to allow determination of the number of dactyls *D. limulurus* possessed.

Rusophycus bilobatum, Type 3 Pl. 1, fig. 2; Pl. 2, figs. 2, 3; Pl. 3, figs. 1, 4

Most *Rusophycus bilobatum* collected from the Herkimer, including the three specimens figured by Hall (1852), bear no characteristics which allow us to assign them to either *D. limulurus* or *T. delphinocephalus*. The form on Plate 3, figure 1 typifies this group. The length is 8.7 cm, the width 6.2 cm. The cast is elevated only about 2 cm off the sole of the bed indicating a shallow burrow, one which does not conform to the true outlines of its maker. The striae are well developed with some bifid imprints clearly visible. Like most Clinton *Rusophycus* the striae are directed transversely. Over two dozen specimens like this one were collected and many more were observed. Some of the forms indicate deeper burrowing but otherwise portray no characteristics which differ from the specimen described above. Because of the variable size, length/width ratio, and lack of casts of spines, the *Rusophycus* included in this group cannot be assigned to a given trilobite species. The large width of most specimens seems to point to *T. delphinocephalus* as most likely, but *D. limulurus* cannot be ruled out.

While Seilacher (1970) did not include *R. bilobatum* in his monographic study, a review of his 10 subgroups leads us to conclude that the species fits best within Group IX, the Pudica Group. The key features are ". . . sharp and multiple endopodal scratches that run mainly transverse." (Seilacher, 1970, p. 471). This is the only subgroup with transverse striae. However, as noted above, if *R. pudicum* and *R. bilobatum* are to be included in this group Seilacher's definition of the group must be modified. The phrase "probably made by calymenid trilobites" should be deleted as neither *Trimerus* nor *Dalmanites* are calymenids. In addition, to accommodate *R. pudicum,* his first sentence should be altered to read "Mainly deep resting tracks, sometimes smooth or with weakly developed striae. Striae can be sharp especially in larger forms. All striae are directed transversely."

Although *Rusophycus* is extremely abundant in parts of the Clinton, the results gathered from this study are somewhat disappointing. These trace fossils manifest no behavioral variations which have not been reported previously in the literature. Moreover, whereas the striae are pronounced in some specimens it is not possible to determine the number of dactyls of the common Clinton trilobites. The ethological significance of *Rusophycus* is covered following the discussion of *Cruziana* and *Diplichnites*.

CRUZIANA d'Orbigny, 1842

Plate 3, figure 3; Plate 4, figures 1, 3

Cruziana d'Orbigny, 1842, p. 30; *partim* James, 1885, pp. 155-157; *partim* Abel, 1935, fig. 223; *partim* Lessertisseur, 1955, pp. 44-47, text-fig. 25 A, B, D, E, pl. VI, figs. 1, 3; Seilacher *in* Seilacher and Schindewolf, 1955, pp. 364-367; Häntzschel *in* Moore, 1962, p. W189, figs. 119-5, 6; Radwanski and Roniewicz, 1963, pp. 267-269, pls. IV-VI; Seilacher and Crimes, 1969, pp. 145-148, pl. 1, figs. 1-6; Crimes, 1970a, pp. 49-53, pls. 5-9, 12 a, b; text-fig. 2; Cowie and Spencer, 1970, pp. 94, 96, 98, pl. 2, figs. d, e; Crimes, 1970b, pp. 111-112, pls. 3, 5; Orłowski, *et al.*, 1970, pp. 350-356, pls. 1-4; *partim* Seilacher, 1970, pp. 447-476, 11 figs.; Selley, 1970, pp. 481-484, pl. 1, figs. 2 b, c; Birkenmajer and Bruton, 1971, pp. 303-319, figs. 5, 10-13; *partim* Bergström, 1973, pp. 55-58.

Partim *Rusophycus* Hall, 1852, p. 23, pl. 8, figs. 1a, b, 2 a, b; *partim* Osgood, 1970, pl. 59, fig. 3; pl. 67, fig. 5.

Cruziana, as defined in this paper, is extremely rare in the Clinton. Aside from the specimens figured by Hall (1852, pl. 8, figs. 1a, b; 2a, b) only Flat Creek (locality 14) yielded *Cruziana*. Although Hall's two species can be reduced to one, *C. clavata*, the Flat Creek forms are different and are placed in *Cruziana* cf. *C. quadrata* Seilacher.

Cruziana clavata (Hall) Pl 3, fig. 3

Rusophycus clavatus Hall, 1852, p. 23, pl. 8, figs. 1 a, b.
Rusophycus subangulatus Hall, 1852, pl. 8, figs. 2 a, b.
Cruziana clavatum (Hall), James, 1885, pp. 154, 156-157.
Cruziana subangulata (Hall), James, 1885, pp. 154, 156-157.
Rusophycus clavatum Hall, Osgood, 1970, pl. 67, fig. 5.
Rusophycus subangulatum Hall, Osgood, 1970, pl. 59, fig. 3.
Cruziana clavata (Hall), Seilacher, 1970, p. 470.

Hall (1852, p. 23) proposed two additional species of *Rusophycus, R. clavatum* and *R. subangulatum*, which we place in *Cruziana*. Both were from Blackstone's quarry and thus from the Upper Sauquoit. Two specimens of each species were figured. Of these four forms, two were illustrated by Osgood (1970) while a third can be found herein on Plate 3, figure 3. The fourth specimen, "*R.*" *subangulatum* (Hall, 1852, pl. 8, fig. 2a) could not be located in any of Hall's collections. This is indeed unfortunate because it is the only one of the four which truly embodies the morphology of *Cruziana*. The other syntypes are either poorly preserved or transitional between *Rusophycus* and *Cruziana*. One of Hall's types of *C. clavata* (Hall, 1852, pl. 8, fig. 1b; herein Pl. 3, fig. 3) consists of two shallow, U-shaped, bilobed burrow casts which are 5-5.5 cm long. The width is 1.4 cm and the lobes do not bear traces of striae. Hall's other syntype for this species (Hall, 1852, pl. 8, fig. 1a; Osgood, 1970, pl. 67, fig. 5) reflects more complex behavior. The two burrow casts are podlike and trilobed. In addition there is a short bilobed segment, 1 cm in width, leading from one of the pods. This segment, which bears weak striae is not included in Hall's lithograph but does show on Osgood's plate. The morphology exhibited by this specimen shows that the trilobite burrowed, backed up, shifted position slightly, and then burrowed again, thus accounting for the unusual trilobed appearance. The same procedure produced the second pod. The short-bilobed segment reveals a reversion to normal furrowing activity, more typical of *Cruziana*. The basically bilobed nature of the syntypes indicates a trilobite origin, but the forms are sufficiently small that they may have been made by the Clinton trilobite.

Hall (1852, p. 23) set *C. subangulata* apart as a separate taxon because forms included in this species were ". . . of equal dimensions throughout and usually more elongate." The specimen which best typifies *Cruziana* is apparently lost and the other (Hall, 1852, pl. 8, fig. 2b; Osgood, 1970, pl. 59, fig. 3), bears only superficial resemblance to Hall's lithograph. This form is a little over 1 cm in width and somewhat discontinuous. While the bilobate nature is clearly evident, the host rock is too coarse to permit preservation of striae on so small a specimen.

Because Hall believed these were fucoids, the morphological differences may have been sufficient under the circumstances to justify separate species. They are clearly of trilobite origin and manifest only slight differences in behavior. We believe that *C. subangulata* should be considered as a junior synonym of *C. clavata*. Seilacher (1970, p. 470), with some reluctance, placed *C. clavata* in his number VIII Quadrata Group, more specifically under *C. quadrata*. The

Clinton specimens, however, do not fit the diagnosis of *C. quadrata* which is: "Deep furrow with rectangular cross section. Narrow endopodal lobe of oblique multiple scratches on either side of the median line. Pleural lobe smooth with few transverse scratches." On the other hand, as we are dealing with a rare, unremarkable group of specimens in the Clinton it does not seem wise either to alter Seilacher's diagnosis or to establish a new Group. Seilacher admitted that the Quadrata Group may be artificial, but to include *C. clavata* in it weakens it even further. For the present we prefer not to place *C. clavata* in any Group but to wait until additional material can be collected.

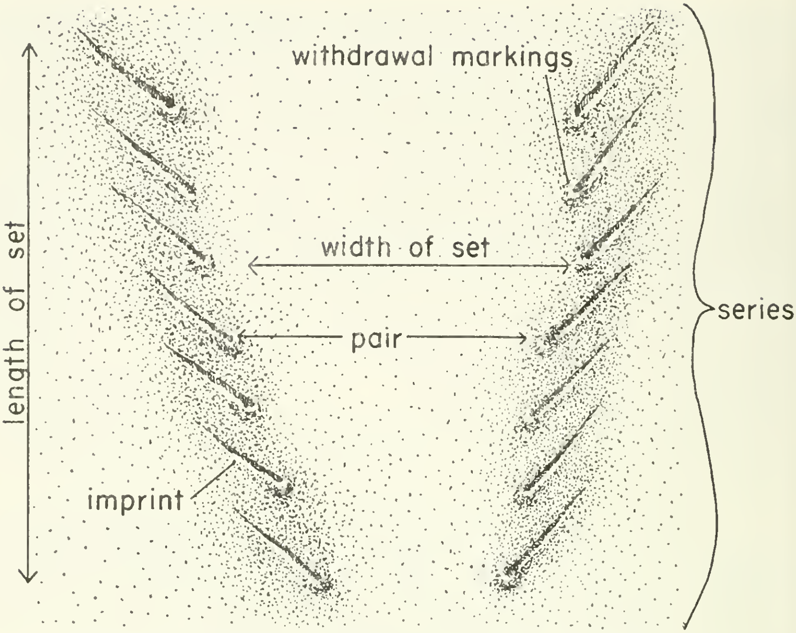
Cruziana cf. **C. quadrata** Seilacher Pl. 4, figs. 1, 3

1970. *Cruziana quadrata Seilacher,* Geol. Jour., Spec. Issue No. 3, p. 470, text-fig. 7, No. 22.
1970. *Non Cruziana* cf. *quadrata* Seilacher, *ibid.,* p. 471.

The only cruzianids actually collected by the authors from the 17 Clinton localities were found in the Otsquago beds at Flat Creek. These occur as convex hyporeliefs on large slabs which were found in close stratigraphic proximity to those bearing the trilobite trackways, *Diplichnites.* The form illustrated on Plate 4, figure 1 is typical. The width is 7 mm. Study of this specimen reveals that this is not a single trail as several of the arcs meet at odd angles. This was either made by several individuals, or if it is the work of one organism the animal must have intermittently lost contact with the depositional interface. The morphology varies from ill-defined tracks, to a bilobed cast flanked by casts of the exopodites or genal spines, to bilobed ridges resting on a quadrate platform with sharply defined margins. This final type of preservation (Pl. 4, fig. 3) occurs only when the cast is elevated well off the sole of the bed. It appears that in deeper furrowing the cephalon acted as a plow. This provides justification for placing the specimens in the taxon. We hesitate to assign them directly to the species because of their small size. Indeed, because of this one could question whether the Flat Creek specimens were even made by trilobites. However, we believe they were as indicated in the final section of this paper.

TRILOBITE TRACKWAYS

In a well-reasoned study using comparisons with Recent arthro-



Text-figure 3. Nomenclature applied to arthropod trackways. See text for more complete definitions (after Osgood, 1970, text-figure 18).

pods, Seilacher (1955) hypothesized that trilobites walked with a wave of motion which proceeded anteriorly from the pygidium toward the cephalon. By the time one wave reached the cephalon another was initiated at the pygidium (Osgood, 1970, pp. 350-354 for a discussion of Seilacher's conclusions). This action resulted in a series of V-shaped markings made by the walking legs; the open end of the "V" points in the direction of movement. To provide a basis for description Seilacher (1955) proposed a series of terms, which were translated by Osgood (1970) and are shown in Text-figure 3. See Osgood (1970, p. 351) for a definition of the terms. The depressions resulting from the contact of the legs with the substrate are termed concave epireliefs.

Several factors influence the final configuration of the trackway, among these being:

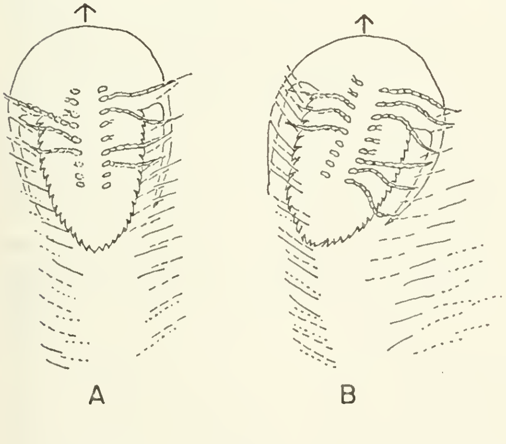
1. The orientation of the body with relation to the direction of movement (see Text-figure 4).

2. The number of dactyls actually making contact with the substrate. A slight rotation of the limb or a change in the angle of penetration can alter the imprints. Therefore, the greatest number of dactyls seen in an imprint provides the best clue as to the number of dactyls possessed by the walking leg.

3. As Crimes (1970a) demonstrated, the speed at which the animal was traveling is also a factor. The faster the movement the more acute the angle of the "V" will become. It may also mean that fewer appendages make contact with the substrate during rapid movement. Therefore, the maximum width of the set may be somewhat less than the actual width of the organism. It is especially difficult to assign a given species of trilobite to a trackway of relatively narrow width.

4. The topography of the depositional interface must also be considered. While there is some debate as to how well trilobites could swim, a series of ripple marks may lead to discontinuous and poorly organized trackways.

5. The type of preservation is also important. Both Osgood



Text-figure 4. Morphology of trilobite tracks. A. Movement parallel to body axis. The results are partially superimposed V-shaped series. B. Direction of movement slightly oblique to body axis. Imprints on one side are clearly defined, those on the other are superimposed. C. Strongly oblique movement resulting in markedly dimorphic imprints (from Osgood, 1970, text-figure 17; A and B after Seilacher, 1955, figs. 1a, e; C after Seilacher, 1955, fig. 2B).

(1970, text-figure 19) and Goldring and Seilacher (1971) demonstrated that arthropod imprints preserved on "cleavage planes" a millimeter or two below the surface can differ markedly from surficial imprints.

The direction in which a trilobite was traveling may be determined by at least two methods. First, if the imprints are arranged in the V-shaped pattern described above, the open end of the "V" points toward the direction in which the trilobite was moving. The second method is useful when complete series of V's are not present. It was postulated by Seilacher (1955) (see also Seilacher, 1962, p. 224) and verified by Osgood (1970). As the dactyls made contact with the substrate the appendage was drawn in toward the body. This action usually resulted in a small welt of sediment being raised as the walking leg lost contact with the bottom (Text-figure 3). These were termed "withdrawal markings" by Osgood, 1970.

Trilobite tracks have been assigned to several genera. As Bergström (1973) stated, probably not all of these are necessary. The two most commonly applied are *Protichnites* Owen (1852) and *Diplichnites* Dawson (1873). Osgood (1970, p. 352) pointed out that for various reasons the type specimens of neither trackway could be assigned to trilobites with any degree of certainty. Instead, he chose to discuss Cincinnatian trilobite trackways within the framework of the several taxa proposed by Miller (1880). However, subsequent authors, Seilacher (1970), Crimes (1970 a, b), and Bergström (1973) have chosen to employ *Diplichnites* for trilobite trackways indicating straight-ahead or slightly oblique movement. *Protichnites* is currently used for trackways with a groove between the arms of the "V". This groove probably is the impression of fleshy caudal cerci or a pygidial spine. As it appears that both genera have gained general acceptance it seems reasonable to assign the Clinton traces to *Diplichnites*. However, the genus has yet to be monographed and as many of the Clinton trackways are somewhat incomplete, no attempt is made here to establish species. Instead, for reasons further justified below, our trilobite trackways are assigned to *Diplichnites* sp. Groups A, B, C.

Two additional genera of trilobite tracks are worthy of mention. They are *Dimorphichnus* Seilacher, 1955 and *Monomorphichnus* Crimes, 1970a. *Dimorphichnus* (Text-figure 4 herein) was erected by Seilacher for trackways in which the body was oriented nearly at right angles to the direction of movement. The resulting trace is a series of long raking imprints made by the appendages on the lee side of the body; the legs of the other side provided body support, thus these imprints resemble a series of small pits. Seilacher interpreted this as a feeding trail where the legs acted as rakes to stir up the nutrient-bearing sediment. Opinions of several authors regarding Seilacher's ethological interpretation are given in Osgood (in press). *Monomorphichnus* is similar to *Dimorphichnus* except that the support imprints are absent. Crimes envisioned a trilobite swimming sideways with only the legs on the lee side of the body making contact with the bottom. Crimes regarded *Monomorphichnus* as a feeding trace. Thus far both genera have been reported only from the Cambrian. Neither genus is present in the Clinton rocks.

CLINTON TRILOBITE TRACKWAYS

DIPLICHNITES Dawson, 1873

Plate 4, figure 4; Plates 5, 6, 7

Diplichnites Dawson, 1873, pp. 19-20, fig. 3; Seilacher *in* Schindewolf and Seilacher, 1955, pp. 342-346, pl. 16, figs. 3, 4, text-figs. 1 b-d, f; Crimes, 1970a, pp. 56-57, pls. 9-13; Crimes, 1970b, pp. 117-119, pl. 5 d; Bergström, 1973, pp. 52, 53, 58, 59, pl. 5, fig. 11.
Partim Asaphoidichnus Miller, 1880, pp. 217-219; *partim* Häntzschel *in* Moore, 1962, p. 184; Osgood, 1970, pp. 356-358, pl. 65, fig. 2, pl. 71, fig. 6, pl. 72, fig. 3, pl. 73, figs. 1, 2, text-figs. 20-A, 21-A, 29-f.
Petalichnus Miller, 1880, pp. 219-221, pl. 13, fig. 5; pl. 14, fig. 3; Häntzschel *in* Moore, 1962, p. W208; Osgood, 1970, pp. 362-366, pl. 73, figs. 5, 6; pl. 74, figs. 2, 4, 5; pl. 75, fig. 4, text-figs. 22, 29 i, j.
Partim Trachomatichnus Miller, 1880, pp. 219-220, pl. 13, figs. 2-4; *partim* Häntzschel *in* Moore, 1962, p. W219; Osgood, 1970, pp. 366-368, pl. 73, figs. 3, 4; pl. 74, fig. 1, text-figs. 20-B, 29 g.
Merostomichnites Packard, Caster, 1938, p. 34, pl. 10, fig. 1.
"Arthropodenfährten" Abel, 1935, fig. 222.
"epichnial tracks" Martinsson, 1965, pp. 207-209, figs. 14-17.

The trackways illustrated by Hall (1852, pls. 15-16) fascinated him to such a degree that he sought opinions on their origin from such luminaries as J. D. Dana, Louis Agassiz, and Charles Lyell. With some hesitation he finally concluded that the markings represented imprints of the fins of fish. A comparison of Hall's comments on the markings (1850, 1852) demonstrates that the thoughts presented in his 1850 paper actually postdate the 1852 volume. In 1850 he admitted that he had considered the impressions to be of crustacean origin (his final conclusion in the 1852 work) but dismissed that hypothesis in favor of the fish origin. Hall admitted that he was confused by the configuration of the individual imprints which varied from monodactyl to pentadactyl. Moreover, he remarked that the number of dactyl imprints varied within the same trail (from monodactyl to tridactyl). One final aspect led him to cast aside an arthropod origin: He pointed out ". . . when we examine a single series of these [imprints] there does not appear to have been as many appendages as are usual in the crustaceans" (Hall, 1852, p. 33).

Little can be gained from a complete redescription of all of Hall's figured specimens. Instead, selected types augmented by material collected by the authors from various Clinton localities will provide the basis for discussion. Generally speaking, trilobite trackways are not as common in the Herkimer as they are in the Sauquoit-Otsquago. The best material was collected from localities 5, 14, 16 and 20a. Nearly all the trackways are preserved as concave epireliefs in fine to medium-grained sandstones whose upper surfaces bear interference ripple marks.

It must be admitted that even with the benefit of the work which has been done on arthropod trails since Hall's time, we still do not completely understand the nature of some of the Clinton trackways. In only a few cases can the specimen be attributed to a given trilobite species commonly found in the Clinton. Further collecting may clarify the situation. For purposes of discussion the trackways are assigned to *Diplichnites* sp. and are separated into three Groups, A, B, and C. Groups A and C are polyphyletic in the sense that they probably contain trackways made by different trilobite species. Group B may be monophyletic.

Diplichnites sp., Group A Pl. 4, fig. 4; Pl. 5, fig. 3, Pl. 7

This group of trackways contains forms where the sets are well organized, *i.e.* the V-shaped pattern is clearly evident. The width of the set varies from 1.3 - 1.5 cm and a series contains 6-11 imprints. The dactyls are unbranched or bifid and short. The group is best typified by the specimens illustrated on Plate 5, figure 3 and Plate 7, figure 3. Although individual imprints of the form seen on

Plate 5, figure 3 are so weakly impressed as to make it impossible to determine the number of dactyls which the appendage possessed, the trackway is remarkable for its length. The same trail and several similar ones on a large slab from loc. 14 (Flat Creek) can be traced for over 25 cm. The organism crossed several ripple crests in its movement without losing contact with the substratum. This is in marked contrast to many other Clinton trilobite trackways where interference ripples had a definite influence on the imprints. Plate 7, figure 3 shows another form from Flat Creek, illustrated by Hall (1852, pl. 16, fig. 3). The trail is shorter and consists of the three well-defined V-shaped sets with 5-6 imprints in each. The dactyls are bifid.

We can state with a high degree of confidence that the two trackways described above are of trilobite origin. They conform in their V-shape, and number of imprints to trilobite trails discussed by Seilacher (1955) and Osgood (1970). The relatively narrow width of the sets suggests *Liocalymene clintoni* or *Dalmanites limulurus,* both of which have been reported from the Sauquoit.

Diplichnites sp., Group B Pl. 5, figs. 1, 4

Only two specimens are assigned to this group which differs basically from the preceding only in the large width of the sets (3.5-4.0 cm). Both forms were figured by Hall (1852, pl. 16, figs. 1, 2; herein Pl. 5, fig. 4; Pl. 5, fig. 1). Photographs of both specimens were taken from latex molds. Thus the directions differ from those given by Hall. The trackway shown on Plate 5, figure 4 does not conform in all respects either to Hall's lithograph or his written description of it. He referred to the short row of imprints on the upper right (as viewed on Pl. 5, fig. 4) as trifid yet the latex mold does not show it. However, a few markings within the trackway give a hint of being bifid. Also, the longer series of imprints near the center of the specimen does not possess the marked chevron shape which Hall illustrated. The large number of imprints in a series (up to 16), as well as the width of the set is indicative of a trilobite origin. Both the orientation of the "V" and the location of the withdrawal markings demonstrate that movement was from the upper left to the lower right, and the body axis was oriented somewhat to the left of the direction of movement (compare with Osgood, 1970, pl. 73, fig. 2).

The other specimen placed in Group B (Pl. 5, fig. 1) is one of the more complete trackways found in the Clinton. The width is 3.5 cm, there are at least 10 imprints per set, and all dactyls seems to be unbranched. The trail appears to start as a shallow *Rusophycus* or "sitzmark" at the bottom of the illustration. The organism then moved toward the top while pivoting to the right. The chevron markings on the left were caused by the legs slicing into the sediment. These legs bore most of the body weight; those on the right reveal longer scratch marks, indicating that they were dragged over the bottom.

The width of the set seems to leave *Dalmanites limulurus* as the most likely candidate for the tracemaker for both specimens.

Diplichnites sp., Group C Pl. 5, fig. 2; Pl. 6

The group includes a number of trails which are not continuous, and with a few exceptions, not well organized. Whereas it is not possible in many cases to see the V-shape of the series or even to measure the width of the set, the individual imprints may be preserved with a remarkable degree of clarity. These imprints range from monodactylous to pentadactylous.

The complexity inherent in *D*. Group C is typified by the form on Plate 6, figure 1. (Hall, 1852, pl. 15, fig. 2). There are at least three trails preserved on the slab. One is visible on the far right of Plate 6, figure 1. This has narrow imprints of bifid dactyls and can be assigned to *D*. Group A. The second trackway, which is somewhat indistinct, is first seen at point "a" on the illustration. It terminates near the upper left margin. These two trails partially obscure a third which traverses the rock from right to left. Many imprints are present, yet V-shaped sets are not apparent. The imprints in the right half of the figure (point "b") are unbranched or bifid, yet near the left-hand margin (point "c" also see Pl. 6, fig. 2 for enlargement), they become trifid and finally pentadactylous, inscribing an arc of greater than 180°! The withdrawal markings (depressed areas on the latex mold) show that the organism was traveling from right to left. These radiating pentadactylous markings are present in other material from Flat Creek as well. Plate 6, figure 3 shows a grouping of such imprints with no obvious organization along the margin of a slab.

On the other hand Hall (1852, pl. 15, fig. 1; herein Pl. 6, fig. 4), illustrated a specimen in which two rows of imprints are clearly evident. The left side is composed of pentadactylous imprints; the other side is unbranched. Withdrawal markings show movement was from top to bottom as viewed on the plate. The best preserved example of pentadactylous imprints (Pl. 6, fig. 5) occurs on another ripple-marked slab collected by the authors from the Otsquago beds at Flat Creek. There is a profusion of imprints on the rock surface, yet two pentadactyl imprints can be clearly seen near the bottom margin. If one follows these toward the center of the plate they revert to a more elongate trifid condition. Markings made by the appendages of the other side of the body are not evident.

It is clear that the forms included in *D.* Group C differ significantly from those of the other two groups. Indeed, one might question whether they are of trilobite origin. Eurypterids and synxiphosurids have not been reported from the Clinton but are present in the Upper Silurian section in New York. However, unless positive evidence to the contrary can be found, we believe that several points favor a trilobite origin. These are: 1) the lack of eurypterid and synxiphosurid body fossils in the Clinton; 2) the complete lack of any markings which could be interpreted as having been made by the long thin telson which many Silurian merostomes possessed (Størmer, 1955); 3) the morphology of the imprints included in *D.* Group C does not conform to the distal portions of the appendages of preserved Silurian merostomes (Størmer, 1955); 4) the Clinton trails do not compare favorably with xiphosurid and eurypterid trails (Caster, 1938; Størmer, 1934); 5) finally and possibly most important, the number of pentadactylous impressions in a series in at least one specimen exceeds the number of pairs of locomotive appendages in the merostomes (3-6). Hall (1852, pl. 15, fig. 5; herein Pl. 5, fig. 2) figured a specimen which shows pentadactylous impressions in a portion of the right hand series of the "V." The number of imprints which can confidently be assigned to a series ranges from 5-10. The overall pattern of the markings does not differ drastically from that seen in *Diplichnites,* Groups A and B. For these reasons, we conclude that *D.* Group C is also of trilobite origin.

If this line of reasoning be correct, how do we reconcile the markings with what is known of the distal portion of trilobite appendages? Also, how do we explain the seemingly unorganized pattern seen in most of the specimens in light of what we understand of trilobite locomotion? The pentadactylous markings, especially those on Plate 6, figures 2, 3, 4 are somewhat reminiscent of forms illustrated by Seilacher (1962) from the Devonian Hunsrück Shale of Germany and attributed to *Phacops*. Study of preserved appendages of *Phacops* (Seilacher, 1962, pl. 24, figs. 1, 2) enabled Seilacher (1962, fig. 1) to reconstruct the walking legs. His figure shows two terminal digits surrounded by a circlet of long slender setae. Seilacher's (1962, pl. 24, fig. 3) illustration demonstrates that when the organism was walking on firm sediment and was being aided by currents or was aided by currents the dactyls alone could support the body weight. In contrast, Seilacher pointed out that the dactyls would provide less support on soft sediment, in which case the circlet of setae served in a manner analogous to a snowshoe distributing the body weight over a larger area (Seilacher, 1962, pl. 25, fig. 1). This provides us with an attractive explanation for some Clinton trackways (Pl. 6, fig. 4) but does not seem adequate for most of the forms placed in *D.* sp. Group C. Instead, it seems that the organism was truly pentadactylous. The specimen seen on Plate 6, figure 5 supports the latter hypothesis since a transition from pentafid to trifid imprints can be observed. There is no evidence of a circlet of setae.

The presence of imprints which range from unbranched to pentadactylous within the same group, and show variation within the same trackway, may at first seem to contradict a trilobite origin. To the best of our knowledge there was no morphological differentiation of the terminal digits of the walking legs within a given trilobite species. The apparent contradicton can perhaps best be explained by trilobite locomotion. It has been demonstrated that the manner in which the walking leg strikes the surface is critical in determining the imprint (Seilacher, 1962, fig. 2 several examples). Osgood (1970) found that it was not uncommon for Cincinnatian trilobite trackways to show a discrepancy in the number of dactyl imprints. In addition, one must recall that the surface upon which the Clinton trackways were made was irregular because of interference ripple marks. In some instances (*D.* sp. Group A) this did not seem to have affected the movement of the organism, but the difference in the number of dactyl impressions, as well as the poorly organized pattern (*i.e.* lack of V-shaped sets), leads us to conclude that the irregular topography of the depositional interface was important in determining the ultimate morphology of some trackways. This effect could even be magnified by rapid movement where the trilobite may have been swimming or was being driven by currents. Such movement would result in the organism skimming across the bottom with only a few appendages striking the substrate, usually near the ripple crests. This provides the most logical explanation for the trails placed in *D.* sp. Group C. Regrettably, it is not possible to accurately identify the trilobite species responsible. Neither *Rusophycus* nor *Cruziana* provides any clues as they bear no trace of pentadactylous imprints. *Dalmanites limulurus* seems unlikely because one would expect to find occasional impressions of the pygidial spine, especially wth the careening type of movement we have postulated. By a process of elimination this leaves *Liocalymene clintoni* as the only other trilobite known to occur in the Sauquoit-Otsquago. Beyond this we have no evidence to indicate the species.

ETHOLOGICAL SIGNIFICANCE OF TRILOBITE TRACE FOSSILS

The ethological significance of *Rusophycus, Cruziana,* and *Diplichnites* has been mentioned briefly. Our purpose here is to see whether the Clinton material matches generally accepted views. Although there is still some disagreement, the prevailing conclusion is that *Rusophycus* represents a method for the trilobite to protect its soft ventral surface by burrowing. *Diplichnites* is regarded as evidence of simple locomotion across the bottom. Likewise, simple cruzianids (*i.e.* gently curved or straight) are thought of as furrowing analogues of *Diplichnites.*

Based on an extensive statistical treatment of Cambrian and Ordovician representatives of the three ichnogenera under consideration, Crimes (1970b, pp. 117-124) formulated an intriguing hypothesis. He concluded that young trilobites, those less than 0.5 cm in width, were planktonic. After some growth they took up the benthonic mode of life. However, their relatively weak musculature and frequency of molting during early ontogeny led them to burrow frequently, resulting in *Rusophycus.* As individuals became larger and stronger, furrowing (*Cruziana*) was possible as was walking (*Diplichnites*). He also concluded that they were able to swim during all stages of the life cycle.

The authors have no argument with Crimes' hypothesis as it applies to his study area in Great Britain. However, the same life cycle cannot be applied to Clinton trilobites. There simply is no discernable pattern with regard to size. *Rusophycus* ranges from 1 cm to more than 10 cm in width. *Cruziana* is rare and the only specimens present are small. Likewise, *Diplichnites* varies greatly in width. Based both on Osgood's 1970 study and the present work, we conclude that *Rusophycus* and *Diplichnites* were produced throughout the trilobite's life, once it became benthonic. The scarcity of *Cruziana* in both the Cincinnatian and the Clinton is perplexing and warrants more study. The paucity of specimens indicates that it could not have represented a common method of feeding or locomotion for Cincinnatian or Clinton trilobites.

Osgood (1970) regarded *Rusophycus* solely as a burrow for protection. However, Bergström (1973, p. 8) pointed out that X-ray examination of certain trilobites, most from the Devonian Hunsrück Shale (Stürmer and Bergström, 1973) reveals that two pairs of appendages have coxal elongations which could well have served as "jaws". Bergström went on to conclude that some *Rusophycus* represent casts of hunting burrows. Bergström (1973, fig. 16) figured a form similar to one of Hall's syntypes (Pl. 1, fig. 1) in which a hemicylindrical burrow cast is associated with the *Rusophycus*. We agree that Bergström may well be correct in his interpretation, although the combination of burrows of other organisms associated directly with *Rusophycus* are as rare in the Clinton as they are in the Upper Ordovician of Ohio. However, some *Rusophycus* specimens from both areas show evidence of vertical or horizontal repetition *i.e.* additional horizontal or vertical movement within the burrow. Whereas these might reflect movement by the trilobite to further escape a probing predator, they might just as easily demonstrate that the trilobite was pursuing softbodied prey (Osgood, 1970, pl. 58, fig. 9; pl. 60, fig. 2). We still generally regard most *Rusophycus* as burrows for protection, but those which show additional movement, as well as forms associated with burrows of other animals, might well represent hunting structures.

TRILOBITE TRACES AND THE DEPOSITIONAL ENVIRONMENT OF THE CLINTON

Trilobites are considered to be organisms which were restricted to a marine environment (Harrington *in* Moore, 1959, p. 040 and annotated bibliography of Brooks *in* Ladd, 1957, pp. 895-919). This conclusion is based primarily on the fauna associated with trilobites (echinoderms, brachiopods) and to a lesser degree on the lithology of the sediments in which they are entombed (limestones and relatively fine-grained clastics). If we accept the assumption cited above, trilobite traces can provide an additional factor for defining the lateral facies relationship within the Herkimer Formation and Sauquoit-Otsquago Formation.

The authors found no evidence which contradicted Zenger's (1971) conclusions concerning the depositional environment of the Herkimer. The Joslin Hill Member contains abundant *Rusophycus,* especially west of locality 8, and thus appears to be an offshore marine facies. Conversely, no trace fossils at all were seen within the massive orthoquartzites of the Jordanville Member. We cannot state categorically that trilobites did not live within the Jordanville sands. Conditions for preservation of sole markings within the Jordanville are poor. There is practically no interbedding of shale and sandstone, the optimum condition for trace fossil preservation.

The paleoecologic setting of the Sauquoit-Otsquago postulated by Muskatt (1972) conflicts somewhat with our findings. He concluded that the Sauquoit was a marine, near-shore and, possibly, tidal flat deposit while the "Otsquago Formation is considered to be a river or distributary channel deposit that occasionally was partly drowned by a shallow sea or encroached into the sea. The darker sandstones are probably brackish, possibly estuarine." (Muskatt, 1972, p. A-12). He cited several lines of evidence to support his conclusion: lack of fauna, type and direction of crossbedding, and the red color of the beds which, according to Muskatt indicates exposure to the atmosphere. Numerous references to work on Recent sediments were provided. On the whole, our work does not negate Muskatt's conclusions for much of the Otsquago. However, we found what we consider to be trilobite traces at three localities which Muskatt calls Otsquago (field notes provided by Muskatt to senior author; see also Text-figure 2). Each of the localities will be described below.

1) Locality 16 — west branch of an unnamed north-flowing creek 1.2 miles SSE of Edicks.

Trilobite trackways (Pl. 4, fig. 4) were found here one meter below the upper contact of the Otsquago and also in a layer 10 meters below the contact. The rock is a red medium-grained irregularly bedded sandstone. The imprints on the figured specimen are bifid. As the direction of movement was parallel to the body axis the sets are superimposed. While it is not possible to determine the exact number of imprints in each set, it is in excess of 11.

2) Locality 14 — Flat Creek.

Details of the section which crops out at Flat Creek can be found in Rickard and Zenger (1964), Zenger (1971), and Muskatt (1972). Detailed field notes provided by Muskatt were most useful. According to Muskatt (personal communication; also Text-fig. 2) 83′ (25.2 m) of strata separate the Herkimer at the top of the waterfall from the uppermost Sauquoit. Rickard and Zenger (1964, pp. 27-32) cited a figure of 61.5′ (18.7 m). Some of the disagreement concerns the thickness of the Herkimer; Muskatt (personal communication) shows 52′ while Rickard and Zenger (1964, p. 32) stated that the Herkimer is only 40′ thick. Thus, between 6.5 m (21.5′) and 9.4 m (31′) of strata separates the base of the Herkimer from the upper contact of the Sauquoit-Otsquago.

Muskatt's field notes show the following section for the Sauquoit-Otsquago facies:

Sauquoit	6′ (1.82 m)
Otsquago	41′ (12.46 m)
Sauquoit-Otsquago	8′ (2.43 m)
Otsquago	15′ (4.56 m)
Sauquoit	15′ (4.56 m)
Sauquoit and Otsquago	9′ (2.74 m)
Sauquoit	20′ (6.08 m)
Sauquoit and Otsquago	3.5′ (1.06 m)
Sauquoit	3.5′ (1.06 m)
Top of Oneida Conglomerate	

We used the clearly-defined base of the Herkimer as our datum (Text-figure 2) and collected specimens from a zone some 7.5 meters thick, 16 meters below the base of the Herkimer. This clearly places our specimens within Muskatt's 12.46 m (41′) thick section of Otsquago. Material collected by the authors consists of numerous trilobite trackways (Pl. 5, fig. 3; Pl. 6, fig. 5), *Cruziana* cf. *quadrata* (Pl. 4, figs. 1, 3) and a single specimen of *Rusophycus* (Pl. 1, fig. 5). The trilobite trace fossils were collected from three different lithologies within this section of the Otsquago: a) *C.* cf. *C. quadrata* occurs on a slightly reddish fine-grained sandstone. The rock bearing *Rusophycus* is similar in lithology but slightly more red in color. b) The trilobite trackways seen on Plate 6, figure 5 occur in what might be termed more typical Otsquago lithology; dark red, medium-grained sandstone with shale clasts. Although it is not possible to know exactly from which horizon Hall collected his material, the lithology, color and shale clasts of this specimen are identical to the lithology of Hall's specimens obtained from the American Museum of Natural History (Pl. 7, fig. 3). c) The longest continuous trackways found by the authors in the Clinton (Pl. 5, fig. 3) occur as concave epireliefs on an even darker red (maroon) fine-grained sandstone, some 5 cm thick, which lacks shale clasts. The upper surface is characterized by uneven but conspicuous interference ripple marks.

To summarize, *Rusophycus* and *C.* cf. *C. quadrata* occur in a Sauquoit-type lithology while the *Diplichnites* are found within the dark red sandstones of the Otsquago. However, all the material occurs within what Muskatt mapped as Otsquago.

3) Locality 20A — Travis Road northeast of Van Hornesville.

Two slabs bearing trilobite trackways were taken from this locality within the Otsquago but were less than one meter from Muskatt's Otsquago-Sauquoit boundary. The form seen on Plate 7, figure 2 is representative. It is a concave epirelief on a moderately red, medium-grained sandstone with interference ripple marks. The width of the trail is 2.5 cm and it consists of several deeply incised imprints indicating a slicing movement of the appendages. The trackway is temporarily terminated by a ripple trough 3 cm wide but the tracks pick up again on the other side.

In light of the evidence presented above, *i.e.* diverse trilobite traces within what Muskatt has termed fluviatile or estuarine deposits, three alternatives appear possible:

1) Trilobites were able to tolerate brackish water.

2) The trackways and what we have called *Cruziana* and *Rusophycus* are of non-trilobite origin and instead were made by fresh or brackish water arthropods.

3) Muskatt's boundaries between the Sauquoit and Otsquago are somewhat in error for the three localities in question.

As regards the first point, there are no well-documented examples of trilobites living in other than marine environments. Although they may have been able to withstand brief incursions of brackish water, there is no evidence to support this contention.

Seilacher (1970, p. 456) declared that there are no criteria except size by which small rusophycids and cruzianids may be attributed to trilobites. He implied that any forms with a width of less than 1 cm are suspect and could have been produced by isopods, a group of arthropods which today inhabit a wide range of aquatic environments. In addition, Crimes (1970b) in his study of Cambrian and Ordovician trace fossils from Wales concluded that trilobite traces less than 0.5 cm were not present. The genus *Isopodichnus* Bornemann, 1889, has been employed by several authors for small forms which apart from size (1-6 mm in width according to Häntzschel, 1962, p. W201) resemble *Rusophycus* and *Cruziana*. *Isopodichnus* has been reported from several localities and horizons; the oldest occurrence is the Upper Silurian of Spitsbergen (Häntzschel, 1962). Admittedly the size of our *Cruziana* cf. *C. quadrata* (width 7 mm) and *Rusophycus* (width 1 cm) places them in a "gray area." They are slightly larger than forms included in *Isopodichnus* yet smaller than most specimens which can confidently be assigned to trilobites. However, two points lead us to conclude that the arthropod traces at Flat Creek were produced by trilobites. First, the quadrate cross section of *Cruziana* cf. *C. quadrata* can best be explained by the shieldlike cephalon of a trilobite acting as a plow. Second, and more important, the *Rusophycus* and *Cruziana* occur in close vertical proximity to trackways (Pl. 5, fig. 3) which in all aspects mirror those of trilobites. Moreover, the trackways at Flat Creek attain a width of 1.5 cm, a measurement well within the trilobite range.

We conclude, therefore, that the arthropod traces from the three localities were made by trilobites and that these zones within the

Otsquago represent a marine facies. Again, this does not necessarily stand in direct contradiction to Muskatt's overall conclusions regarding the Otsquago. Most of the Otsquago we sampled was barren of trace fossils. Moreover, as Text-figure 2 demonstrates, he was working in an area with extensive and complex lateral interfingering between marine and non-marine units. Nevertheless, we feel that some readjustment of his Sauquoit-Otsquago facies boundaries is necessary. Our primary goal in undertaking this study was to describe and interpret the trace fossils of the Clinton Group, and we do not have the detailed stratigraphic and sedimentological data to suggest specific changes. It should be apparent, though, that trilobite trace fossils can be useful tools in working out complex facies relationships.

APPENDIX

LOCALITY DATA

To provide uniformity we have adopted the locality numbers used by Zenger (1971), and to conserve space are listing only those localities actually cited in this paper. Two localities, 4A and 20A, were not included by Zenger. In addition to the list below we visited the following localities: 1, 3, 6, 9, 15, and 19. Material was collected from some of these but, as it does not add significantly to the study it is not specifically mentioned.

The reader is referred to Zenger (1971) for the complete locality list and also to Muskatt (1972). Muskatt's localities reflect a comprehensive sampling of the Clinton but they are identified by the New York State coordinate system which, while accurate, may be unfamiliar to the reader. For this reason we elected to use Zenger's locality numbers with some additions. The descriptions below are largely from Zenger (1971, pp. 55-58).

2. Section with considerable covered intervals, outcropping along stream flowing north to Lairdsville at which point it bends toward the east; about 5.6 kilometers (3.5 miles) NW of Clinton; SW 1/9 Rome 15′ quadrangle (C 1/9 Clinton 7 1/2′ quadrangle); Willowvale, Dawes, Kirkland, Herkimer (Joslin Hill Member), and Ilion; base of Herkimer at about 660 feet.

4. Sherman Brook (known also as Dawes Quarry Creek) both east and west of bridge on north-south road (Dawes Ave.) which crosses a creek 2.8 kilometers (1.8 miles) east of village square in

Clinton. A quarry adjacent to the creek on the north bank some 30 meters downstream from the bridge was productive, yielding many *R. bilobatum;* C 1/9 Rome 15′ quadrangle (W 1/9 Utica West 7 1/2′ quadrangle); upper Willowvale, Dawes, Kirkland, lower and middle Herkimer (Joslin Hill Member); base of Dawes at about 685 feet.

4A. Cleary Road Quarry. Proceed east from Clinton Village on Brimfield Street for 3.0 km (1.9 miles). Turn south on Cleary Road for 0.8 km (0.5 miles). Quarry is located where Cleary Road is crossed by a small stream; (W 1/9 of Utica West 7 1/2′ quadrangle). Some 2-3 meters of Herkimer is uncovered over a wide area.

5. Section along "The Glen," an east-flowing tributary of Sauquoit Creek at Chadwicks (formerly known as Willowvale), 3.2 kilometers (2 miles south of New Hartford; SE 1/9 Rome 15′ quadrangle (SE 1/9 Utica West 7 1/2′ quadrangle); Sauquoit, Willowvale, Kirkland, lower Herkimer (Joslin Hill Member); base of Herkimer at about 815 feet.

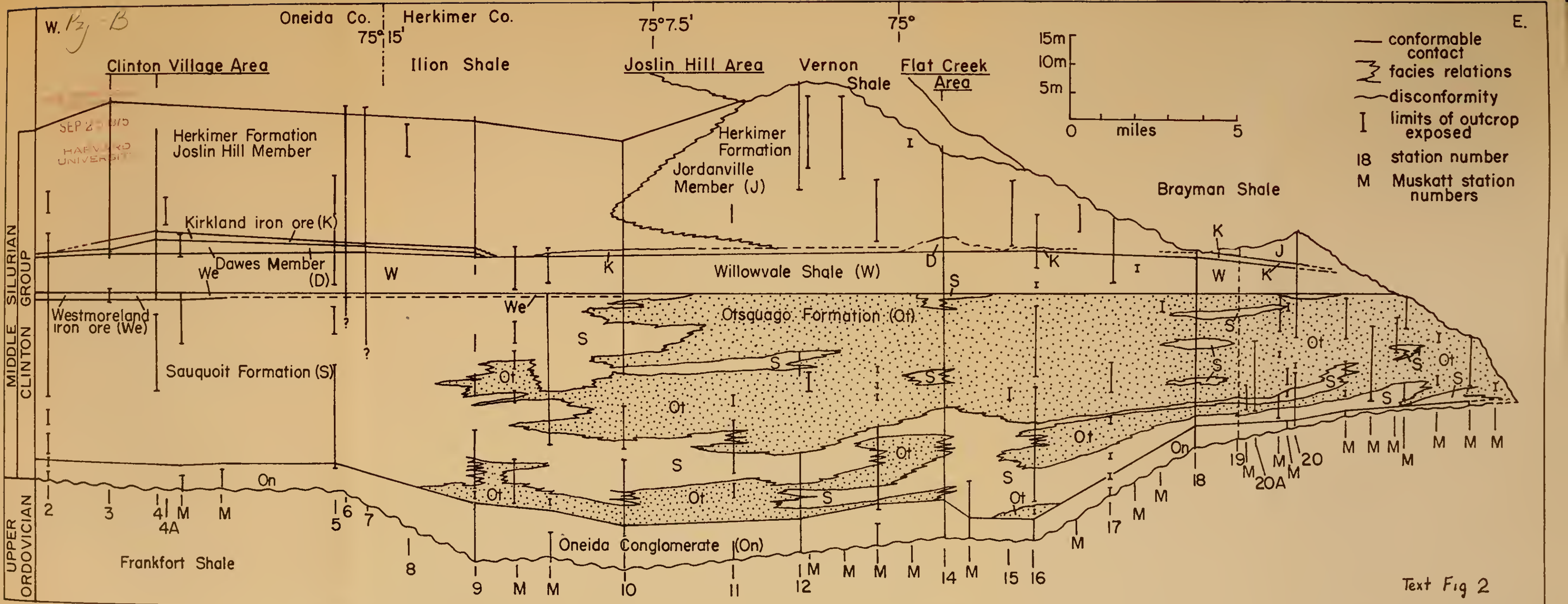
7. West-flowing tributary of Sauquoit Creek, midway between and parallel to Roberts Road and Laughlin Road, about 1.6 kilometers (1 mile) NNE of Sauquoit; SE 1/9 Rome 15′ quadrangle and SW 1/9 Utica 15′ quadrangle (SE 1/9 Utica West 7 1/2′ quadrangle and SW 1/9 Utica East 7 1/2′ quadrangle, respectively); Sauquoit, Willowvale, Kirkland, Herkimer (Joslin Hill Member), Ilion; base of Herkimer just below 840 feet.

8. Abandoned quarry in middle (?) Herkimer (Joslin Hill Member) just east of Tilden Road about 0.24 kilometer (0.15 mile) northeast of junction of Tilden and Higby Roads on hill overlooking Utica; SW 1/9 Utica 15′ quadrangle (W 1/9 Utica East 7 1/2′ quadrangle); top of quarry at about 1130 feet; similar quarry just west of Tilden Road.

10. South branch of Moyer Creek about 2.1 kilometers (1.3 miles) ENE of Parker Corners; S 1/9 Utica 15′ quadrangle (SE 1/9 Utica East 7 1/2′ quadrangle); Sauquoit-Otsquago, Willowvale, Kirkland, Herkimer (Joslin Hill Member), Ilion; base of Herkimer at about 1000 feet.

11. Composite section along Steele Creek (Ilion Gorge), a northeast-flowing tributary of the Mohawk River, between 4.8-5.6 kilometers (3-3.5 miles) SW of Ilion; (NW 1/4 Millers Mills 7 1/2′

W. P2 -B



Text Fig 2

quadrangle) data taken from the following: SE-flowing tributary of Steele Creek immediately SW of Ilion Fish and Game club on Barringer Road, uppermost Herkimer at about 1090 feet; abandoned quarry immediately north of bend in Barringer Road 1.6 kilometers (1 mile) ESE of Kinne Corners, top of quarry at about 1080; banks of Steele Creek proper between 915 and 930 feet about one-half mile north of Beckus Gulf; also ledges on hills between these localities, on northwest side of Steele Creek; upper Willowvale, Kirkland, Herkimer (Joslin Hill and Jordanville transitional), Ilion.

14. Flat Creek just north of paved road 4 kilometers (2.5 miles) NNW of Jordanville; NW 1/9 Richfield Springs 15′ quadrangle (W 1/9 Jordanville 7 1/2′ quadrangle); Sauquoit-Otsquago, Willowvale, Herkimer (Jordanville Member), Vernon; top of Herkimer (Jordanville Member) capping falls at about 1250 feet.

16. Section along west fork of north-flowing creek at waterfall about 1.9 kilometers (1.2 miles) SSE of Edicks; NW 1/9 Richfield Springs 15′ quadrangle (C 1/9 Jordanville 7 1/2′ quadrangle); Sauquoit-Otsquago, upper Willowvale, lower Herkimer (Jordanville Member); Willowvale-Herkimer contact at about 1310 feet.

18. Discontinuous section along Ohisa Creek from just east of road crossing 3.4 kilometers (2.1 miles) SW of Cramer Corners on downstream to about 1300-foot elevation; N 1/9 Richfield Springs 15′ quadrangle (W 1/9 Van Hornesville 7 1/2′ quadrangle); Sauquoit-Otsquago, Willowvale, Brayman.

20A. Travis Road, the first road on the north side of New York State Route 80, 0.8 km (0.5 miles) east of Van Hornesville; outcrop is 1.4 km (0.9 miles) from the intersection at the 1300′ contour. Trilobite traces taken from outcrop on northwest side of road (S 1/9 Van Hornesville 7 1/2′ quadrangle); Sauquoit-Otsquago.

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EXPLANATION OF PLATE 1

Figure

1-4. **Rusophycus bilobatum** (Vanuxem), 1842

1. *R. bilobatum* — Type 3
   Convex hyporelief associated with hemicylindrical burrow cast. Specimens like this may reflect efforts of the trilobite to attack soft-bodied prey. Syntype (Hall, 1852, pl. 9, fig. 1). "Gaylord and Norton's quarry near New-Hartford, Oneida county." (Hall, 1852, p. 23). According to Chadwick (1918, fig. 2) this would place the specimens in the lower Herkimer. NYSM 31, × 1.
2. *R. bilobatum* — Type 3
   Convex hyporelief of an incomplete specimen preserved in a coarse-grained quartz sandstone. The striae on the lobes are strongly developed and indicate powerful ?bifid dactyls. Herkimer Fm., Dawes Creek quarry (loc. 4). NYSM 13237, × 1.
3. *R. bilobatum* — Type 2
   Convex hyporelief; the sharp ridge located between the lobes near the posterior margin is interpreted as a cast of the pygidial spine of *Dalmanites limulurus*. Herkimer Fm., Dawes Creek (loc. 4). NYSM 13238, × 0.7.
4. *R. bilobatum* — Type 2
   Convex hyporelief showing casts of genal and pygidial spine of *D. limulurus*. Herkimer Fm., Dawes Creek Quarry (loc. 4). NYSM 13239, × 1.

5. **Rusophycus pudicum** Hall, 1852

Concave epirelief of a small specimen with no discernible striae. Otsquago Fm., Flat Creek (loc. 14). NYSM 13245, × 1.

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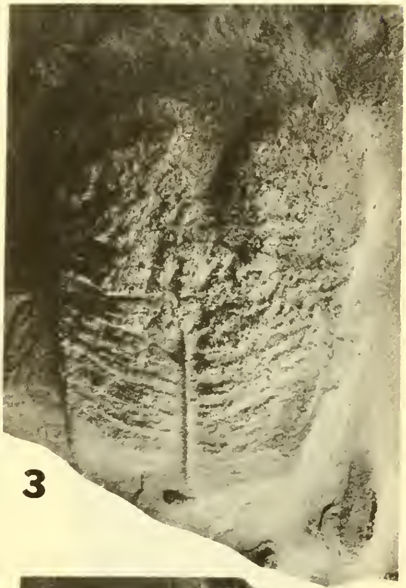

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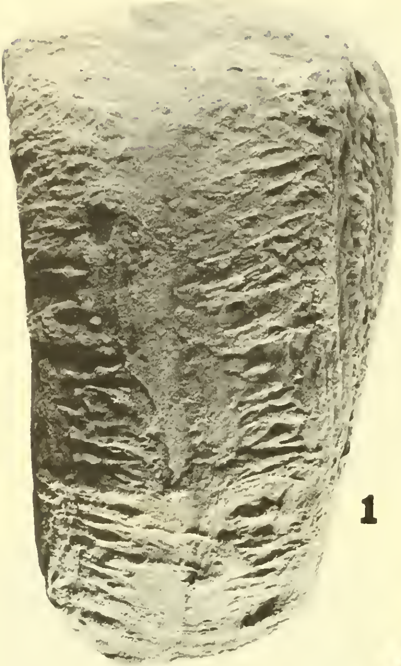

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EXPLANATION OF PLATE 2

Figure

1-4. **Rusophycus bilobatum** (Vanuxem), 1842

1. *R. bilobatum* — Type 1
Convex hyporelief in which the lobes and striae are clearly evident. The large size as well as the general outline indicate that *Trimerus delphinocephalus* was responsible for this specimen. Herkimer Fm., Dawes Creek quarry (loc. 4). NYSM 13240, × 0.5.
2. *R. bilobatum* — Type 3
Convex hyporelief; the cast of a shallow burrow and thus one which does not reflect the true dimensions of the tracemaker. Note the cylindrical burrow filling between the lobes. Syntype (Hall, 1852, pl. 9, fig. 2). Locality and horizon same as Pl. 1, fig. 1. NYSM 32, × 0.8.
3. *R. bilobatum* — Type 3
Convex hyporelief; a representative specimen where the striae on the lobes are directed transverse. Syntype (Hall, 1852, pl. 9, fig. 2). Locality and horizon same as Pl. 1, fig. 1. NYSM 32, × 0.8.
4. *R. bilobatum* — Type 2
Convex hyporelief showing forward movement by the organism within the burrow. The prominent lateral margins are attributed to the genal spines of *Dalmanites limulurus*. Herkimer Fm., Dawes Creek quarry (loc. 4). NYSM 13241, × 0.75.

Explanation of Plate 3

Figure

1. **Rusophycus bilobatum** (Vanuxem), 1842 — Type 3

   Convex hyporelief; one of the few Clinton *Rusophycus* on which evidence of bifid dactyls is clearly present. See bottom (posterior) half of left lobe. Herkimer Fm., Dawes Creek quarry (loc. 4). NYSM 13242, × 0.9.

2. **Rusophycus bilobatum** (Vanuxem), 1842 — Type 1

   Convex hyporelief which conforms well to both the size and body outline of *Trimerus delphinocephalus*. Herkimer Fm., Dawes Creek quarry (loc. 4). NYSM 13243, × 0.5.

3. **Cruziana clavata** (Hall), 1852

   Convex hyporelief of two specimens which possess U-shaped profiles. The lobes are moderately developed with weak striae. Syntype. Hall (1852, pl. 8, fig. 1b) overstresses the striae. "Blackstone's quarry, New-Hartford, Oneida county." (Hall, 1852, p. 23). Stratigraphic horizon is Sauquoit according to Chadwick (1918, fig. 2). USNM 41116, × 1.

4. **Rusophycus bilobatum** (Vanuxem), 1842 — Type 3

   Convex hyporelief; a typical specimen with pronounced nearly transverse striae on the lobes. Herkimer Fm., Dawes Creek quarry (loc. 4). NYSM 13244, × 0.85.

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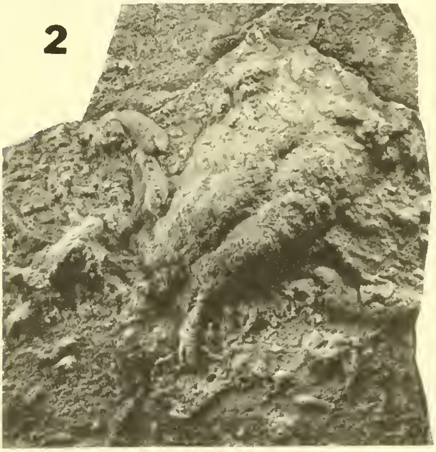
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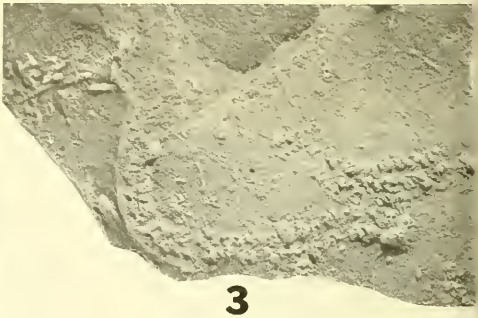
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EXPLANATION OF PLATE 4

Figure

1. **Cruziana** cf. **C. quadrata**

   Convex hyporelief; the best developed *Cruziana* found in the Clinton thus far. The acute angles of juncture of the arcs indicate that this specimen does not represent the continuous trace of a single organism. Several similar, shorter arcs were found on the sole of the same bed. Otsquago Fm., Flat Creek (loc. 14). NYSM 13247, × 0.9.

2. **Rusophycus pudicum** Hall, 1852

   Convex hyporelief which closely resembles the specimen figured by Hall (1852, pl. 8, fig. 6a: Osgood 1970, pl. 58, fig. 6). This form is tentatively attributed to *Liocalymene clintoni.* Sauquoit Fm., Ohisa Creek (loc. 18). NYSM 13246, × 0.9.

3. **Cruziana** cf. **C. quadrata**

   Convex hyporelief showing the platform adjacent to the bilobate ridge. It is postulated that the trilobite employed the anterior margin of the cephalon as a plow. This best explains the quadrate cross section of the cast. Otsquago Fm., Flat Creek (loc. 14). NYSM 13248, × 0.75.

4. **Diplichnites** sp. Dawson, 1873 — Group A

   Concave epirelief in dark red sandstone. Although the V-shape of the sets is not readily apparent, close study reveals that a minimum of eight imprints can be assigned to each set. Dactyls bifid, direction of movement left to right. Otsquago Fm., unnamed north-flowing stream SSE of Edicks (loc. 16). NYSM 13249, × 1.

Explanation of Plate 5

Figure

1-4. **Diplichnites** sp. Dawson, 1873

1. *D.* sp. — Group B
Latex mold of a concave epirelief; large specimen with sets clearly evident. The trilobite moved from bottom to top and the body axis was angled to the right of the direction of movement. Syntype (Hall, 1852, pl. 16, fig. 2). ?Otsquago Fm., Flat Creek (loc. 14). AMNH $\frac{1604}{1}$, × 0.8.

2. *D.* sp. — Group C
Latex mold of a concave epirelief; direction of movement from top to bottom. Note V-shaped sets and casts of imprints of polydactylous leg (upper right). The number of imprints in a series varies from 5-10. Syntype (Hall, 1852, pl. 15, fig. 5). Otsquago Fm., Flat Creek (loc. 14). AMNH $\frac{1604}{1}$, × 1.

3. *D.* sp. — Group A
Latex mold of a concave epirelief representing a small portion of a much longer trackway which crosses over interference ripple marks. Direction of movement from lower right to upper left. Note V-shaped sets and the large number of imprints/set. Otsquago Fm., Flat Creek (loc. 14). NYSM 13250, × 1.

4. *D.* sp. — Group B
Latex mold of a concave epirelief where the direction of movement was from upper left to lower right. Body axis was angled to the left of the direction of movement (compare with Text-figure 4B). A minimum of 14 imprints can be assigned to a series thus demonstrating a trilobite origin. Syntype (Hall 1852, pl. 15, fig. 1). ?Otsquago Fm., Flat Creek (loc. 14). AMNH $\frac{1604}{1}$, × 0.85.

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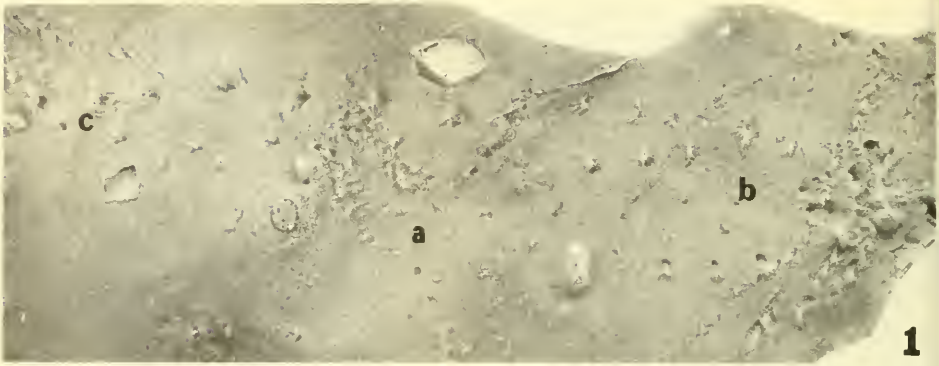

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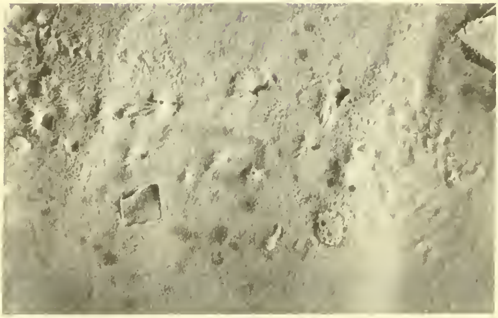

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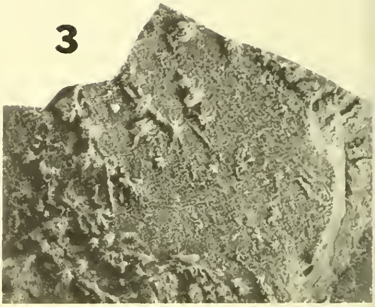

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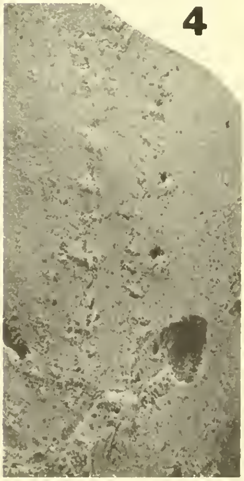

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EXPLANATION OF PLATE 6

Figure

1-5. **Diplichnites** sp. Dawson, 1873 — Group C

1. Latex mold of a concave epirelief bearing at least three trackways (pages 326-329 for a complete discussion). The direction of movement of the *D*. sp. — Group C trackway was right to left. See fig. 2 below. Syntype (Hall, 1852, pl. 15, fig. 2). ?Otsquago Fm., Flat Creek (loc. 14). AMNH $\frac{1604}{1}$, × 0.8.
2. Enlargement of upper left portion of fig. 1 above showing multifid dactyls. Withdrawal markings (depressions on the mold) permit determination of the direction of movement; × 1.
3. Convex hyporelief of a seemingly unorganized group of multifid dactyls. Otsquago Fm., Flat Creek (loc. 14). NYSM 13251, × 1.25.
4. Latex mold of a concave epirelief. Dactyl imprints of left series are multifid; those on the right are not. The arrangement of the imprints in two straight, parallel rows makes this specimen unique among Clinton trackways. Withdrawal markings indicate that movement was from top to bottom. Syntype (Hall, 1852, pl. 15, fig. 1). Otsquago Fm., Flat Creek (loc. 14). AMNH $\frac{1604}{1}$, × 1.
5. Concave epireliefs on a fragment of a large ripple mark (crest near top of photo). Note the remarkably clear impressions of pentafid dactyls near the lower margin center. Two trifid dactyl impressions can be seen near center of photo. This row which trends toward upper right corner is interpreted as imprints belonging to the same series. Otsquago Fm., Flat Creek (loc. 14). NYSM 13252, × 1.

EXPLANATION OF PLATE 7

Figure

1-3. **Diplichnites** sp. Dawson, 1873 — Group A

1. Concave epirelief in a coarse sandstone. Note the quartz pebble adjacent to the figure number. The direction of movement was from bottom to top. Sauquoit Fm., unnamed north-flowing creek SSE of Edicks (loc. 16). NYSM 13253, × 0.7.
2. Concave epirelief where the trackway is interrupted by a deep ripple trough. The direction of movement is from bottom to top. Otsquago Fm., Travis Rd. east of Van Hornesville (loc. 20A). NYSM 13254, × 0.75.
3. Concave epirelief where the V-shape of the sets is apparent and the dactyls are bifid. The direction of movement is from bottom to top. Note the indistinct trackway near the right margin. Syntype (Hall, 1852, pl. 16, fig. 3). AMNH $\frac{1604}{1}$, × 1.5.


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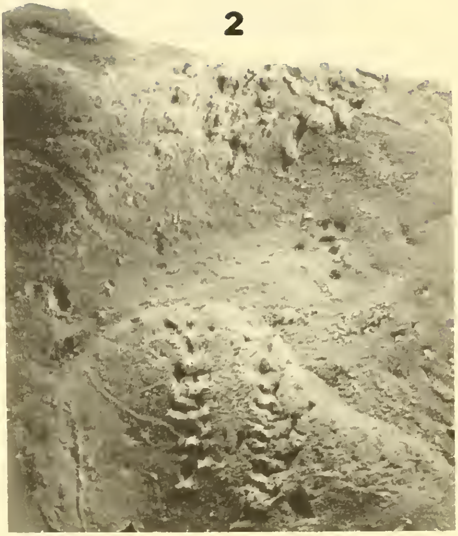
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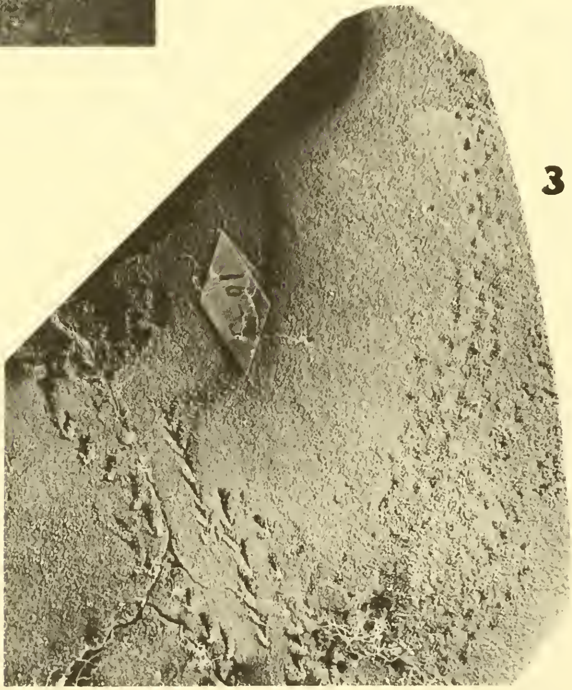
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SYSTEMATICS AND FUNCTIONAL MORPHOLOGY OF *COLUMBOCYSTIS,* A MIDDLE ORDOVICIAN "CYSTIDEAN" (ECHINODERMATA) OF UNCERTAIN AFFINITIES

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ABSTRACT

Columbocystis Bassler is a Middle Ordovician "cystidean" of uncertain affinities but is more closely related to the Eocrinoidea than to any other pelmatozoan echinoderm group. It is characterized by an ovoid theca made of irregularly arranged non-pored plates and a raised transversely offset ambulacral platform with five food grooves; the exothecal appendages are unknown. There are two species, *C. typica* Bassler and *C. ovata,* n. sp. *Allocystites hammelli* Miller, a diploporid from the Niagaran of Indiana, is a heterochronous homeomorph.

Columbocystis is believed to have been adapted to living in moderate unidirectional currents with the ambulacral appendages extending down current, partly shielded by the theca.

INTRODUCTION

Among the stalked sessile Echinodermata, in part, the Pelmatozoa of the older literature, there are a number of Paleozoic classes that contain only a few genera. These classes (such as the Edrioblastoidea Fay, 1962, Paracrinoidea Regnèll, 1945, Parablastoidea Hudson, 1907) differ significantly in the construction of the subvective appendages and theca, from the larger classes (such as Crinoidea Miller, 1821, Blastoidea Say, 1825, and Cystoidea von Buch, 1846).

Some of the smaller "pelmatozoan" classes have been restudied recently, *e.g.,* the Eocrinoidea Jaekel, 1918 (Ubaghs, 1968; Sprinkle, 1973), and the Paracrinoidea (Parsley and Mintz, in press). The result is that these classes are now more precisely defined and certain genera have either been added or removed.

Ubaghs, 1968, with some reservations followed Bassler, 1950, in placing *Columbocystis* along with *Springerocystis* Bassler, 1950, *Bockia* Gekker, 1938, and *Foerstecystis* Bassler, 1950, in the eocrinoid family Springerocystidae Bassler, 1950. With the exception of *Bockia* these genera were only provisionally assigned to this class (Ubaghs, 1968, pp. 477-478). Sprinkle, 1973, removed *Bockia* from the family but retained it in the Eocrinoidea. The other genera he transferred to the Paracrinoidea.

Parsley and Mintz (in press) in their review of the Paracrinoidea do not include *Columbocystis* in that class. Reasons for excluding it from the paracrinoids will be given below. I prefer not to leave *Columbocystis* in the Eocrinoidea and accept Sprinkle's opinion that it does not easily fit into the class as it is now defined. Classification at the class level must wait until the subvective appendages are known (Ubaghs, 1968, p. S487; Parsley, 1969, pp. 277-278; Sprinkle, 1973, p. 138).

Columbocystis is herein considered to be of uncertain higher taxonomic affinities, although for reasons given below, it seems closer to the eocrinoids than any other "pelmatozoan" class.

ACKNOWLEDGMENTS

The generous aid of several individuals and their institutions made this study possible. Porter M. Kier of the National Museum of Natural History, Washington, D.C., kindly lent specimens and facilitated the study while I was at the Museum. John Pojeta of the U.S. Geological Survey aided in the loan of important material. Mathew H. Nitecki lent material from the Field Museum in Chicago. This study was begun while I was a graduate student at the University of Cincinnati, under the direction of Kenneth E. Caster. His help and encouragement is gratefully acknowledged. E. R. Dalvé drew the text figure and Sofia Baltodano typed the manuscript.

SYSTEMATIC PALEONTOLOGY

Phylum ECHINODERMATA

Class, Order, Family Uncertain

Genus **COLUMBOCYSTIS** Bassler, 1950

Type species: *Columbocystis typica* Bassler, 1950, by original designation.

Diagnosis. — Theca subovate to pyriform, with about 40 to 60 non-pored, variably sized thecal plates, three basals. Raised ambulacral platform of six plates (orals consist of four peristomals, two lateral exserts), offset to left from distal apex; five subvective grooves, with two unequal facets for exothecal arms at distal ends. Hydropore on margin of oral platform between the peristomals in the *CD* interray.

Occurrence. — Middle Ordovician (Blackriverian) Ottosee Formation and Benbolt Formation, Virginia and Tennessee. All stratigraphic and locality data used in this report for *Columbocystis* and *Allocystites* come from museum labels.

Description. — Theca subovate to pyriform or fusiform, varying in profile according to species and subcircular in cross section. Composed of about 40 to 60 non-pored plates including three basal and six oral plates that vary from triangular (new intercalates) to heptagonal; hexagonal plates are the most common. Except for basals, orals and possibly periproctals the thecal plates are arranged without obvious order. Thecal plates, especially larger ones, are thickened at their centers and large plates have a low rounded central boss. Fine pustulose prosopon on unweathered external plate surfaces. Thecal growth effected by peripheral growth of plates and by intercalation (at the juncture of three plates) which occurs over the entire surface.

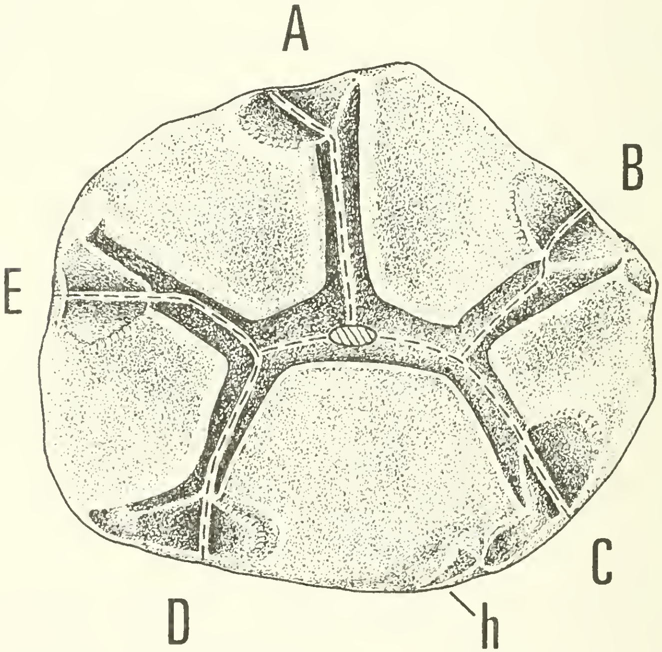
Raised oral platform has five subvective grooves radiating from the central peristome. At ends of grooves are asymmetrical facets presumedly for anchoring exothecal arms or brachioles (Text-fig. 1). Platform is offset to left from distal apex of theca. Slitlike hydropore in the *CD* interray defines posterior end of animal; *A* ray or groove is anterior. Ambulacral platform composed of six thick oral plates. Four plates make up peristome, two are lateral and presumably exserted (Text-fig. 1). The four peristomal plates are subtrapezoidal and the two exsert plates are subtriangular. Sutures between these plates are located on the bottoms of the five ambulacral grooves except for the suture that extends from the peristome through the slitlike hydropore and the base of the oral platform in the *CD* interray area. This suture is offset slightly to right from axis of symmetry and is sufficiently ankylosed as to be normally indistinct. At end of each groove is a broad "V"-shaped exothecal appendage seat which is incised into the suture. Dextral side of each food groove is slightly undercut, and the groove extends above the right side of the incised appendage base and terminates at a rounded base, juxtaposed to it.

Lateral and posterior grooves (*B, C,* and *E, D,* in the Carpenter system) branch off the main transverse arm groove which has the transversely oval peristome at its midpoint. Adjacent to the peristome, and bisecting the main transverse groove, is the anterior, *A* ambulacrum.

Periproct above ambitus and consistently located proximal to the right posterior (or *C*) ambulacrum. Number of periproctal plates variable. Anal pyramid, made up of eight triangular plates.

Column unknown, but attachment scar on basals indicates it was circular and of small diameter.

Discussion. — The general outline of the ambulacra is similar to some genera of other primitive pentaradial echinoderms, especially in edrioasteroids, eocrinoids, and diploporid cystoids where there is a marked transverse food groove off of which the food grooves branch. The significance of the two distinctly different bases for exothecal appendages at the ends of the sessile ambulacral grooves is not clear. The main incised "V"-shaped base is doubtlessly for an exothecal arm or brachiole while the smaller seat may be for a smaller but similar structure. Perhaps, as Sprinkle (1973, p. 138, fig. 33) pointed out, the seats are for asymmetrical arms. Whether one is dealing with one exothecal extension or two, per sessile ambulacrum, the food groove



Text-figure 1. *Columbocystis typica* Bassler. Details of the ambulacral platform. Lettering of the ambulacra *A* - *E* follows the standard Carpenter system. The hydropore, labeled *h,* is in the *DC* interray and between two oral plates. The suture between these two orals is essentially ankylosed and usually not visible. Dashed lines are plate sutures. Drawing is based on a topotype (Pl. 1, fig. 7).

includes both the incised "V" and the rounded bases. In all probability the entire sessile ambulacral area was roofed over by covering plates of the same type that were probably present on the exothecal appendages. As noted above, this genus is not readily assignable to any "pelmatozoan" class as now defined.

Placement of *Columbocystis* in the Paracrinoidea by Sprinkle (1973) is understandable because of the homeomorphic left-side offset of the peristome and the column attachment, as well as the asymmetrical thecal profile. These features are especially evident on the type species *C. typica.* The ambulacral platform and nature of the facets is similar to the genus *Achradocystites* Gekker, 1938, a "paracrinoid" with typical thecal pores and hydropore-gonopore arrangement from the Middle Ordovician of Estonia. The platform in this case has three ambulacral grooves. (In *Achradocystites* exothecal appendages may be biserial instead of the normal unserial condition of paracrinoids; the classification of the genus is, therefore, problematic.)

Parsley and Mintz (in press) have redefined the paracrinoids; on the basis of its thecal characteristics *Columbocystis*, despite its homeomorphic features, does not easily fit into this class for the following reasons.

1. The hydropore arrangement is different than that of a paracrinoid. Paracrinoids usually have a prominent hydropore and gonopore situated on the posterior lip of the peristome with the gonopore being in the plane of symmetry. There is no visible gonopore at this location instead, as noted below, it may be in a lateral position on the *BC* oral plate. Also in paracrinoids the hydropore is located at the juncture of three plates, not between two.

2. Presence of an ambulacral platform is different than any other known paracrinoid with non-pored thecal plates. *Columbocystis* does, however, have four peristomals as is typical of paracrinoids.

3. The angle of the basals and column attachment, as well as the overall shape of the theca, suggests that (especially in *C. typica*) it is the periproct and not the peristome which was uppermost in life. If this interpretation be correct, it represents a habitus feature different from that of any known paracrinoid.

4. Paracrinoids are usually protuberant on their right lateral sides because of considerable intercalation of smaller plates; *Colum-*

bocystis is similarly protuberant but lacks the markedly increased plating.

Other genera usually allied to *Columbocystis* in the Springerocystidae are so poorly known that their mutual affinities are problematic, and none of them may be closely related to each other. My examination of *Springerocystis* indicates that it is not synonymous with *Columbocystis* as suggested by Sprinkle (1973, p. 138). The attenuated oral area of *Springerocystis* probably does not have a sessile, five groove ambulacrum as in *Columbocystis*. Instead, the arms or brachioles appear to have extended, exothecally, from directly adjacent to the peristome. (Bassler, 1950, p. 275, fig. 3.)

The position of the probable gonopore in the *BC* interray is atypical of both paracrinoids and eocrinoids. A similar opening is, however, present on the DE interray oral plate in *Cryptocrinites* von Buch, 1846 (Ubaghs, 1968, p. S488, p. S486, fig. 316, 3, 4). It is the general similarity of the ambulacra, position and morphology of the hydropore and to a lesser degree the gonopore, and the plating of the theca to that of *Cryptocrinites* and related eocrinoids which suggests that *Columbocystis* is more closely akin to the Eocrinoidea than any other "pelmatozoan" class.

Columbocystis typica Bassler, 1950
Pl. 1, figs. 1-9; Pl. 2, figs. 6-9; Text-fig. 1

Cystid, genus and species undetermined, Butts, 1941, p. 90, pl. 89, figs. 16, 17, p. 91.

Columbocystis typica Bassler, 1950, pp. 273-275, figs. 1, 2; Ubaghs, 1968, p. S487, p. S485, fig. 315, 1a-c, p. S463, fig. 298, 1; Sprinkle, 1973, p. 138, fig. 33 [non holotype specimen].

Diagnosis. — *Columbocystis* with prominent oral platform offset to the left; right side of theca protuberant, ambitus of theca above midline.

Occurrence. — Middle Ordovician (Blackriverian), Benbolt Formation, known primarily from Brick Church in Rye Cove, Scott County, Virginia. Ottosee Formation and Benbolt Formation, Luttrell, Union County, Tennessee.

Description. — *Columbocystis typica* has about 40 thecal plates exclusive of the three basals and six peristomals. In profile theca protuberant on right side; left side shorter and straighter due to offset to left of oral platform and basals (Pl. 1, figs. 4, 6; Pl. 2, figs. 8, 9).

Ambitus above midline and proximal end of the theca broadly conical. Most thecal plates have prominent central boss. Plating is tightly sutured. Specimens range from 12 to 35 mm in height.

Massive ambulacral platform slightly wider (transversely) than long (antero-posteriorly). Distinct transverse food groove at ends of which ambulacrum, *A*, bisects the transverse groove at peristome. Hydropore between ambulacra *D* and *C*. In one specimen (Pl. 2, figs. 6, 7) a single small pore is located near edge of oral platform, between rays *B* and *C*. This may be the gonopore.

Periproct located above ambitus, below *BC* interray. Approximately five plates in periproct series. In holotype (Pl. 1, figs. 1, 2) periproct covered by anal pyramid of approximately eight wedge-shaped platelets.

Material. — This species is represented by approximately 25 known specimens, of which about one-fourth are sufficiently well preserved to be useful for description. Most of the material comes from the church yard and immediate area around Brick Church in Rye Cove, Scott County, Virginia.

Columbocystis ovata, n. sp. Pl. 1, fig. 10; Pl. 2, figs.1-5

Diagnosis. — *Columbocystis* with small ambulacral platform, only slightly offset to left, ovoid to fusiform in profile.

Occurrence. — Middle Ordovician (Blackriverian), Ottosee Formation and Benbolt Formation, northeast of Washburn, Granger County, Tennessee.

Description. — Ovoid to fusiform in profile with ambitus usually at middle of theca. Ambulacral platform and basals-column attachment seat only slightly offset to the left. About 60 thecal plates, including basals and orals, and they tend to be regular, usually hexagonal, in outline. Thecal plates more numerous than the type species. Central bosses on most thecal plates.

Larger than *C. typica*. Specimens greater than 40 mm in height are known and one incomplete specimen (Pl. 1, fig. 10) was probably about 80 mm high.

Ambulacral platform similar to that of *C. typica* except that it is relatively smaller, less elevated, and does not extend laterally beyond its base as it does in some specimens of the type species.

Transverse food groove associated with the peristome in *C.*

typica is essentially absent and all of the ambulacral grooves radiate outward from the transversely ovoid peristome.

Periproct located high on right side of theca, proximal to *BC* interray oral plate. In holotype (Pl. 2, figs. 1-3) there are five periproctal plates including a small quadrate plate on proximal margin. Anal pyramid unknown.

Discussion. — Poor preservation of the material precludes discussion of the facets for the exothecal appendages at the distal ends of the sessile food grooves. They are probably similar to those of *C. typica*. Also, poor preservation precludes discussion of the hydropore or a possible gonopore.

Material. — This species is represented by six specimens which are well enough preserved to be assigned to the genus. Complete specimens range from 27 to 44.5 mm in height. All specimens according to the museum labels are from the Ottosee Formation and Benbolt Formation, northeast of Washburn, Granger County, Tennessee.

FUNCTIONAL MORPHOLOGY AND MODE OF LIFE

The left-right asymmetry seen in *Columbocystis* is present in other "pelmatozoans" with exothecal ambulacral appendages. This asymmetry is manifest by the position of the peristome (sometimes associated with some type of ambulacral platform) and the basals-column attachment seat. Examples include most of the paracrinoids with recumbent arms and exothecal pinnules, the diploporid cystoid *Allocystites* Miller, 1889 (Pl. 2, figs. 10-14) and possibly the rhombiferan cystoid *Echinosphaerites* Wahlenberg, 1818 (Kesling, 1968, p. 233). These forms which show this evolutionary convergence are interpreted to be adapted to an essentially unidirectional rheophilic mode of life, *i.e.*, living in moderate, unidirectional currents above the sea bottom.

In genera such as *Columbocystis* and *Allocystites* where the ambulacral platform is present, the position of the column and thecal asymmetry indicates that the periproct was uppermost, or nearly so, and the subvective appendages subapically extended from the theca, presumably in a down current direction. The ambulacral platform insures that the appendages would have been firmly anchored and would remain fairly close together in a current. The appendages probably did not form a broad fan but took advantage of the slowed water and back-eddies on the down-current side of the theca. The proximity of the appendages would have served to further slow the currents flowing around them and thus would have created a quiet water/back-eddy "feeding cone" between the endotomously grooved appendages. This is in harmony with observations of modern rheophile crinoids where feeding is usually done with the pinnule food grooves in a down-current position. (Meyer, 1973, Macurda, 1973, 1974 for discussions on this matter.)

Columbocystis typica was probably better adapted to living in stronger currents than was *C. ovata* as suggested by the smaller ambulacral platform and lesser offsets of the theca in the latter species.

In paracrinoids the left side of the theca probably faced into the current. The pinnules of the left arm thereby had their food grooves facing down-current. The grooves on the right arm pinnules faced up-current but into slower water and back eddies caused by the pinnules of the left arm (the proximal pinnules of the right arm high on the theca) and the down-current side of the theca (the distal pinnules), *e.g.*, *Amygdalocystites* Billings, 1854, and *Platycystites* Miller, 1889. In genera with ambulacral platform, *i.e.*, *Columbocystis* and *Allocystites*, it is the right side that faced into the current.

Allocystites hammelli Miller, 1889, which is Niagaran (Middle Silurian) in age appears to have been adapted for life in a moderately strong, unidirectional current (Pl. 2, figs. 10-14). The inclusion of this monotypic species in the Diploporida is tenuous but features such as plate outlines are similar to other genera in the Sphaeronitida and despite the poor preservation, caused by dolomitization, there are raised pustules which may be remnants of raised diplopore rims. Sprinkle (1973, p. 186) suggested that this species may be a paracrinoid. I contend that the similarity of its morphology is a result of adaptation to similar paleoecological conditions.

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EXPLANATION OF PLATE 1

Figure

1-9. **Columbocystis typica** Bassler

Specimens in figures 1-7 are from the Benbolt Formation, Brick Church in Rye Cove, Scott County, Virginia. 1, 2. Oblique and normal view of the right face of the holotype. USNM 93407; × 3 and × 2 respectively. 3-6. Left, anterior, right, and posterior faces of topotype. Note the irregular outlines of some thecal plates caused by triangular intercalates. USNM 93407; × 1.5. 7. Apical view of the same specimen. The facets for the exothecal appendages are well developed; × 4.5. 8, 9. Posterior and apical view of a small specimen. The slitlike hydropore is well preserved. Ottosee-Benbolt formations, Luttrell, Union County, Tennessee. USNM 93402; × 3 and × 4 respectively.

10. **Columbocystis ovata,** n. sp.

Apical view of an incomplete theca. Note that the ambulacral platform is smaller and simpler than in *C. typica.* Ottosee-Benbolt formations, northeast of Washburn, Granger County, Tennessee. USNM 25935; × 1.25.


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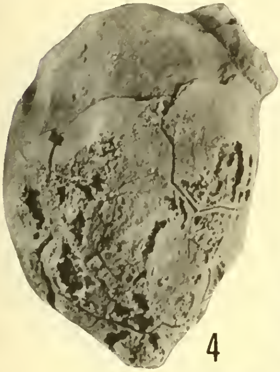
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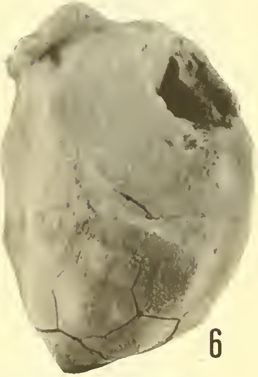
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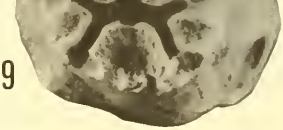
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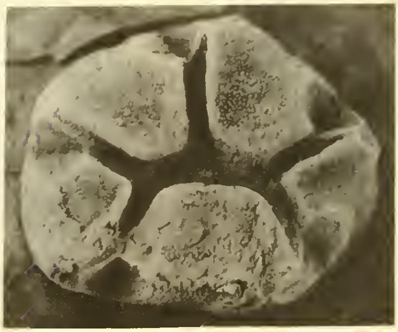
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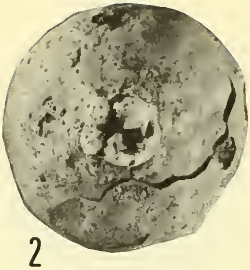
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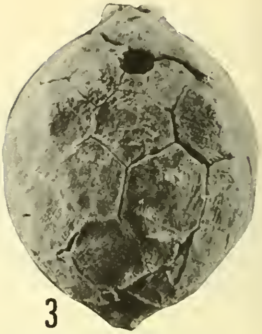
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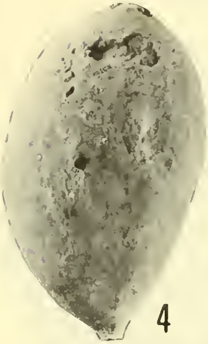
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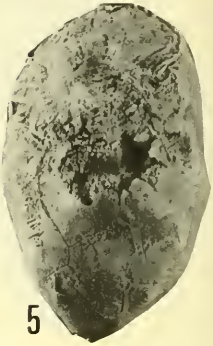
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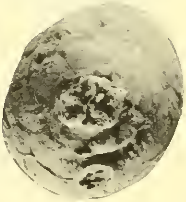
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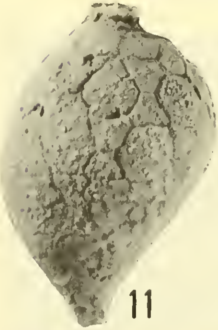
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EXPLANATION OF PLATE 2

Figure

1-5. **Columbocystis ovata,** n. sp.

These specimens are from the Ottosee-Benbolt formations northeast of Washburn, Granger County, Tennessee. 1-3. Posterior, dorsal, and right faces of the holotype. USNM 25935; × 1.5. 4, 5. Two large eroded specimens which show the typical profile. USNM 93403 and USNM 93404 respectively; × 1.

6-9. **Columbocystis typica** Bassler

Specimens are from the Benbolt Formation, Rye Cove, Scott County, Virginia. 6, 7. Side and apical views of an incomplete ambulacral platform. Complete *B* and *C* rays are visible. Note the small possible gonopore on the *BC* oral. USNM 97469a; × 1.25.

10-14. **Allocystites hammelli** Miller

Niagaran, Jefferson County, Indiana. Apical, left, posterior, anterior, and right faces of the holotype. FMNH(UC)6006; × 1.5.

FORDILLA TROYENSIS BARRANDE AND EARLY PELECYPOD PHYLOGENY

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ABSTRACT

The various Cambrian fossils placed in the class Pelecypoda are briefly reviewed, and it is shown that at present only *Fordilla troyensis* Barrande can be unequivocally regarded as a pelecypod. The systematics of *Fordilla* are reviewed in detail, as is its geographic and stratigraphic distribution; *Fordilla* has been reported only from Lower Cambrian rocks. The phylogenetic importance of *Fordilla* is considered—its relation to younger pelecypods and to the rostroconch mollusks. *Fordilla* is regarded as ancestral to the pelecypod subclasses Heteroconchia, Pteriomorphia, and Palaeotaxodonta; it was probably derived from the rostroconch *Heraultia* Cobbald.

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INTRODUCTION

This work is the outgrowth of a paper by Pojeta, Runnegar, and Kriz (1973) which briefly outlined the pelecypod features of *Fordilla troyensis* Barrande. I intend to expand upon this paper and to review information on other Cambrian animals which have been called pelecypods.

Some 20 generic names have been applied to Cambrian (pre-Tremadocian) animals which at one time or another have been regarded as pelecypods. Of these *Cambridium* Horný, *Bagenovia* Radugin, and *Stenothecoides* Resser were placed in the molluscan class Stenothecoida by Yochelson (1968, 1969). *Ozomia* Walcott, *Ribeiria* Sharpe, and *Wanwania* Kobayashi are placed in the molluscan class Rostroconchia by Pojeta and Runnegar (in preparation). *Ambonychia macroptera* Tate from the Lower Cambrian rocks of South Australia is regarded as a brachiopod by Daily (1956, 1957).

Delgado (1904) placed many small specimens from the Lower

Cambrian rocks of Portugal in the genera *Ctenodonta* Salter, *Davidia* Hicks, *Fordilla* Barrande, *Modiolopsis* Hall, *Posidonomya*(?), and *Synek*(?). Teixeira (1952) restudied Delgado's material and dealt with all species except *Ctenodonta geikiei* Delgado. He placed Delgado's taxa in two species, "*Modiolopsis*" *bocagei* Delgado and Lamellibranchiata(?) sp. I have not seen Delgado's material, but on the basis of his figures and those of Teixeira the specimens are not well enough preserved to show the critical features of dentition or muscle scars that would allow one to determine whether or not they are pelecypods. Vogel (1962, p. 202) discussed and figured a Delgado specimen of *Ctenodonta geikiei;* he noted that it did not preserve any of the dentition and was so deformed that it was not possible to be certain about its systematic placement.

Emmons (1855) described a species from his Taconic system which he placed in *Cypricardia* Lamarck. I have not been able to locate Emmons' specimen; however, his drawing is that of a pelecypod. The Cambrian age of this form is uncertain and probably unlikely, as Wilmarth (1938, p. 2107) noted that the Taconic system of Emmons included rocks ranging in age from Early Cambrian to Late Ordovician. Matthew (1899) described *Modiolopsis thecoides* from the Lower Cambrian rocks of Newfoundland. Ulrich and Bassler (1931) could not locate Matthew's specimen and came to the conclusion that it may have been a hyolithid. Matthew noted that the specimen could easily be mistaken for a hyolithid. Rusconi (1950a, b; 1951; 1952) described three species from the Middle and Upper Cambrian of Argentina which he placed in *Ctenodonta* and *Palaeoneilo* Hall and Whitfield. His figures of these forms leave doubt as to their placement in the Pelecypoda, and his material is in need of restudy. Vologdin (1955) described *Palaeoconchiella* from the northern Tyan'-Shan Mountains of Kirgiziya, USSR; however, his figure is only a drawing of a cross section of two valves. Zhuravleva (1970) referred to *Palaeoconchiella* as being of problematic affinities. Cox (1959) noted that *Tellinomya lingulicomes* McCoy from the *Lingulella* flags of North Wales, was known only from some flattened impressions, apparently of Lamellibranchia, and that the Cambrian age of this form was uncertain because of faulting which brings Cambrian and Ordovician slates into close proximity; he also noted that *Grammysia heathcotiensis* Chapman from the Middle Cambrian of Australia may not even be of organic origin.

Vogel (1962) described *Lamellodonta simplex* from the base of the Middle Cambrian of Spain. He regarded *Lamellodonta* as a pelecypod and gave it an important place in the phylogeny of the class. I have examined most of the specimens figured by Vogel and have discussed them with several pelecypod and brachiopod specialists.

Lamellodonta has elongate ridges on either side of the umbo (Pl. 1, figs. 5-7; Pl. 4, fig. 7) which are usually preserved as depressions because the specimens are internal molds. Some specimens show a median elevation which is also preserved as a depression on the internal molds, extending from the umbo toward the margin of the shell (Pl. 1, figs. 6, 7). Vogel interpreted the ridges on either side of the umbo as pelecypod teeth; he also noted that all specimens are deformed, and thus it is difficult to reconstruct their original shape. Although Vogel showed adductor muscle scars on his reconstruction of *Lamellodonta* (p. 233), he noted (p. 217) that the impressions of the adductor muscles and the pallial line are not preserved on any of his specimens.

Obolellid brachiopods have posterior ridges equally developed to either side of the umbo and a median elevation extending toward the margin of the shell (Pl. 1, fig. 8; Cooper, *et al.,* 1952, pl. 12, figs. 20, 21). The specimens of *Lamellodonta* that I have seen could as readily be interpreted as inarticulate brachiopods as pelecypods; they occur with acknowledged obolellids (Vogel, 1962), and I do not regard them as pelecypods.

Zhuravleva (1970, p. 424) noted that pelecypods were reported from the Lower Cambrian by Meshkova (1969). However, the Meshkova reference cited by Zhuravleva seems to be an unpublished dissertation.

Poulsen (1967, p. 17) described, but did not name, a small shell from the Lower Cambrian of Denmark, which he noted had six poorly developed teeth to one side of the umbo. He suggested that this form "may be referred to the taxodont group of pelecypods." The figured specimen has the general appearance of a pelecypod, but the six taxodont teeth cannot be readily seen on his figure.

Pojeta, Runnegar, and Kriz (1973) noted the pelecypod features of *Fordilla troyensis* Barrande from the Lower Cambrian rocks of New York State. *Fordilla* is a bivalved animal (Pl. 4, fig. 4) with adductor (Pl. 1, figs. 1-3; Pl. 3, fig. 3; Pl. 4, figs. 1, 2) and pedal retractor (Pl. 1, figs. 1-3) muscle scars, and a pallial line (Pl. 1, figs. 1-3; Pl. 3, fig. 3; Pl. 4, figs. 1, 2). To date it is the only known Cambrian animal that shows unequivocal pelecypod characteristics. *Modioloides prisca* (Walcott) is also from Lower Cambrian rocks of New York State. It is known from one small poorly preserved specimen (Pl. 1, fig. 4), which does not show an anterior adductor muscle scar or pallial line as thought by Walcott (1887). Younger specimens of *Fordilla troyensis* have the beaks in a more central position (Pl. 4, fig. 3) than do larger specimens (Pl. 2, figs. 1-4), and *Modioloides* may be a young *Fordilla.*

SYSTEMATIC PALEONTOLOGY

Phylum MOLLUSCA Cuvier

Subphylum DIASOMA Runnegar and Pojeta

Class PELECYPODA Goldfuss

Subclass HETEROCONCHIA Hertwig

Pojeta (1971) recognized six subclasses of pelecypods. Since then, one of these has been raised to class status, the Rostroconchia (Pojeta, Runnegar, Morris, and Newell, 1972). *Fordilla* is herein placed in the Heteroconchia, primarily because its shell shape is similar to some cycloconchids (Pojeta, 1971) and because some cycloconchids have a thickened pallial line reminiscent of the pallial line of *Fordilla.*

Order FORDILLOIDA, n. ord.

Primitive cycloconchiform pelecypods lacking anterior and posterior lateral teeth and with a posteriorly expanded pallial line. Presently known only from Lower Cambrian rocks.

Family **FORDILLIDAE,** n. fam.

This is the only known family in the order Fordilloida and has the characteristics and stratigraphic range of the order.

Genus **FORDILLA** Barrande, 1881

Type species: *Fordilla troyensis* Barrande, 1881, pl. 361, by monotypy.

Description. — Shell equivalved, inequilateral; beaks prosogyral, not terminal; obliquity prosocline; ornament consisting of comarginal growth lines. Ligamental areas erect; anterior adductor muscle scar smaller than posterior, small pedal retractor muscle scar dorsal to anterior adductor scar; pallial line integripalliate, and moniliform and expanded posteriorly; lacking anterior and posterior lateral teeth.

Distribution. — In the United States, *Fordilla* is presently known only from the Lower Cambrian rocks of New York State. Lochman (1956) reported *Fordilla* from the Schodack lithofacies in the Kinderhook, Shushan, and Cambridge quadrangles of the Taconics. She noted that the Schodack lithofacies is part of the *Elliptocephala asaphoides* fauna which she assigned to the upper *Olenellus* subzone of late Early Cambrian age. Howell, *et al.* (1944) showed the Schodack Formation as of Early Cambrian age. Potter (1972) noted the occurrence of *Fordilla* in the West Castleton Formation of the Hoosick Falls area in the east-central Taconics. Fisher (1962) regarded the West Castleton Formation as being Early Cambrian in age. Rasetti (1967) noted that the oldest Early Cambrian fauna in the Taconic sequence is believed to be the *Elliptocephala asaphoides* assemblage. I have found *Fordilla troyensis* in the section along New York Route 9J south of Schodack Landing, 0.45 mile south of the Rensselaer County-Columbia County boundary (USGS 8043-CO) in what Bird and Rasetti (1968) regarded as Lower Cambrian rocks. Walcott (1886) also collected *Fordilla* south of Schodack Landing, as well as east of Troy, New York.

Elsewhere in North America, *Fordilla* occurs in the Lower Cambrian rocks at Conception Bay, Newfoundland (USNM 207679), and the Bastion Formation (Lower Cambrian) of Greenland (Poulsen, 1932). The specimen assigned to *Fordilla* from the Lower Cambrian rocks at North Attleboro, Massachusetts, by Shaler and Foerste (1888) is probably a rostroconch mollusk similar to *Heraultia* Cobbald or *Watsonella* Grabau (Pojeta and Runnegar, in preparation); this was noted by Grabau (1900) in his description of *Watsonella.*

Outside of North America, the only well-documented occurrence of *Fordilla* is from the Lower Cambrian rocks of Bornholm, Denmark (Poulsen, 1967). Cobbald (1919) tentatively placed one specimen in *Fordilla* from the Lower Cambrian rocks at Hartshill, Warwickshire, England. Delgado (1904) tentatively placed some of his specimens from the Lower Cambrian of Portugal in *Fordilla;* many of the specimens that Teixeira (1952) placed in "*Modiolopsis*" *bocagei* Delgado and some of those that he placed in Lamellibranchiata ? sp. show at least a superficial resemblance to *Fordilla.* However, the material does not appear to be well preserved and needs to be reillustrated. Sampelayo (1933) noted the occurrence of *Fordilla* in the Cambrian of Spain (Valdemiedes, Zaragoza); on the basis of his illustrations. His specimens are not well preserved, and it is difficult to determine their systematic position. Rozanov, *et al.* (1969, p. 35) noted the occurrence of *Fordilla* in the Atdabanian Stage of the Lower Cambrian of Siberia in a range chart.

Fordilla troyensis Barrande, 1881
Pl. 1, figs. 1-4; Pls. 2, 3; Pl. 4, figs. 1-6; Pl. 5

Bivalve of uncertain class, gen. nov. ? Ford, 1873, p. 139.

Fordilla troyensis Barrande, 1881, pl. 361, figs. 1, 2, a-c; Walcott, 1886, p. 125, pl. 11, figs. 3, 3 a-c; 1890, p. 615, pl. 73, figs. 2, 2 a-c, *non* fig. 1; Lesley, 1889, p. 251, fig.; Miller, 1889, p. 480, fig. 825; Grabau and Shimer, 1909, p. 389, fig. 495; Ulrich and Bassler, 1931, p. 97, pl. 4, figs. 14, 15; Poulsen, 1932, p. 16, pl. 3, figs. 3-5; Shimer and Shrock, 1944, p. 660, pl. 279, figs. 5, 6; Lochman, 1956, p. 1372, pl. 1, figs. 5-10; Poulsen, 1967, p. 15, pl. 2, fig. 1; Pojeta, Runnegar, and Kříž, 1973, p. 866, fig. 1A-D.

? *Fordilla troyensis,* Delgado, 1904, p. 358, pl. 4, figs. 23, 25; Cobbald, 1919, p. 156, pl. 4, fig. 33.

? *Modioloides prisca* Walcott, 1887, p. 191, pl. 1, fig. 19; 1889, p. 29; 1890, p. 615, pl. 73, fig. 3; Ulrich and Bassler, 1931, p. 98, pl. 4, fig. 16; Kobayashi, 1954, p. 129.

Non Fordilla troyensis, Shaler and Foerste, 1888, p. 28, pl. 1, fig. 4; Gorham, 1905, pl. 3, fig. 4.

Diagnosis. — Small *Fordilla* with thick shell, prominent growth lines, and ovate outline.

Types and materials. — I have examined approximately 350 specimens of *Fordilla troyensis* from various localities in the Taconics of New York State and Conception Bay, Newfoundland. These include silicone and latex replicas of the specimens from New York State figured by Barrande (1881, pl. 361). The specimen used for Barrande's figure "a" (Pl. 2, fig. 1, herein) measures 3.5 mm long and 2.5 mm high; the specimen used for his figure "b" (not figured herein) measures 4.5 mm long and 3.2 mm high; the one used for his figure "c" (Pl. 2, fig. 2, herein) is 3.7 mm long and 2.3 mm high;

the specimen used for Barrande's figure "1" (Pl. 4, figs. 1, 2, herein) is 3.6 mm long and 2.3 mm high and is herein chosen as the lectotype of the species; the one used for his figure "2" (Pl. 4, fig. 5, herein; Pojeta, Runnegar, and Kriz, 1973, fig. 1D) is 4.9 mm long and 3.5 mm high.

The specimen shown on Plate 1, figures 1-3, herein, preserves the impressions of most of the musculature of the right valve of *Fordilla troyensis*, including both adductor muscle insertions, the moniliform pallial line, and the anterior pedal retractor muscle insertion. Plate 1, figures 1, 2, show the specimen as photographed by light photography; in figure 2, the muscle scars are inked in. This specimen was also prepared for Scanning Electron Microscope photography (SEM). In this process much of the matrix surrounding the specimen had to be removed, and the specimen was damaged. Plate 1, figure 3, shows the extent of the damage; most of the posterior adductor impression was destroyed, as was most of the moniliform portion of the pallial line. The anterior adductor and pedal retractor muscle insertions remain intact as does the anterior part of the pallial line.

The specimens that best illustrate the musculature of the left valve are shown on Plate 3, figure 3, and Plate 4, figures 1, 2. The anterior adductor and pedal retractor insertions are preserved on both specimens, as is the anterior part of the pallial line. In addition, the specimen shown on Plate 4, figures 1, 2, preserves the anterior part of the moniliform part of the pallial line. Pojeta, Runnegar, and Kriz (1973) discussed the functional significance of the moniliform part of the pallial line. The specimen shown on Plate 4, figures 1, 2, also shows a gradual increase in the width of the pallial line until it grades almost imperceptibly into the anterior adductor muscle scar; this supports Yonge's concept (1953) that the adductor muscles are cross-fused and hypertrophied pallial muscles.

Only one articulated specimen of *Fordilla troyensis* is known (Pl. 4, figs. 3, 4). It clearly shows that *Fordilla* is equivalved.

Three specimens give indication of the lack of anterior and posterior lateral teeth in *Fordilla troyensis*. The specimen shown on Plate 3, figure 3, is a left valve, preserving impressions of the anterior musculature. Although most of the dorsal margin of this shell is broken and missing, the extreme anterior and posterior parts are present, and they show a lack of dentition. The specimen shown on Plate 4, figures 5, 6, are internal molds of left valves which preserve impressions of the posterior and anterior parts of the dorsal margin, respectively; in neither case are there impressions of any teeth. On the basis of these three specimens I interpret *Fordilla troyensis* as lacking anterior and posterior lateral teeth. No specimens of *Fordilla* seen by me preserve the part of the dorsal margin in the vicinity of the beaks, and it is not known whether *Fordilla* had cardinal teeth.

A reconstruction of the right valve of *Fordilla troyensis* was published by Pojeta, Runnegar, and Kriz (1973, fig. 2).

Distribution. — *Fordilla troyensis* is known from various localities in the Lower Cambrian rocks of the Taconics of eastern New York State; it also occurs in the Lower Cambrian rocks of Newfoundland (USNM 207679), Greenland, and Denmark (Poulsen, 1932, 1967). It has questionably been reported from the Lower Cambrian rocks of Portugal (Delgado, 1904), and England (Cobbald, 1919).

Fordilla ? marini Sampelayo, 1933

This name was applied to one figure by Sampelayo (1933). The specimen is unusually large for *Fordilla,* measuring almost 8 mm long, and the beak is almost central, creating an equilateral shell; it is doubtful that this specimen belongs to *Fordilla.* The shell is from the Spanish Cambrian at Valdemiedes (Zaragoza).

PALEOECOLOGY

None of the specimens of *Fordilla troyensis* that I have seen appear to be part of *in situ* or life assemblages. At Schodack Landing, *Fordilla* occurs in a silty limestone as disarticulated valves together with small fragments of trilobites (USGS 8043-CO); this is the only locality at which I have been able to find *Fordilla* in the field. The matrix associated with *Fordilla* in museum specimens is silty limestone, a shell hash, or sparry limestone in which the larger fossils are broken up and *Fordilla* is disarticulated. The single known articulated specimen of *Fordilla* is free of all matrix.

Morphologically, *Fordilla* resembles younger pelecypods that are adapted for infaunal life. *Fordilla* is laterally compressed, has a well-developed anterior end with attendant musculature, and shows no sign of a byssus. The anterior adductor is slightly smaller than the posterior adductor, and the beaks and umbo are closest to the anterior end of the shell. All these features suggest an animal that lived in the sediment rather than on top of it. The general morphology of *Fordilla* also suggests a suspension feeding mode of life rather than deposit feeding.

PHYLOGENY

The systematic position of *Fordilla* has long been in dispute, although until recently it was usually regarded as a bivalved arthropod. Ford (1873, p. 139) was the first to suggest that *Fordilla* might be an arthropod, although he felt that this was unlikely. Barrande (1881) and Walcott (1886) regarded *Fordilla* as a pelecypod. Later, Walcott (1887, 1890) expressed some doubts about including *Fordilla* among the pelecypods and suggested that it might be allied to the crustaceans. Ulrich and Bassler (1931) placed *Fordilla* firmly in the conchostracan crustaceans because they felt it had a "calcareo-phosphatic" shell like various conchostracans which they placed in the Limnadiidae. Shimer and Shrock (1944) in their widely used text on *Index Fossils of North America* included *Fordilla* in the branchiopod crustaceans. Raymond (1946), in a review of fossil conchostracans, noted that *Fordilla* might be ancestral to the group. Kobayashi (1954, p. 183) noted that Howell had a chemist test the shell of a specimen of *Fordilla* for phosphorus but could find none. Kobayashi (1972) considered *Fordilla* to be one of the ancestral conchostracans. Lochman (1956, p. 1373) felt it would be unwise to arbitrarily reject *Fordilla* as a member of the Pelecypoda. Poulsen (1932, 1967) supported the placement of *Fordilla* in the Pelecypoda, particularly because of the thickness of its shell, and he noted that the Greenland specimens of *Fordilla* lacked phosphate. Pojeta, Runnegar, and Kriz (1973) noted that *Fordilla* was a pelecypod because of its musculature which consists of anterior and posterior adductors, pedal retractors, and a pallial line; this position is further documented and supported herein.

There is a significant stratigraphic gap in the fossil record of pelecypods between the occurrence of *Fordilla* in the late Early Cambrian and the Early Ordovician (Tremadocian-Arenigian) when the pelecypods undergo a major radiation.

The literature about Early Ordovician pelecypods is not large, and little is known about Tremadocian (early Early Ordovician) forms. Harrington (1938) described three species from the lower Tremadocian rocks of Argentina: *Ctenodonta famatinensis, Palaeoneilo iruyensis,* and *Cosmogoniophorina tenuicostata.* The first two species have shapes similar to the genera to which they are assigned and probably are palaeotaxodonts, although Harrington's figures do not show taxodont dentition. *Cosmogoniophorina* is an isofilibranch genus, and the Argentinian specimens probably do not belong in this genus. One of Harrington's figures of *C. tenuicostata* (1938, pl. 3, fig. 4) suggests the presence of taxodont dentition, and the shape of the species is similar to such palaeotaxodonts as *Deceptrix* Fuchs; however, the Argentinian form has fine radial ribs which are not present in *Deceptrix.* It seems likely that Harrington's *Cosmogoniophorina tenuicostata* belongs to an as-yet-unnamed genus of palaeotaxodonts.

Thoral (1935) noted the presence of two pelecypods in the upper Tremadocian rocks of France: the heteroconchian *Babinka* and a palaeotaxodont which he placed in *Nucula*(?). Soot-Ryen (1969) noted that Thoral's specimens of *Babinka* probably are Arenigian (late Early Ordovician) in age and not Tremadocian. Hicks (1873) described a pelecypod fauna from rocks which he regarded as Tremadocian in age from Wales; this fauna was restudied by Carter (1971), who regarded it as Arenigian in age. Termier and Termier (1971) described the palaeotaxodont *Afghanodesma* from the Tremadocian rocks of Afghanistan. They did not give photographic illustrations of the form, but their drawings show taxodont dentition.

Thus, the earliest Ordovician record of pelecypods is based upon a maximum of five known species, all of which are probably palaeotaxodonts. By the end of Arenigian time, palaeotaxodonts are reported from Argentina (Harrington, 1938), France (Thoral, 1935; Barrois, 1891; and Babin, 1966), Wales (Hicks, 1873; Carter, 1971), and Malaysia (Pojeta, 1971, p. 16). Babinkid heteroconchs are known from the Arenigian of France (Thoral, 1935; Soot-Ryen, 1969), and Sweden (Soot-Ryen, 1969); redoniid heteroconchs are known from Arenigian rocks in France (Barrois, 1891; Babin, 1966; Thoral, 1935; Dean, 1966, p. 348); lyrodesmatid heteroconchs are known from the Arenigian of France (Barrois, 1891; Babin, 1966;

Pojeta, 1971); and cycloconchid heteroconchs are known from France (Barrois, 1891; Babin, 1966), and perhaps Wales (Carter, 1971). Isofilibranchs are known from the Arenigian of France (Barrois, 1891; Babin, 1966), perhaps Wales (Hicks, 1873; Carter, 1971), and perhaps Argentina (Harrington, 1938). The reported occurrences of other higher level taxa in the Arenigian are all equivocal at this time.

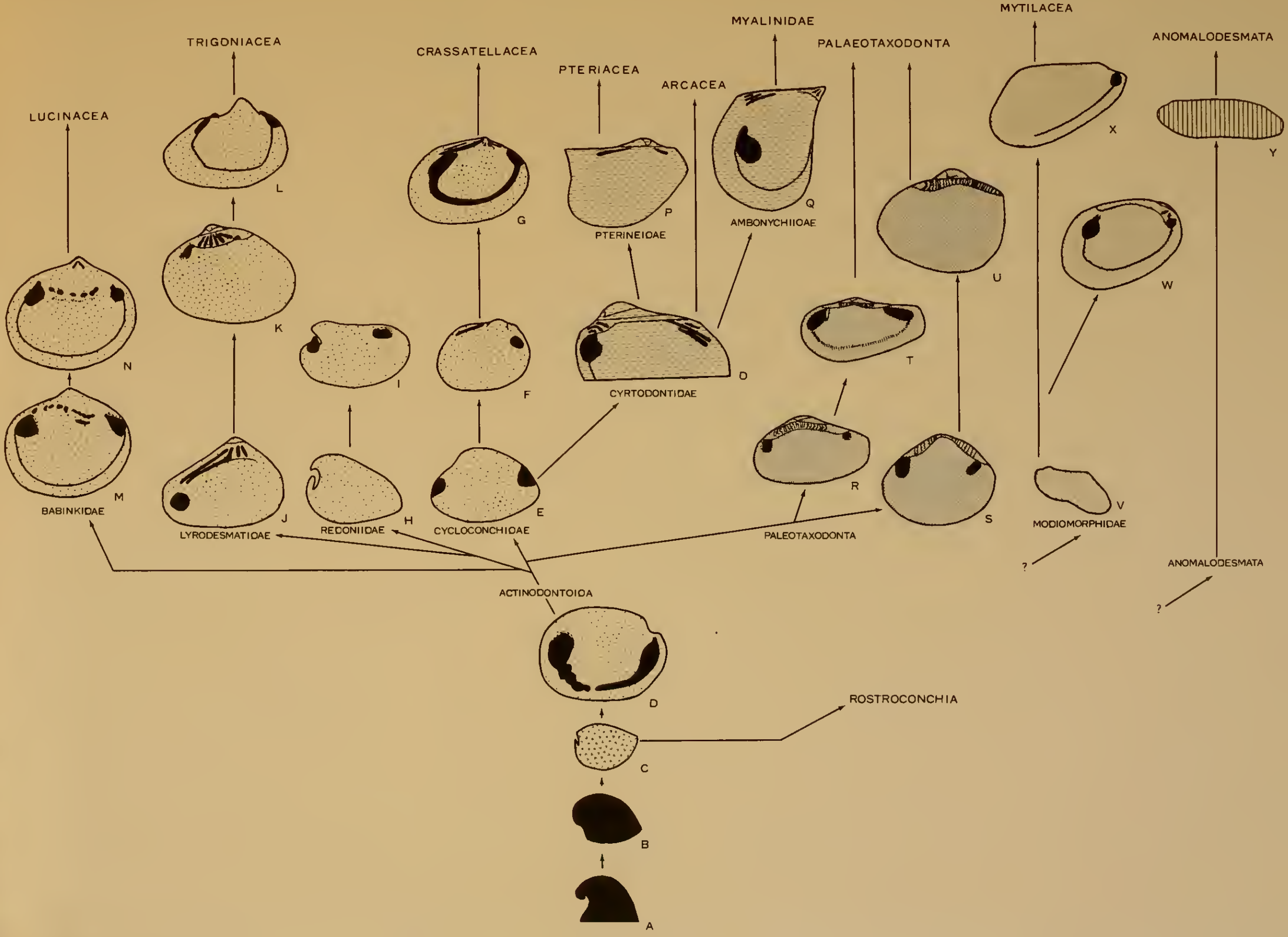
The pelecypods were actively radiating by Early Ordovician time, and they diversified further and spread out geographically in the Middle Ordovician (Pojeta, 1971, fig. 6). Also by Middle Ordovician time, all the subclass-level taxa were established (Pojeta, 1971, fig. 5). *Fordilla* gives us only one point in the development of pelecypods in the Cambrian, and all the diversity of pelecypods present in the Early Ordovician cannot be related to this one point (Text-fig. 1).

The general shape of *Fordilla* is similar to such Arenigian cycloconchid heteroconchs as *Actinodonta secunda* (Salter) and such Middle and Late Ordovician forms as *A. naranjoana* (de Verneuil and Barrande) (Llandeilian), *Cycloconcha mediocardinalis* Miller, *C. ovata* Ulrich (Edenian), and *C. milleri* (Meek) (Richmondian). Further, some cycloconchids such as *C. mediocardinalis* have a broadly inserted pallial line (Pojeta, 1971, pl. 3, figs. 1, 2) reminiscent of the broadly inserted pallial line of some specimens of *Fordilla* (Pl. 1, figs. 1, 2), although the pallial line of *Cycloconcha* is not moniliform (Text-fig. 1).

It is reasonable to regard *Fordilla* as ancestral to the Cycloconchidae (Text-fig. 1) for the reasons cited above. To this family, Pojeta (1971) related the Lyrodesmatidae, Redoniidae, and Babinkidae, all of which were united in the order Actinodontoida. *Fordilla* differs from the actinodontoids in lacking a well-developed and extensive dentition.

Relating the isofilibranchs, pteriomorphs, palaeotaxodonts, and anomalodesmatans to *Fordilla* is more difficult than showing relationships to the actinodontoids and heteroconchs (Text-fig. 1). It is postulated that the retention of the byssus in adult pelecypods is a neotonous feature (Yonge, 1962; Stanley, 1972). Pteriomorphs could be derived paedomorphically from the actinodontoids as most Ordovician pteriomorphs have well-developed dentition (Pojeta, 1971).

Text-figure 1. — Postulated phylogeny of the Pelecypoda during the Cambrian and Ordovician. All figures semidiagrammatic and taken from the authors indicated. Black pattern used for the Class Monoplacophora, chevron pattern used for the Class Rostroconchia, all other patterns indicate subclasses of the Pelecypoda. From left to right, coarse stippled pattern used for the subclass Heteroconchia, horizontal dashed line pattern used for the subclass Pteriomorphia, fine stippled pattern used for the subclass Palaeotaxodonta, oblique dashed line pattern used for the subclass Isofilibranchia, vertical line pattern used for the subclass Anomalodesmata. A. *Latouchella* Cobbald (Tommotian, Lower Cambrian); B. *Anabarella* Vostokova (Tommotian, Lower Cambrian); C. *Heraultia* Cobbald (Georgian, Lower Cambrian); D. *Fordilla troyensis* Barrande (upper Lower Cambrian); E. *Actinodonta secunda* (Salter), after Babin, 1966, pl. 9, fig. 7 (upper Arenigian); F. *Actinodonta naranjoana* (deVerneuil and Barrande), after Babin, 1966, pl. 10, fig. 10 (Llandeilian); G. *Cycloconcha* Miller, composite diagram from Pojeta, 1971, pl. 2, fig. 14; pl. 3, fig. 1 (Cincinnatian); H. *Redonia prisca* Thoral, after Thoral, 1935, fig. 7 (lower Arenigian); I. *Redonia bohemica* Barrande, after Barrande, 1881, pl. 268, fig. 2 (Llanvirnian); J. *Lyrodesma armoricana* deTromelin and Lebesconte, after Barrois, 1891, pl. 1, fig. ID (upper Arenigian); K. *Lyrodesma conradi* Ulrich, after Pojeta, 1971, pl. 3, fig. 20 (Edenian); L. *Lyrodesma poststriatum* (Emmons), after Pojeta, 1971, pl. 3, fig. 18 (Maysvillian); M. *Babinka oelandensis* Soot-Ryen, after Soot-Ryen, 1969, text-fig. 1 (upper Arenigian); N. *Babinka prima* Barrande, after McAlester, 1965, text-fig. 1 (Llanvirnian); O. *Cyrtodonta* cf. *C. huronensis* Billings, after Pojeta, 1971, pl. 7, fig. 2 (Wildernessian); P. *Palaeopteria,* after Pojeta, 1971, pl. 11, fig. 9 (Barneveldian); Q. *Ambonychia radiata* Hall, after Pojeta, 1962, pl. 22, fig. 6 (Cincinnatian); R. *Ctenodonta,* after Pojeta, 1917, pl. 4, fig. 20 (upper Canadian); S. *Deceptrix? oehlerti* (Barrois), after Babin, 1966, fig. 4, (upper Arenigian); T. *Ctenodonta nasuta* (Hall), after Pojeta, 1971, pl. 4, fig. 10 (Mohawkian); U. *Deceptrix* aff. *D. hartsvillensis* (Safford), after Pojeta, 1971, pl. 5, fig. 20 (Barneveldian); V. *Modiolopsis davyi* Barrois, after Barrois, 1891, pl. 3, fig. 7a (upper Arenigian); W. *Modiolodon oviformis* (Ulrich), after Pojeta, 1971, pl. 13, fig. 6 (Barneveldian); X. *Modiolopsis modiolaris* (Conrad), after Pojeta, 1971, pl. 16, fig. 2 (Maysvillian): Y. *Rhytimya mickelboroughi* (Whitfield), after Pojeta, 1971, pl. 16, fig. 10 (Maysvillian).


LUCINACEA
TRIGONIACEA
CRASSATELLACEA
PTERIACEA
ARCACEA
MYALINIDAE
PALAEOTAXODONTA
MYTILACEA
ANOMALODESMATA
L
G
P
PTERINEIDAE
Q
AMBONYCHIIDAE
X
Y
U
W
N
K
I
F
CYRTODONTIDAE
D
T
M
BABINKIDAE
J
LYRODESMATIDAE
H
REDONIIDAE
E
CYCLOCONCHIDAE
R
S
PALEOTAXODONTA
V
MODIOMORPHIDAE
?
ANOMALODESMATA
?
ACTINODONTOIDA
D
ROSTROCONCHIA
C
B
A

Ordovician isofilibranchs do not have well-developed dentition (Pojeta, 1971) and were probably not derived from the actinodontoids. They may have arisen from *Fordilla* by the paedomorphic retention of the byssus by the adult, or they may have arisen from as-yet-unknown Cambrian forms. The development of taxodont dentition is a recurrent feature of pelecypod evolution and has developed independently in the palaeotaxodonts, arcaceans (Cox, 1959), and unionaceans (*Iridina* Lamarck). In both the arcaceans and unionaceans, taxodont teeth seem to have developed from a dentition consisting of cardinal and lateral teeth with the latter approximately parallel to the dorsal margin. By inference, the taxodont dentition of palaeotaxodonts could have arisen from the cardinal and lateral teeth of actinodontoids. The morphology of Ordovician anomalodesmatans is poorly known, and their relationship to other Ordovician pelecypods or *Fordilla* is uncertain.

In summary (Text-fig. 1), it is postulated that *Fordilla* gave rise to the cycloconchid pelecypods and through them to the rest of the Actinodontoida. The byssate ambonychiid, cyrtodontid, and pterineid pteriomorphs of the Ordovician have well-developed dentition consisting of cardinal and lateral elements; they could have been derived from the actinodontoids paedomorphically by the neotonous retention of the larval byssus throughout life. Ordovician isofilibranchs are either edentulous or have only cardinal teeth; they may have been derived from the actinodontoid stem stock before dentition became well developed by neotonous retention of the larval byssus throughout life, directly from *Fordilla* by the same process or from as-yet-unknown Cambrian forms. The palaeotaxodonts may have been derived from the actinodontoids by a rearrangement of dental elements like the development of taxodont dentition in arcaceans and unionaceans.

Runnegar and Pojeta (in press) noted the similarities of *Fordilla* to the oldest known rostroconch mollusk *Heraultia* Cobbald. Both have laterally compressed shells of about the same size and similar lateral profiles, and both are of about the same age (Text-fig. 1). They differ in that *Heraultia* has a univalved larval shell, lacks a dorsal commissure as an adult, and it is thus pseudobivalved. *Heraultia* is in effect a laterally compressed univalve with anterior, posterior, and ventral gapes; it can be related to such laterally compressed monoplacophorans as *Anabarella* Vostokova (Rozanov, 1969) which have a curved ventral margin. I envisage such forms as *Anabarella* as giving rise to *Heraultia,* and *Heraultia* in turn by mutation producing a flexible hinge in the larval shell giving rise to *Fordilla*. The main difference between pelecypods and rostroconchs is that in pelecypods the shell is bivalved from the beginning of its formation. Once a flexible ligament was established in the larval shell, all adult features of a pelecypod would follow in short order. This change probably occurred in the Early Cambrian when *Fordilla* evolved from *Heraultia* or some closely related form.

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EXPLANATION OF PLATE 1

Figure

1-3. **Fordilla troyensis** Barrande, 1881

Right valve showing muscle scars, × 13, USNM 15372. 1. Light photograph of specimen. 2. Same view of same specimen with muscle scars outlined in ink. 3. Same view of same specimen showing damage suffered after preparation for SEM photography. The museum label gives the horizon and locality as "Lower Cambrian, Troy, New York."

4. **Fordilla troyensis** Barrande, 1881

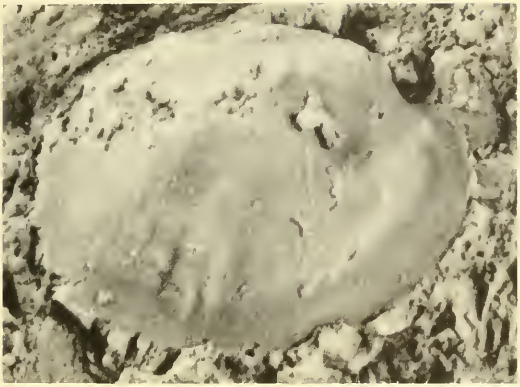
Right(?) valve, × 10, USNM 17445. Holotype and only known specimen of *Modiolopsis*? [*Modioloides*] *prisca* Walcott. The museum label gives the horizon and locality as "Lower Cambrian, Whitehall, Washington Co., New York."

5-7. **Lamellodonta simplex** Vogel, 1962

5. A paratype showing ornament and posterior ridges, × 2, UT La 1228/10; this specimen was figured by Vogel (1962, pl. 2, fig. 2). 6. A paratype showing posterior ridges and midumbonal elevation, × 3.5, UT La 1228/11; this specimen was figured by Vogel (1962, pl. 2, fig. 3, 4, 9). 7. A paratype showing posterior ridges and midumbonal elevation, × 4, UT La 1228/8; figured by Vogel (1962, pl. 1, fig. 9). All specimens from the Middle Cambrian rocks of Spain.

8. **Obolella mexicana** Cooper, 1952

Paratype showing posterior ridges and midumbonal elevation for comparison with *Lamellodonta simplex* in figures 5-7 above, × 8, USNM 116041d. Puerto Blanco Formation (Lower Cambrian), Sonora, Mexico.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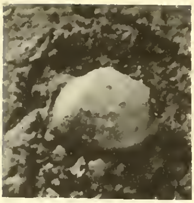
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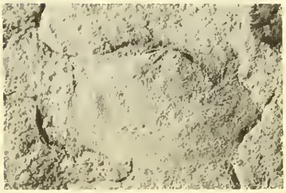
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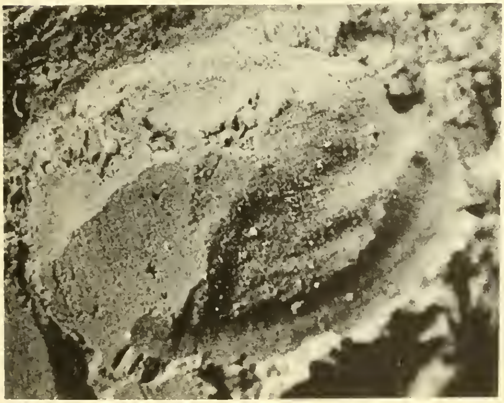
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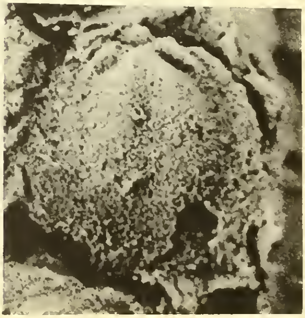
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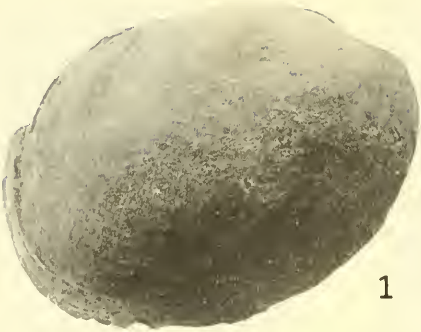
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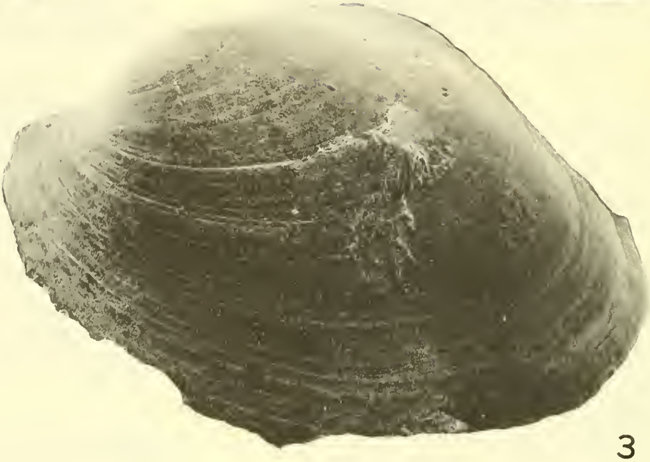
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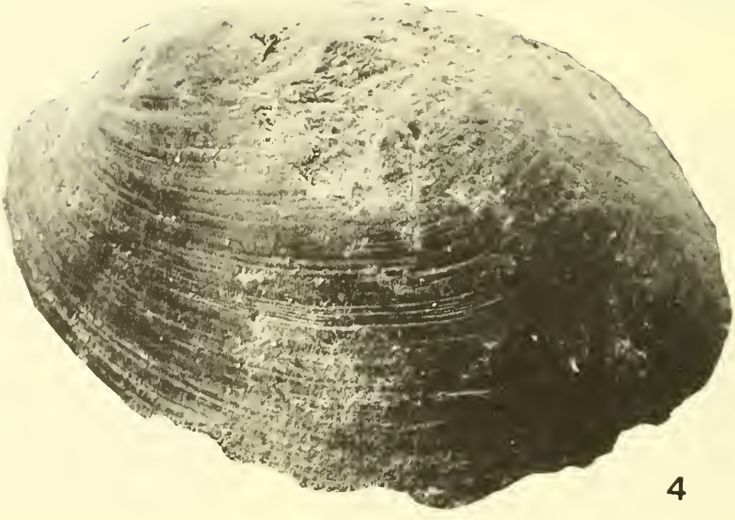
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EXPLANATION OF PLATE 2

Figure

1-4. Fordilla troyensis Barrande, 1881

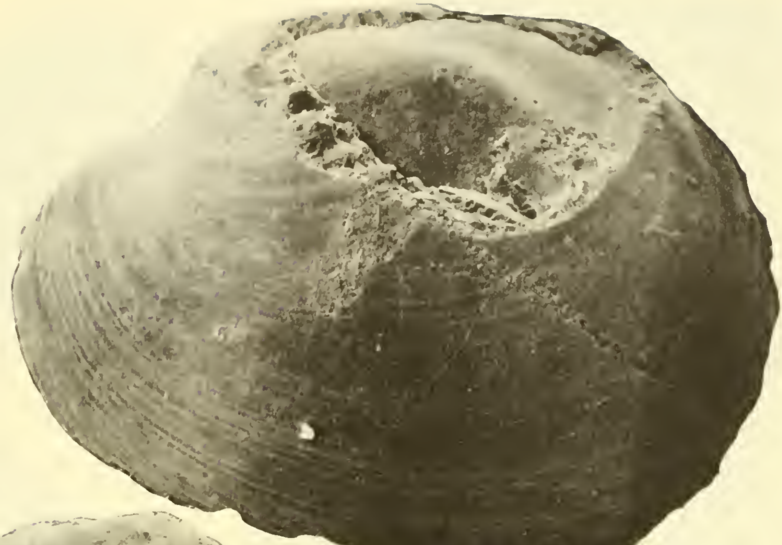
1. Latex replica of a paralectotype of the species, right valve, × 15, USNM 207680; Barrande, 1881, plate 361, figure "a". 2. Latex replica of a paralectotype of the species, left valve, × 16, USNM 207681; Barrande, 1881, plate 361, figure "c". 3. Left valve exterior, × 17, USNM 207682, Lower Cambrian, Troy, New York. 4. Left valve exterior, × 25, USNM 207683, Lower Cambrian, Troy, New York.

EXPLANATION OF PLATE 3

Figure

1-3. **Fordilla troyensis** Barrande, 1881

1. Left valve exterior, × 23, USNM 207684. 2. Right valve exterior, × 16, USNM 207685. 3. Left valve interior showing anterior muscle scars, × 25, USNM 207686. All specimens from Lower Cambrian, Troy, New York.



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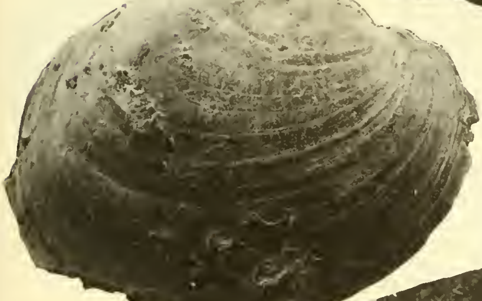

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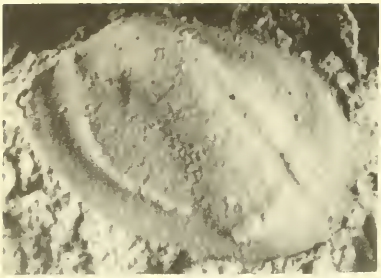
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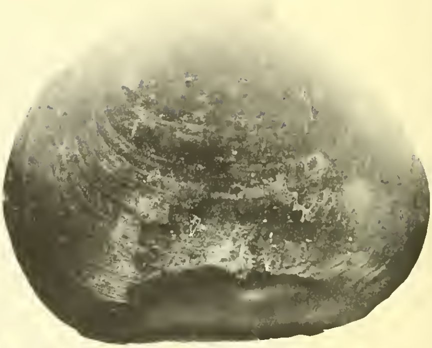
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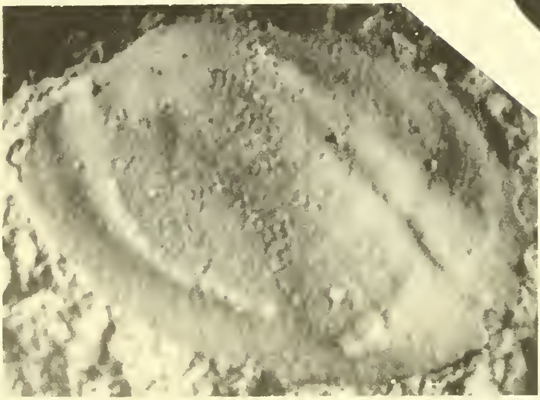
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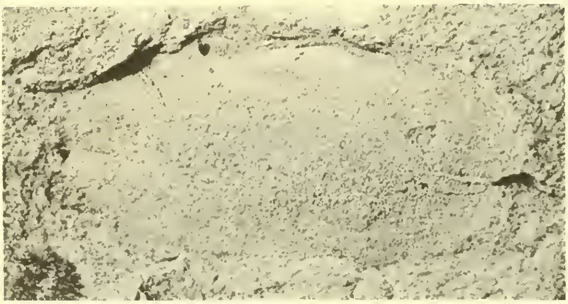
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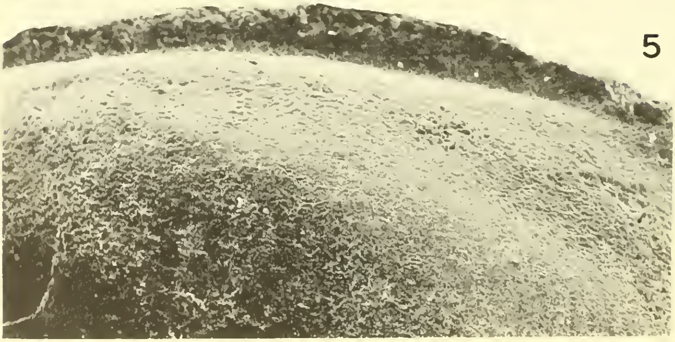
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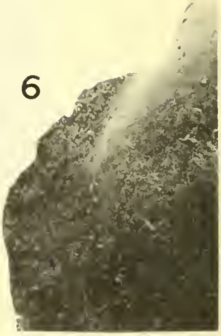
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EXPLANATION OF PLATE 4

Figure

1-6. **Fordilla troyensis** Barrande, 1881

1. Latex replica of the lectotype of the species, left valve showing anterior muscle scars, × 12.5, USNM 207687; Barrande, 1881, plate 361, figure 1. 2. Same as figure 1, × 18.5. 3. Right valve of an articulated specimen, × 20, MCZ 7424, Lower Cambrian, Troy, New York. 4. Dorsal view of the articulated specimen shown in figure 3 above, × 20. 5. Latex replica of a paralectotype, internal mold of a left valve showing the posterodorsal portion with an impression of the erect ligamental area and lacking any indication of posterior lateral teeth, × 39, USNM 207688; Barrande, 1881, plate 361, figure 2. 6. Internal mold of a left valve showing the impression of the anterodorsal part of the shell and lacking any indication of anterior lateral teeth, × 22, USNM 207689, Lower Cambrian, Troy, New York.

7. **Lamellodonta simplex** Vogel, 1962

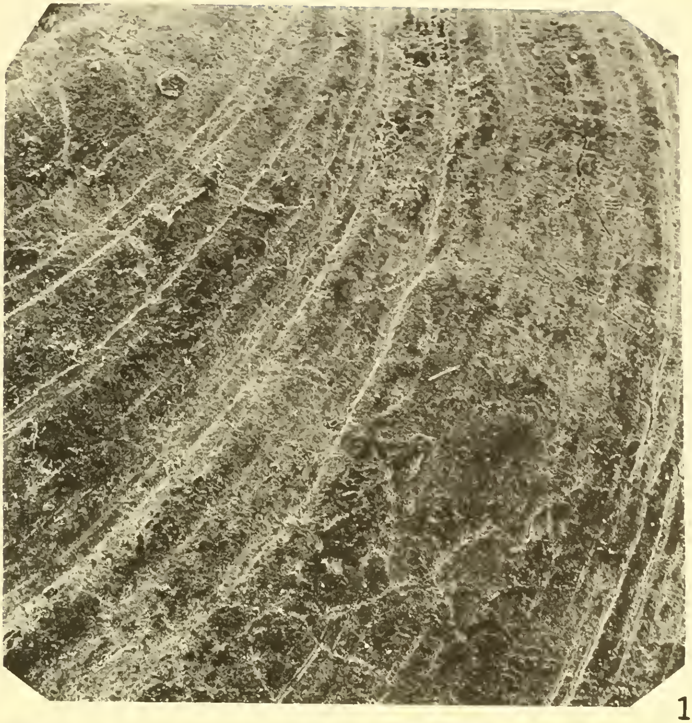
Holotype of the species showing the posterior ridges, × 5, UT La 1228/1, figured by Vogel (1962, pl. 1, fig. 1), from the Middle Cambrian of Spain.

EXPLANATION OF PLATE 5

Figure

1, 2. **Fordilla troyensis** Barrande, 1881

1. Enlargement of growth lines on the anterior part of the right valve shown on Plate 3, figure 2, × 80, USNM 207685, Lower Cambrian, Troy, New York. 2. Enlargement of growth lines along the midventral portion of a right valve, × 80, USNM 207690, Lower Cambrian, Troy, New York.



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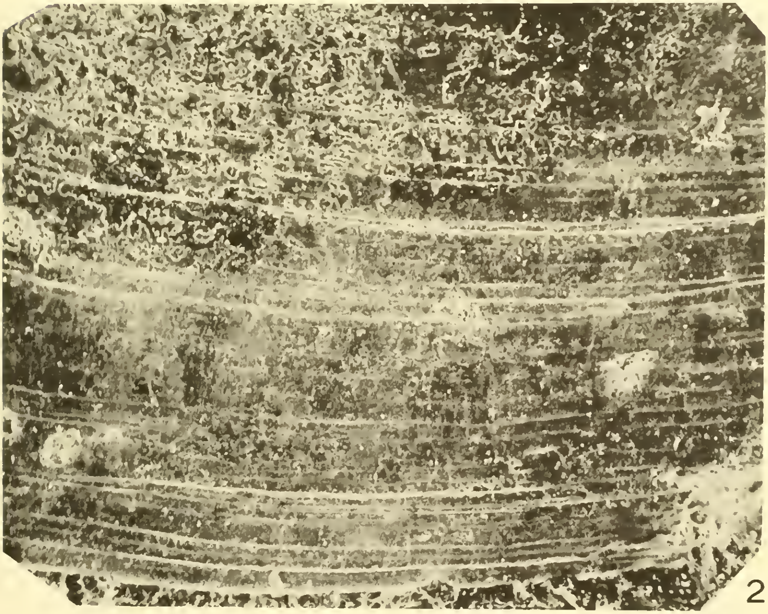

2

EVIDENCE FOR RELATING THE LEPIDOCOLEIDAE, MACHAERIDIAN ECHINODERMS, TO THE MITRATE CARPOIDS

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ABSTRACT

The Machaeridia has been allied to the chitons, barnacles, annelids, and trilobites but generally is accepted today as a class of the Echinodermata. Lepidocoleid machaeridians are tentatively regarded herein as a system of plates that enveloped the posterior spines of "carpoids" of the order Mitrata. Many strobili of *Lepidocoleus* Faber have been discovered in association with plates of *Enoploura* Wetherby, an anomalocystitid mitrate, in the Waynesville Formation, Upper Ordovician, at Cincinnati, Ohio, and St. Marys, Indiana. The broken ends of some of these strobili expose internal rods interpreted to be the posterior spines of *Enoploura*. The population of strobili is divisible into left and right enantiomorphs. Serial and longitudinal markings on isolated posterior spines possibly indicate an enclosing structure. The texture and appearance of the surfaces of the strobili and mitrate plates are similar.

INTRODUCTION

The general morphology of the Machaeridia is well documented in Withers' *Catalogue of the Machaeridia* (1926). General descriptions of the Machaeridia published subsequently, *e.g.*, Termier and Termier (1953) and Nichols (1962), have not added substantially to our understanding of machaeridian structure.

As there is no important dissension among authors regarding the morphology of the fossils of this group, it is surprising that opinions differ so greatly as to their zoological affinity. Tangible features, as the shape of the strobilus (a complete set of machaeridian plates, so-called for its similarity in form to a conifer cone) and the shape of individual plates, as well as deductive conclusions as to the form of the alimentary and respiratory systems and the position of the plates on the animal during life have led authors to assign the machaeridians to the polyplacophorans, cirripeds, annelids, trilobite appendages, carpoid peduncles and posterior processes, ophiocistioid tube feet and unknowns. The concept relating the Machaeridia to the Echinodermata was so convincingly expressed by Withers (1926) and also by Bather in his involvement of the group in his "dipleurula theory" in the introduction to Withers' *Catalogue,* that the alliance of the Machaeridia to the echinoderms has remained popular to this day without significant additional evidence.

Recent discovery of a population of machaeridians affords an opportunity to reinvestigate their zoological affinity.

In about 1952, Joseph Stocker, Jr., of Cincinnati, found a locality in the western area of Cincinnati, Hamilton County, Ohio, which quickly became, and for a decade remained, one of the most intensively searched sites in this region. This Boudinot Avenue locality, originally a hillside that had been scraped to bedrock, today lies below an apartment development.

The principal attraction at the Boudinot Avenue locality was the abundance of complete specimens of the trilobite *Flexicalymene meeki* (Foerste) found in mudstone of the Waynesville Formation, Upper Ordovician, near the top of the exposure. While washing the trilobite-bearing mudstone, Stocker and a collecting companion, William Deak, discovered a great number of mitrate carpoid plates, incomplete mitrate thecae and aulacophores, and plates and sections of strobili from a biserial machaeridian. Subsequently, Stocker and Deak found and collected a similar assemblage from a second locality, also in the Waynesville Formation, at St. Marys, Franklin County, Indiana.

Today, through the diligence of Stocker, Deak, and other collectors, the University of Cincinnati Geology Museum and the Miami University Geology Museum possess thousands of mitrate plates, a number of incomplete thecae and aulacophores, and over 50 incomplete machaeridian strobili from these localities. The lepidocoleid machaeridians and mitrate posterior spines from these localities considered in this study are at the University of Cincinnati Geology Museum (UCGM 42701-42754).

The occurrence of isolated machaeridian plates, especially *Lepidocoleus jamesi* (Hall and Whitfield), and mitrate plates in washings from shales of the Cincinnatian Series is not unusual, but the joint occurrence of thousands of mitrate plates and of machaeridian plates assembled into strobili from Cincinnatian rocks is unique. I attach less significance to description of the machaeridian species and its population than to its association with mitrate remains which affords evidence to support the conjectured origin of machaeridians as appendages of the mitrate animal.

Remarks originally by Louis B. Kellum and recently by Georges Ubaghs (1967, p. 52) and Stefan Bengtson (1970, p. 386) have convinced me that my original statement (Pope, 1962) regarding the mitrate-lepidocoleid liaison needs amplification.

ACKNOWLEDGMENTS

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The late William H. Shideler stimulated my interest in the Machaeridia with a gift of specimens from the Upper Ordovician, Kope Shale. Prof. Shideler left many machaeridan plates and a fine specimen of *Lepidocoleus jamesi* in the collections of the Miami University Geology Museum. The rock section at the Boudinot Avenue locality was measured and described by Mark Schweinfurth (1958). Melinda R. Tucker carefully reconstructed *Enoploura* thecae from isolated plates from St. Marys, Indiana.

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GROUP MACHAERIDIA WITHERS, 1926

Small, elongated, sabreblade-shaped to cylindrical strobili constructed of two or four columns of many, strongly imbricated, calcitic scales or plates. Range: Middle Ordovician to Late Mississippian.

In view of the relationship of the Machaeridia to the Mitrata propounded herein, it does not seem appropriate to give the Machaeridia formal taxonomic rank.

Genera of the Machaeridia include *Lepidocoleus* Faber (1886, Middle Ordovician to Middle Devonian), and *Aulakolepos* Wolburg (1938, Lower Devonian), with two columns of plates, and *Turrilepas* Woodward (1865, Middle Silurian to Lake Mississippian), *Plumulites* Barrande (1872, Middle Ordovician to Middle Devonian), *Deltacoleus* Withers (1926, Middle and Upper Ordovician, possibly Late Silurian), and *Sokolophocoleus* Pope (1960, = *Lophocoleus* Ruedemann, 1942, Middle Ordovician), with four columns of plates. Genera that are probably machaeridians but which need additional documentation include *Strobilepis* Clarke (1888, Middle Devonian) and *Clarkeolepis* Elias (1958, Late Mississippian). Genera that upon occasion have been referred to the Machaeridia but which are rejected herein include *Leckwyckia* Termier and Termier (1951; included tentatively in the Machaeridia by Termier and Termier, 1953, p. 1005; rejected because of possible arenaceous composition and lack of plates), *Anatifopsis* Barrande (1872; referred to the Machaeridia by Lamont and Gilbert, 1945, p. 643; probably the theca of a lagynocystid carpoid, from personal examination of latex molds of type specimens in the University of Cincinnati Geology Museum), and *Virgulaxonia* Yin (1937, = *Virgulaxonaria* Fisher, 1962, p. W127-W128, incorrect spelling; placed in the Machaeridia in the *Zoological Record* for 1937; placed in the Hyolithida by Fisher, 1962, p. W128).

Family **TURRILEPADIDAE** Withers, 1926

Machaeridia with four columns of strongly imbricating plates. Range: Middle Ordovician to Late Mississippian. Not considered further herein.

Family **LEPIDOCOLEIDAE** Withers, 1926

Machaeridia with two columns of imbricating plates. Range: Middle Ordovician into Lower Devonian.

Genus **LEPIDOCOLEUS** Faber, 1886

Lepidocoleus Faber, 1886, p. 15; Withers, 1926, pp. 6-9; Termier and Termier, 1953, p. 1004.

Type species: *Lepidocoleus jamesi* (Hall and Whitfield), by monotypy.

Diagnosis. — Strobilus generally cordiform in transverse section; plates gently convex, lacking sharply angular fold parallel to fixed margin; external ornament of plates continuous to fixed margin. Lacks deep, longitudinal groove along fixed margin and strongly infolded hinge-flaps of *Aulakolepos* Wolberg.

Remarks. — A more complete synonymy for *Lepidocoleus* was presented by Withers (1926, p. 6). Many species of *Lepidocoleus, e.g., L. ulrichi* Withers and *L. sarlei* Clarke, have a shallow groove along the fixed margin, but no species has a groove as deep as that of *Aulakolepos*. Plates of *Lepidocoleus jamesi* (Hall and Whitfield) have a slight fold along the fixed margin, but this fold is not as angular as in *Aulakolepos*. The surface ornament on plates of *L.*

jamesi continues across the fold to the fixed margin of the plates whereas the surface ornament of *Aulakolepos* ceases at the fold.

Lepidocoleus strictus Withers, 1926
Pl. 1, fig. 1; Pl. 2, figs. 1-18; Pl. 3, figs. 2-20

Lepidocoleus strictus Withers, 1926, p. 17, pl. 2, figs. 13-14.

Diagnosis. — Strobilus small, slender and subcylindrical; inflated cordiform to elliptical in transverse section. Umbo of plates low, not sharply pointed. Growth lines fine, faint to absent. Exposed edges of plates closely spaced along length of strobilus.

Dimensions. — Length of longest strobilus, 20.4 mm (UCGM 42750); other strobili broken, length not meaningful. Greatest diameters of strobili, 1.8 mm (UCGM 42750, 42701) to 2.2 mm (UCGM 42709, 42702); mean diameter about 2.0 mm. Distance between exposed edges of plates along length of strobilus, calculated as (length of strobilus / number of plates), from .52 mm (UCGM 42750) to .97 mm (UCGM 42701); mean distance about .73 mm. Greatest number of plates in a column, 39 (UCGM 42750).

Repository. — University of Cincinnati Geology Museum (UCGM), 42701-42738, 42748, 42750, *L. strictus* from Boudinot Avenue locality; 42739-42740, 42751-42754, *L. strictus* from St. Marys, Indiana. Other specimens considered herein, 42741, *L. jamesi* from Boudinot Avenue locality; 42742-42747, 42749, posterior spines of *Enoploura* from Boudinot Avenue locality.

Age and locality. — Upper Ordovician, Waynesville Formation. The Boudinot Avenue locality was situated on the western corner of the intersection of Westwood-Northern Boulevard and Boudinot Avenue, almost precisely on the western boundary of the City of Cincinnati, Green Township, Hamilton County, Ohio (SE¼ SW¼ sec. 10 and NE¼ NW¼, sec. 9, FR2 T2, Cincinnati West Quadrangle, 7.5 Minute Series). The St. Marys, Indiana, locality lies along the lower end of Russell Branch of Pipe Creek, about 400 m east of St. Marys School, Butler Township, Franklin County, Indiana, (SE¼ NW¼ and SW¼ NE¼ sec. 5, T.10 N., R.13 E., Spades Quadrangle, 7.5 Minute Series).

Paleoecology and preservation. — According to Schweinfurth (1958), about 56 feet (from about 895 feet to 950 feet above sea level) of lower Richmondian (Upper Ordovician) rock was exposed at the Boudinot Avenue locality. The section extended from the

Retrorsirostra carleyi Zone of the Arnheim Formation without interruption to the *Treptoceras duseri* Zone (= *Orthoceras fosteri* Zone) in the Waynesville Formation.

The machaeridians and mitrate plates were distributed uniformly throughout the base of a soft, light olive-gray mudstone about 12 to 15 feet thick at the top of the section, in the Waynesville Formation. These fossils were associated with, among others, complete trilobites, whole crinoid calyces and sections of starfish arms, indicating that the conditions of deposition of the mudstone were favorable for preservation of delicate creatures.

The fossils from this fauna are generally large, unbroken and undeformed. The surfaces of specimens lack tightly adhering clay and calcite crusts, and generally are free of large and numerous epizoans. These fossils also show some evidence of attack by ground water in being yellowish from oxidation, slightly etched and stained (Pl. 3, fig. 20, specimen deeply stained). The surface etching generally obscures cleavage reflections and the iridescent diffraction colors arising from the labyrinthine stereom of the echinoderm remains, but the echinoderms, including the machaeridians, show their crystallinity in cleavage fractures (Pl. 2, fig. 15).

About 12 feet (from about 765 feet to 777 feet above sea level) of light green to blue mudstone and thin, discontinuous limestone strata of the Waynesville Formation is exposed at St. Marys, Indiana. The mitrate and machaeridian remains occur in randomly distributed, thin lenses and streaks in this mudstone. These lenses are noticeable as concentrations of angular fossil fragments.

In contrast to the Boudinot Avenue fauna, that from St. Marys is poorly preserved. Specimens commonly are disarticulated, fragmentary, deformed, and coated with a thin, tightly adhering crust of clay and fine-grained, gray calcite (Pl. 2, fig. 18, calcite crust on specimen). Echinoderm fragments from St. Marys, especially the mitrate plates and machaeridians, show glittering reflections probably caused by filling of the stroma canals with calcite in crystallographic continuity to the stereom. The trilobites, brachiopods, tentaculitids, and bryozoans from St. Marys do not show crystalline reflections.

Many plates, but no large sections of strobili, of *Lepidocoleus jamesi* (Hall and Whitfield) (Pl. 3, fig. 1) were found in washes containing the mitrate plates and *Lepidocoleus strictus* Withers from the Boudinot Avenue and St. Marys localities.

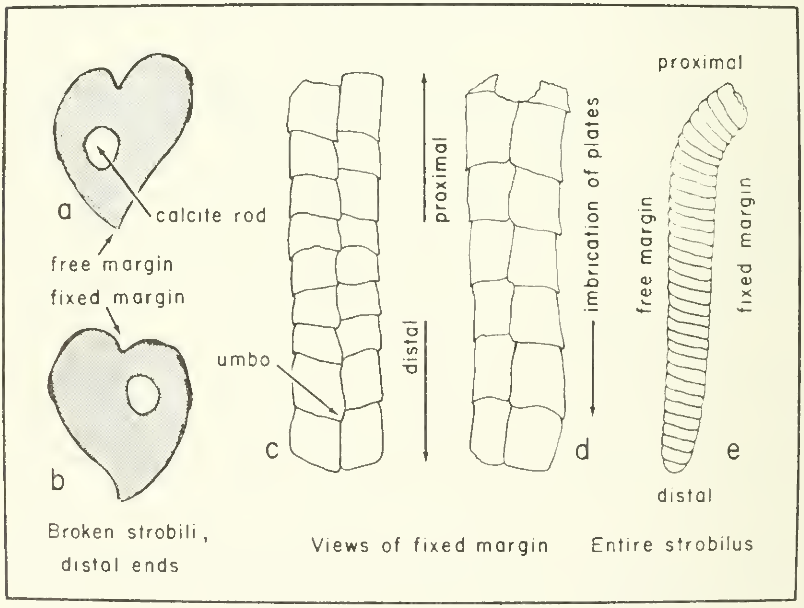
Remarks. — Certain specimens in the collections of *Lepidocoleus strictus* from the Boudinot Avenue and St. Marys localities, if found singly, might be assigned to other species of *Lepidocoleus.* The specimens shown on Plate 3, figure 20 (UCGM 42702) resembles *L. ulrichi* Withers (Withers, 1926, pl. 1, figs. 2-3) from the Middle Ordovician, Prosser Limestone, of Minnesota. The specimen on Plate 3, figure 20, is more slender than *L. ulrichi* and not as constricted at the proximal end. The specimens shown on Plate 2, figures 6, 16-17 and Plate 3, figure 9 (UCGM 42706, 42734, 42725) resemble *L. grayae* Withers (Withers, 1926, pl. 1, figs. 7-10) from the Upper Ordovician, Drummuck Group, of Scotland. These specimens (this report) are smaller, more elliptical in transverse section, and have fewer, fainter longitudinal surface markings than *L. grayae.*

GENERAL MORPHOLOGY OF THE LEPIDOCOLEIDAE

Text-figure 1

The lepidocoleids are small, elongated, sabreblade-shaped strobili constructed of two columns of many, slightly to strongly imbricated scales or plates (Pl. 3, figs. 14-15). The columns of scales are articulated along one edge of the strobilus to form the fixed margin (Pl. 2, figs. 7, 9-10, 12) and gap or are free (Pl. 3, figs. 2, 9, 13), thus forming a commissure, along the opposite edge, the free margin (Pl. 2, fig. 14). The cross-sectional shape of the strobilus of well-preserved specimens is flattened (Withers, 1926, pl. 4, figs. 2, 4) to almost circular and cordiform (Pl. 3, figs. 2-13) in this family as opposed to subtriangular to subquadrate in the turrilepadids. The distal end of the body tapers gently to abruptly into a point (Pl. 1, fig. 1; Pl. 2, figs. 3-5). The exposed edges of the imbricating plates are always directed toward the distal end (Pl. 1, fig. 1). The opposed, proximal end is straight to abruptly flexed and commonly constricted (Pl. 3, fig. 17; Faber, 1886, pl. 1, figs. A-B; Withers, 1926, pl. 4, figs. 1-2). The direction of curvature of the proximal end is not consistent in *Lepidocoleus,* being toward the fixed margin in *L. strictus* Withers and *L. britannicus* Withers and toward the free margin in *L. jamesi* (Hall and Whitfield) and *L. sarlei* Clarke. In no known specimen is the proximal end convincingly complete. Several specimens do have one or more smaller, somewhat rounded plates set at an odd angle to the longitudinal axis of the fossil at their proximal ends (Withers, 1926, pl. 1, fig. 4; pl. 4, fig. 2).

The lepidocoleids are not bilaterally symmetrical. The plates of the two columns are not opposite nor are they exactly alternate, that is, exactly one-half plate out of phase. The terminal plates of the columns thus must be different. Moreover, asymmetry is found in the cross-sectional shape of strobili. While the cross-sectional shape of a strobilus is approximately cordiform, the halves of the heart rarely will be identical (Pl. 3, figs. 2, 5, 7). The plates of one column will be more convex than those of the other column and this dominance will continue along the length of the strobilus. Additionally, in the populations of *L. strictus* studied, the column that is dominant is not consistent, there being an almost even distribution of strobili with left or right dominant columns, suggesting enantiomorphism (left and right handedness) (Text-fig. 1).



Text-figure 1. — Shape, orientation, and enantiomorphism of strobili. (a-b) Broken, distal ends of strobili. (a) Right column dominant; (b) left column dominant. (c-d) Views of fixed margin. (c) Left column advanced; (d) Right column advanced. (e) Reconstruction of shape of a complete strobilus of *Lepidocoleus strictus,* lateral view. Length-width proportion and number of plates based upon UCGM 42750 (Pl. 1, fig. 1).

The plates are subtriangular, isosceles or equilateral, to subrectangular in plan shape. Withers' comparison of the shape of the plates to the flap of a saddle is appropriate. The exterior surface of the plates may be smooth (Pl. 2, figs. 4-5, 7-8) or may bear any combination of weak to strong varices or low, longitudinal ridges (Pl. 3, fig. 1; Pl. 2, fig. 6). The margins of the plates are smooth.

As few as two to as many as four or even five plates may be imbricated (Pl. 3, figs. 14-15). Thus in some strobili much of the surface area of each plate is covered. There are no apparent articulatory structures as teeth and sockets or denticles along the fixed margin of a plate. Each plate bears an umbo which in the lepidocoleids lies at the corner formed by the distal and fixed edges of the plate (Pl. 3, fig. 1). The commissure along the free edge of complete, undistorted specimens is sealed by the closely appressed edges of the plates of the two columns (Pl. 2, fig. 14). On the internal surface of each plate of some species, but apparently not *L. strictus* considered here, there is a circular, shallow pit presumed to be a myophore (Withers, 1926, pl. 1, fig. 6).

The plates are thin and owing to this and their imbrication, difficult to study in transverse section. They seem to be composed of two layers of shell matter. The outer layer is thin, dense, and probably not holocrystalline. It commonly has a different color and surface texture than the inner layer. The outer layer seems to cover only that part of the plate which was exposed to the exterior. The inner layer is thicker, holocrystalline, finely labyrinthine stereom. Cleavages of the inner layer project through the outer layer as straight, regularly oriented fractures (Pl. 2, fig. 15). The internal surface of plates commonly shows crystalline reflections and the pastel iridescence produced by diffraction from labyrinthine stereom.

A longitudinal rod of coarsely crystalline calcite passes along part of the length of the interior cavity of some strobili of *L. strictus* (Pl. 3, figs. 3-6, 11-12).

ORIENTATION

There is no discrepancy among authors in the use of the terms "proximal" and "distal", and "free margin" and "fixed margin" in respect to the Machaeridia. The exposed edges of the imbricating plates on the external surface of individuals are directed distally, and it is the distal end which tapers to a point in complete specimens.

The opposite end is proximal. The fixed margin of the strobilus is the margin along which the plates are conceived to have articulated. The fixed margin is commonly grooved along its length. The umbo of each plate of the lepidocoleids is adjacent to the fixed margin. The free margin of a strobilus is the edge along which the plates are conceived to have opened.

In the conventional view of machaeridian organization, after Withers (1926), the animal was conceived to have been bilateral and sessile. Hence, Withers and others equate proximal to "base", the functional posterior, and the distal end to the functional anterior. The columns of plates are denoted "right" and "left" in a way that requires the fixed margin to be equated to "dorsal" and the free margin to "ventral".

Bengtson (1970, pp 387-388) in comparing machaeridians, especially turrilepadids, to mitrosagophorans regards machaeridians as having been vagile. In this reorientation (p. 388), the left and right columns of plates of Withers are reversed to right and left, and thus the distal end of the strobilus becomes functionally posterior and the proximal end anterior. The fixed edge remains functionally dorsal and the free edge ventral.

The orientation propounded by Bengtson is followed herein for convenience but for different reasons. If, as proposed, machaeridian strobili are a system of plates which covered the posterior spinous processes of mitrates then the proximal end of a strobilus is its most anterior part and the distal end is posterior. Evidence is not available to permit determination of the relationship of the columns of plates in the strobilus to the superior and inferior faces of mitrate thecae. It seems probable but by no means certain that the fixed margin of the strobilus was lateral relative to the theca and that the free margin of the strobilus faced medially, *i.e.,* toward the longitudinal axis of the theca. As these relationships are deductively determined, it is appropriate to maintain for convenience reference to the columns of plates as left and right and the margins of strobili as fixed (dorsal) and free (ventral) while recognizing that these terms may not be biologically accurate.

EVIDENCE FOR MITRATE RELATIONSHIP

The Machaeridia have been placed in various higher taxa by many authors. Withers (1926, pp. 76-84) reviewed in detail all systematic assignments of the group made up to the date of his publication and at the same time emphasized their echinodermal attributes. In summary, up to 1926 the group had been referred by authors to the polyplacophorans, cirripeds, annelids, trilobites (as appendages), and carpoids or "cystids" (as peduncles or posterior processes) or declared *incertae sedis.* Before 1926, the cirriped relationship was most commonly supported. Subsequent to 1926, Nichols (1962, p. 164) offered the only truly novel affinity, that "these structures are isolated tube-feet of their contemporaries, the ophiocistioids. In these, the tube-feet are abnormally large, and some are plated in a manner very similar to the plating of machaerids." This suggestion is worthy of consideration in the case of the turrilepadids where, in some, there is not convincing evidence of a fixed and free margin. Wolburg (1938) (*fide* Regnell, 1945, p. 49) believed they were mollusks, possibly close to the polyplacophorans or pelecypods. Regnell (1945, pp. 47-49) did not advance an opinion of the affinity of the machaeridians but did reject them from the echinoderms because he had not observed crystalline cleavage in their plates. Whitehouse (1941) related the carpoids and machaeridians in the homalozoan echinoderms. Termier and Termier (1953) compared them to the living plated annelids. Elias (1958) placed *Turrilepas* and *Clarkeolepis* in the Thoracica (cirripeds). Ubaghs (1967, pp. S5, S51-S52), in the *Treatise on Invertebrate Paleontology,* provisionally included the Machaeridia within the echinoderms, discussed them generally, but did not advance a personal opinion of their affinity. Moreover, no section in either Volume S (Echinodermata 1, Homalozoa-Crinozoa), Volume U (Echinodermata 3, Asterozoa-Echinozoa), or Volume W (Miscellanea) of the *Treatise* considers the Machaeridia in detail. Finally, Bengtson (1970) presented analysis of the Machaeridia while comparing them to his newly erected Order Mitrosagophora. He concluded that among living animals only the scale-bearing annelids have dorsal, paired, metameric sclerites resembling the machaeridians and mitrosagophorans.

Lepidocoleid plates from Boudinot Avenue and St. Marys, Indiana, clearly are holocrystalline as evidenced by their cleavage and crystalline reflection. It is unlikely that this is the result of recrystallization as other fossils from these deposits, except echinoderms, are not coarsely crystalline. Lepidocoleid plates, especially those from St. Marys, show iridescent diffraction colors, as do associated echinoderm pieces. Fragments of plates crushed in immersion oil and examined petrographically (up to ×400) showed faint, fine, irregular tubules but not large, regularly placed stroma canals. Among these fragments examined petrographically, the smaller showed complete extinction as the stage was rotated; the larger showed weak extinction. Lepidocoleid plates, thus, structurally resemble echinoderm remains.

Woodward (1871, p. 72, figs. 1-7; figures repeated 1880) first indicated the possible relationship of the lepidocoleids to the mitrates. In figure 6 of that page, he showed three views of a probable machaeridian. Ambiguous wording in his explanation of the figure leaves unresolved the exact origin of the specimen which was from the same locality as the mitrate theca he figured. Unfortunately, Woodward did not specify if the machaeridian had come from the same block as a mitrate theca or even if originally it had been attached to a theca. He did remark upon the similarity of sculpture of the machaeridian and the mitrate. Figure 7 of that page shows a posterior spinous process of a mitrate which in the explanation Woodward stated had been attached to a theca. Figure 7 shows a scale at the base of the spine which could be a machaeridian plate.

The occurrence of isolated, perfectly preserved machaeridian plates, especially *Lepidocoleus jamesi* (Hall and Whitfield), and mitrate plates in washes from shales of the Cincinnatian Series is not unusual, but the joint occurrence of thousands of mitrate plates and machaeridian strobili from Cincinnatian rocks has never before been found. The collections from Boudinot Avenue and St. Marys offer an opportunity to test the hypothetical amalgamation of the two groups. Clearly, lepidocoleids are not appendages of the anterior region or aulacophore of mitrates but they may be a system of plates ("cover plates" implies a homology I wish to avoid) that enveloped the posterior spines of these animals. The evidence for this is circumstantial as there are no known specimens of strobili fixed in an appropriate position to mitrate plates nor unquestionable machaeridian plates fixed to posterior spines. The populations of strobili and posterior spines (Pls. 1-3) do offer indirect evidence of the relationship but leave unresolved several objections to the hypothesis.

If the machaeridia are mitrate appendages, it follows that as mitrates are essentially bilateral and have superior and inferior surfaces, there should be asymmetrical features of the strobili which would permit division of their population into enantiomorphs (left-handed and right-handed forms).

Machaeridian scales tend to alternate in position along the fixed margin of the strobilus. As the distal direction along the strobilus can always be distinguished from the direction of overlap of the scales, strobili may be oriented to determine if the left or right column of plates is advanced. This presumes that plates most nearly opposite each other across the fixed margin are couplets. Of 39 strobili examined, 18 showed advancement of the left column and eight advancement of the right column. The 13 remaining specimens include individuals with damaged or covered fixed margins, or with plates so nearly perfectly opposite or alternate as to render the advanced column indistinguishable. The relative amount of offset of plates changes along the length of several specimens. It is evident, therefore, that some longitudinal slippage of the columns of plates could occur and that the columns of plates were neither articulated firmly together nor fixed firmly to any internal structure.

The cross-sectional shape of strobili, asymmetrically cordiform, provides evidence of enantiomorphism also (Pl. 3, figs. 2-13). Of 39 strobili, 26 were judged to be asymmetrical in cross-section and sufficiently free of distortion for analysis. The broken ends of these strobili were examined for evidence of asymmetry. Of these, 13 show enlargement of the left column of plates adjacent to the fixed margin and 13 show enlargement of the right column of plates. Of the 13 showing enlargement of the left column adjacent to the fixed margin, 11 show overlap of the left column by the right along the free margin. Of the 13 showing enlargement of the right column adjacent to the fixed margin, eight show overlap of the right column by the left along the free margin (compare a and b, Text-fig. 1). Several specimens are so symmetrical that the dominant column cannot be determined. In no strobilus does the dominant column change sides along its length. The position of fracture across the strobilus, whether toward the distal or proximal edges of plates, does not seem to control the apparent dominance of the column. The cross-sectional asymmetry thus may be better evidence of enantiomorphism than is the advancement of the columns of plates.

TABLE 1. Strobili containing internal rods

UCGM Number, Plate, figure	Length, mm	Number of plates	Remarks
42701 2; 9	14.6	about 15	Rod exposed, proximal end; distal end damaged
42709 2; 10-11 3; 2-3	6.0	8	Rod exposed, proximal end; distal end weathered
42710 2; 8 3; 4-6	6.6	8	Rod exposed, both ends
42712 2; 14 3; 7-8	4.8	6	Rod exposed, both ends
42715 2; 2	6.8	12	Rod exposed, distal end; possibly proximal end, proximal end crushed
42734 2; 16 3; 10-12	6.1	8	Rod exposed, distal end, stained, possibly at proximal end, weathered

The broken terminations of six strobili, Table 1, show the broken ends of crystalline calcite rods which longitudinally traverse the internal cavity of the specimens (Pl. 3, figs. 2-8, 11-12). These rods are coarsely crystalline, milky calcite that commonly are outlined by staining. They resemble in cross-sectional shape and color the broken ends of posterior spinous processes. The rods are not translucent pseudospar as commonly fills other fossils from Cincinnatian rocks. Neither the rods nor the posterior spinous processes of mitrates are holocrystalline calcite.

The posterior spinous processes of *Enoploura* (Pl. 1, figs. 2-9), in length, diameter, curvature, and cross-sectional shape, would fit compatibly into any of these strobili. The spines range in length from 7.4 mm (UCGM 42744) to 14.8 mm (UCGM 42743), whereas the longest, and possibly only complete strobilus in the population is 20.4 mm long (UCGM 42750). (Most of the broken strobili in these collections have diameters larger than UCGM 42750, thus probably were initially longer than 20 mm.) The spines are straight throughout most of their length except at the base (proximal end) which is slightly curved in a manner resembling the bent proximal ends of strobili. The spines are flattened or ovoid in cross-sectional shape. The proximal curvature lies in the plane which includes the major axis of the oval, just as it does in strobili (compare Pl. 1, fig. 4; Pl. 3, fig. 17). The posterior spines vary greatly in cross-sectional shape, from flat (Pl. 1, fig. 2) to almost terete (Pl. 1, fig. 7) as do the strobili. The posterior spines are not strikingly enantiomorphic except in the position and marginal rim of the ball-joint at the proximal end and the short longitudinal ridge along the concave edge of a spine at its proximal end (Pl. 1, figs. 2-3). If machaeridians are mitrate appendages, it is likely that their enantiomorphism would be obscure.

Several spines show faint, serial, transverse to diagonal constrictions along their lateral surfaces (UCGM 42742, 42744, 42746, 42749) and faint scallops along their convex edges (UCGM 42743, 42744, 42747) when viewed in bright light directed parallel to their length. These marks may be related to some structures which originally covered the spine, muscle attachments, organs or the plates of strobili. Some spines (UCGM 42745, 42746) also show faint longitudinal grooves along their concave edges which also might evidence some enclosing structure. The concave edge also is commonly darkly stained and smoother than the rest of the surface of the spine (Pl. 1, figs. 6, 8) which may evidence some adhering structure. Much of the surface of some spines has a hackly or hispid texture (Pl. 1, fig. 7) which would not have been likely to have survived abrasion if present on the exposed surface of the living animal.

The plates and strobili of *Lepidocoleus strictus* from St. Marys, Indiana, have the same surface texture, reflectance and color as the associated mitrate plates. Glittering reflections from the surfaces of these fossils are not observed on other fossils, as trilobites and brachiopods, from the locality. Similarly, the machaeridian and mitrate remains from Boudinot Avenue have the same surface appearance. Except for occasional cleavage reflections, they have the same color and surface texture as other fossils from the deposit.

Finally, there is no substantial inconsistency in the stratigraphic ranges of the lepidocoleids, Middle Ordovician to Middle Devonian, and the anomalocystitid mitrates, Middle Ordovician to Lower Devonian, considering that good specimens of both groups are so unusual.

Several objections that are not easily explained may be offered to uniting the lepidocoleids and the mitrates. The most serious is simply that of the many anomalocystitid mitrate specimens known, none bear posterior strobili. Apparently the posterior spinous process was not strongly fixed to the theca as evidenced by the many specimens of thecae which lack spines. Moreover, if strobili did enclose spines, it is likely, as has been implied, that they were united only by soft tissue and thus subject to disassociation. The posterior appendages may have been capable of reflexive detachment as in the case of the arms of some living crinoids and ophiuroids.

Bengtson (1970, p. 386) questioned "why lepidocoleid plates are often found in sediments devoid of any plates that could be regarded as representing the rest of the carpoid skeleton". In the case of the Upper Ordovician rock of the Cincinnati Province, this objection is not warranted. Disassociated carpoid thecal plates exist in a sediment-size grade that is not commonly searched for microfossils as ostracods, conodonts, and scolecodonts, yet which is generally smaller than most of the macrofossils. Additionally, the irregularly polygonal outline of carpoid plates is not likely to attract attention. On the other hand, lepidocoleid plates occur in sediments searched for microfossils and their distinctive ornament, especially that of *Lepidocoleus jamesi,* makes them visible. It is doubtful that our information regarding the abundance of either group is adequate to substantiate Bengtson's objection. The fact is, they do occur together in large numbers at the Boudinot Avenue and St. Marys localities.

Not all strobili contain internal rods of calcite, interpreted herein as posterior spines. It is likely, as previously noted, that the spines and strobili were not firmly united but held together by flesh. The two structures may have been easily disassociated. In particular, spines would not be visible in strobili broken near their distal end as the spines are not as long as the strobili.

Strobili enclosing the posterior spines of mitrates have no known function nor is there a precedent for such a structure elsewhere in the Echinodermata. The fact is, there is little precedent elsewhere in the Echinodermata for the entire carpoid animal, much less individual structures of carpoids. The structure of the entire posterior edge of mitrate thecae is obscure. The function of the posterior spines is not known although functions have been proposed and others may be imagined. Addition of a strobilus around each posterior spine does not conflict with what is known of mitrate morphology or way of life. The proposed addition of a strobilus, especially one curved with the free margin along the outside (convex) edge, does require mental reconstruction of a most curious appearing mitrate.

The strobili of *Lepidocoleus strictus* Withers from the Boudinot Avenue and St. Marys localities are varied in form. The variation seems to be great enough to possibly encompass several of the species of *Lepidocoleus* described by Withers. Eventually, when all species of the Lepidocoleidae are restudied in detail, even if the family is not subsumed into the Mitrata, several of the species will undoubtedly become synonyms. The affinity of the turrilepadid machaeridians cannot be determined at this time. Their relationship to the lepidocoleids is not positively established.

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EXPLANATION OF PLATE 1

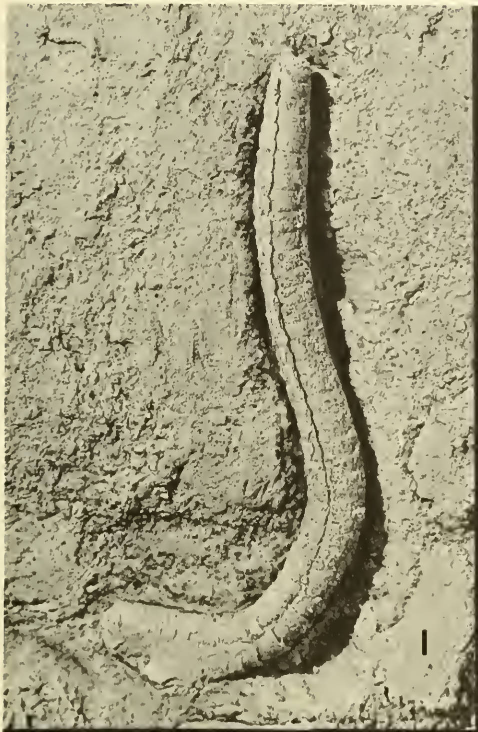
Figure

1. **Lepidocoleus strictus** Withers

   Complete specimen. Conventional orientation, distal end up. Whitened with ammonium chloride. Richmond Group, Waynesville Fm., Boudinot Ave., Cincinnati, Ohio. UCGM No. 42750, × 5.

2-9. **Enoploura** sp.

   Posterior spinous processes of mitrate carpoid. Oriented with proximal end up. All specimens whitened with ammonium chloride except 6 and 8. Figure 6 and 8 not whitened in order to show dark stain along outer edge of spine. All specimens figured × 5 except 6 and 8, × 7. Richmond Group, Waynesville Fm., Boudinot Ave., Cincinnati, Ohio. All specimens in UCGM: 2, No. 42742; 3, No. 42744; 4, No. 42746; 5-6, No. 42745; 7, No. 42743; 8-9, No. 42747.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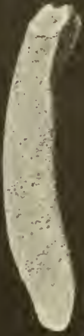
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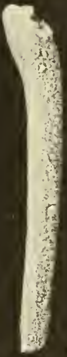
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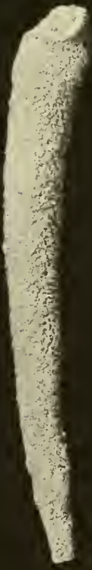
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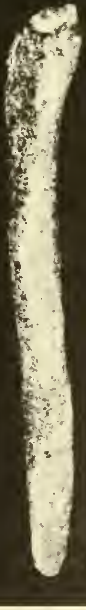
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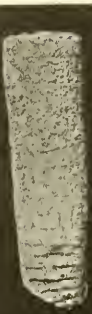
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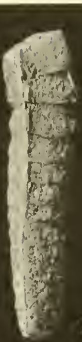
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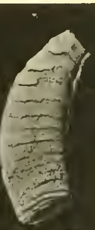
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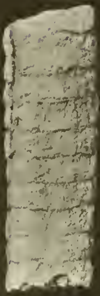
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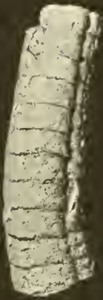
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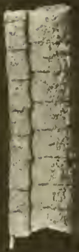
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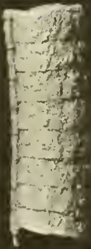
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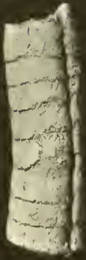
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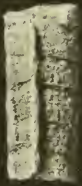
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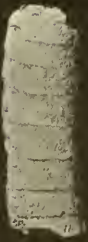
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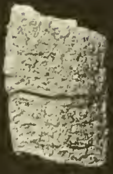
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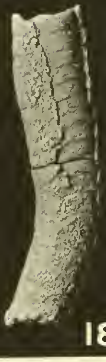
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EXPLANATION OF PLATE 2

Figure

1-5. **Lepidocoleus strictus** Withers

Distal ends of strobili. Oriented with distal end down. Whitened with ammonium chloride. All specimens figured × 5. Richmond Group, Waynesville Fm. 1-4. Boudinot Ave., Cincinnati, Ohio. 5. St. Marys, Ind. All specimens in UCGM: 1, No. 42705; 2, No. 42715; 3, No. 42728; 4, No. 42729; 5, No. 42752.

6-18. **Lepidocoleus strictus** Withers

Sections from middle of strobili. 6, 8, 11, 15-18. Side views. 7, 9, 10, 12-13. Fixed margins. 14. Free margin. Oriented with distal end down. Whitened with ammonium chloride. All specimens figured × 5. Richmond Group, Waynesville Fm. 6-17. Boudinot Ave., Cincinnati, Ohio. 18. St. Marys, Ind. All specimens in UCGM: 6, No. 42706; 7, No. 42708; 8, No. 42710; 9, No. 42701; 10-11, No. 42709; 12-13, No. 42711; 14, No. 42712; 15, No. 42722; 16, No. 42734; 17, No. 42725; 18, No. 42751.

Explanation of Plate 3

Figure

1. **Lepidocoleus jamesi** (Hall and Whitfield)

Lateral view of two joined plates. Oriented with distal end down. Whitened with ammonium chloride. Richmond Group, Waynesville Fm., Boudinot Ave., Cincinnati, Ohio. UCGM No. 42741, × 7.

2-13. **Lepidocoleus strictus** Withers

Broken ends of strobili. Whitened with ammonium chloride except figures 3, 4, 6, 8 and 12, not whitened to show filling and dark rods or staining within strobili. All figures × 7. Richmond Group, Waynesville Fm., Boudinot Ave., Cincinnati, Ohio. All specimens in UCGM. 2-3. Proximal end, No. 42709. 4. Proximal end. 5-6. Distal end, No. 42710. 7. Distal end. 8. Proximal end, No. 42712. 9. Proximal end, No. 42725. 10. Proximal end. 11-12. Distal end, No. 42734. 13. Distal end, No. 42730

14-15. **Lepidocoleus strictus** Withers

Internal surfaces of broken strobili. At least four plates overlap in each specimen. No muscle pits are visible. Oriented with distal end down. Whitened with ammonium chloride. Both figures × 7. Richmond Group, Waynesville Fm., St. Marys, Ind. 14. UCGM No. 42740. 15. UCGM No. 42739.

16-20. **Lepidocoleus strictus** Withers

Proximal ends of strobili. Oriented with proximal end up. Whitened with ammonium chloride. All specimens figured × 5. Richmond Group, Waynesville Fm. 16-18, 20. Boudinot Ave., Cincinnati, Ohio. 19. St. Marys, Ind. All specimens in UCGM. 16. No. 42737. 17. No. 42724. 18. Proximal end exfoliated, No. 42707. 19. Specimen crushed, No. 42753. 20. Exfoliated largely internal mold, dark staining on filling, No 42702.


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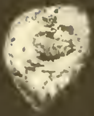
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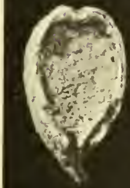
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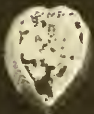
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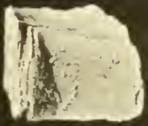
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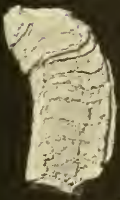
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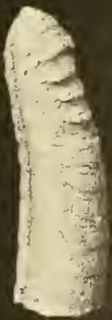
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THE GENUS *PLUMALINA* HALL, 1858 (COELENTERATA) — RE-EXAMINED

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ABSTRACT

Upper Devonian strata in western Steuben County, New York State, have yielded new fossil material of the genus *Plumalina,* provisionally assigned herein to the species *P. densa* Hall, 1878. The specimens occur with the sponge *Clathrospongia ? sp.* in a thin sandstone bed virtually devoid of other fauna. The occurrence of macroscopic surface features, referred to as papillae, are reported from specimens of *P. plumaria* Hall and *P. densa* Hall. The papillae are suggested to be poorly preserved polyp bases. The history of *Plumalina* is reviewed and its possible affinities explored.

ACKNOWLEDGMENTS

The authors are grateful to John W. Wells for his wise counsel and the loan of specimens from his collections. Robert Conrad of the New York State Museum and Science Service kindly prepared latex molds of the types and sent both the molds and the specimens to Alfred for examination and comparison with material collected in Steuben County. Paul A. Gignac of The State University of New York, College of Ceramics, at Alfred, provided the photographs for Plates 2 and 3. Joanne Reinauer typed the manuscript and provided helpful criticism. The Alfred University Research Foundation generously provided funds for travel and specimen exchange. The senior author recalls with fondness the knowledge and discipline imparted by K. E. Caster of the University of Cincinnati to whom both this work and volume are dedicated.

PREVIOUS HISTORY OF THE GENUS

Bayer (1956, p. F212) commented that the genus *Plumalina* Hall, 1858 has been assigned to the family Gorgoniidae Lamouroux (Alcyonaria) by some authors but probably belongs to the Hydrozoa. Hill and Wells (1956, p. F81), in the same volume, considered the genus as being of uncertain systematic position within the Hydroida. Uncertainty as to the taxonomic assignment of *Plumalina* is understandable if one follows the changes which have taken place in establishing the relationships of this perplexing genus over more than a century.

Without attempting to assign a name to the specimen, Vanuxem (1842, p. 175, fig. 41) illustrated and discussed a fossil from the

Middle Devonian "Ithaca Group" which, although looking like a fern, he speculated might be intermediate between the crinoids and the corals. Hall (1843, p. 273, fig. 125) figured and discussed a similar specimen from the same sequence and was unable to decide as to its affinities. Shumard (1855, p. 208, Pl. A, fig. 11) described a specimen from the Devono-Mississippian (?) Louisiana Limestone which he compared favorably with the fossil described by Hall. He named the fossil *Filicites gracilis* — apparently deciding that it was a fern. Three years later Hall (1858, pp. 175, 176) provisionally established the genus *Plumalina* assigning the specimen figured in 1843 to *Plumalina plumaria,* the type for the proposed genus, and renamed Shumard's specimen *P. gracilis;* he did not differentiate between the two species and considered them to be graptolites.

In 1862 Dawson (p. 314, pl. 17, fig. 57) erected the species *Lycopodites vanuxemii* which he considered a plant and for which he cited the illustrations of Vanuxem (1842) and Hall (1843). He was apparently unaware of or dissatisfied with Hall's designation of *Plumalina plumaria.* S. A. Miller (1877, pp. 31, 54, 59) questionably placed *Filicites gracilis* Shumard, 1855 in synonymy with *Plumalina plumaria* Hall, 1858 in the class Polypi, order Alcyonaria, family Graptolitida and listed *Lycopodites vanuxemi* Dawson, 1862 separately as a plant.

Hall (1878, pp. 255-256, pl. 4, figs. 1-5) reviewed the issue noting that he had proposed the generic name *Plumalina* in 1858 for the forms called *Filicites* and *Lycopodites* by other authors. He recognized Shumard's *Filicites gracilis* as a species of *Plumalina* and asserted that he could identify at least six species. After promising to illustrate them in a future report he established an additional species — *P. densa* (1878, pl. 4, fig. 6). *Plumalina densa* was differentiated from *P. plumaria* by virtue of its less rigid rachis and pinnules which were described as being longer and more crowded. The type was recorded as obtained from the Hamilton Group (Middle Devonian) without the designation of a specific locality.

Williams (1884, p. 13) made a note of the "famous *Lycopodites* beds of Professor Hall . . . where great numbers of *L. Vanuxemi* in very perfect condition occur." The reference was to the area around Ithaca, New York, but no attempt was made to assign the fossils to a particular higher taxon. In a subsequent publication (Williams, *et al.*, 1909, p. 62) he did refer to *Plumalina plumaria* Hall and used the fossil, along with *Lingula complanatum* Williams to define the base of the Ithaca Shale. Harris (1899, p. 22, pl. 8, fig. 62) noted the occurrence of *P. plumaria* in the middle to lower Portage Formation (Upper Devonian) and related it to the Hydrozoa noting that it had been regarded as a fern. *P. densa* is listed as a diagnostic species for the Canadaway Group (Upper Devonian) by Chadwick (1935, p. 324). He suggested that this was the last appearance of the genus in the New York section but did not assign it to a particular formation or horizon.

Ruedemann (1916, pp. 10-12) reviewed the literature with respect to *Plumalina plumaria* Hall and cited Hall's 1878 description of the characteristics of the genus. He suggested that the genus compared favorably with the Gorgoniidae and could be assigned to the order Alcyonaria. More recently Glinski (1956) assigned the species *Plumalina conservata* from the Middle Devonian of the Eifel to the Gorgonaria.

The characteristics of the genus were described by Hall (1878, p. 255) as follows:

> In all the species observed, the usual form is that of a simple frond or hydrocaulus, with narrow, linear pinnulae diverging from each side, essentially in the same plane, and more or less ascending. Rare examples are bifurcating or otherwise branching, and the specimen shown on plate 4, fig. 1, is the most remarkable example of this kind observed. Although usually occurring singly, it is evident from the figure given in the Report of the Fourth Geological District, as well as from other specimens known, that they may grow in tufts. No evidence of fertile cells or hydrothecae has been seen, and no distinct serration of the pinnulae can be made out in the specimens examined. From certain appearances upon some specimens, I infer that the pinnulae were cylindrical, and probably tubular, their present appearance being due to extreme compression.

Plumalina densa Hall, 1878 Pl. 2, figs. 1, 3; Pl. 3, figs. 2, 3

1878. *Plumalina densa* Hall, 30th Ann. Rept., New York State Museum of Natural History, p. 255, pl. 4, fig. 6.
1935. *Plumalina densa* Hall, Chadwick, Geol. Soc. America, Bull., vol. 46, pp. 324, 326.

Description. — The type specimen (NYSM No. 301) shows no evidence of the preservation of either the distal or proximal extremities. (Pl. 3, fig. 2) The rachis is flexed, 14 cm long, averages 1 mm in width, and shows no evidence of bifurcation. The margins of the "frond" are indistinct with the maximum width approximately

35 mm. The pinnae were apparently rounded prior to burial and average 20 mm in length. They form an axillary angle of 50° with the rachis, and average 30 oppositely attached per cm of rachis. The pinnae are not constricted at the point of juncture with the rachis.

When the specimen was coated with ammonium chloride and illuminated with low angle oblique lighting, some pinnae (Pl. 3, figs. 2, 3) revealed heretofore undetected macroscopic surface features. They may be described as linear sequences of papillae, in some cases giving a slight moniliform appearance to the pinnae. In certain of the papillae, a central pore may be discerned (Pl. 3, fig. 3) and the entire structure (papilla plus central pore) could be interpreted as a polyp base. Other discernable surface features include irregular prominences attached to the rachis and pinnae — some of which have been identified as embryonic brachiopods.

Another figured specimen (Pl. 2, fig. 3) matches the general characteristics ascribed above to the type of *P. densa.* Specimens collected from a single site in western Steuben County, New York, (to be discussed below) also conform to the general description of *P. densa* and have, therefore, been provisionally identified as belonging to that species. The Steuben County material (Pl. 2, fig. 1) is more coarsely preserved than material from elsewhere and has vestiges of carbonized organic material along the rachis.

Discussion of species. — The description of *Plumalina densa* is, out of necessity, based upon external morphology. Hall (1878) emphasized its flexible rachis and narrow and crowded pinnules as salient characteristics differentiating this species from others. The writers have considered additional characteristics and find that the differences between *P. densa* and other species warrant its separation from them.

The type of *Plumalina plumaria* (Pl. 3, fig. 1) shows a less flexible rachis than *P. densa;* one which is distinct, measures 1 mm thickness and bifurcates (as Hall indicated). The margins of the main axis of the "frond" are relatively distinct with the maximum width approximately 20 mm. The pinnae approximate 10 mm in length; they form an axillary angle of 70° with the rachis and average 20 oppositely attached per cm of rachis. The pinnae are constricted at the point of juncture with the rachis. The second figured specimen of *P. plumaria* (Pl. 2, fig. 2), among others examined, also conforms to the general characteristics of the type.

A third species *Plumalina conservata* Glinski (1956, pl. 1, figs. 1, 2) differs markedly from the two species described above. The rachis is 1.5-1.6 mm wide, the "frond" 30 mm from edge to edge. The pinnae are 15 mm long with a special separation of 0.1 to 0.2 mm between adjacent pairs. The pinnae are constricted at the point of attachment to the rachis. Glinski stated that the axillary angle approximates 65-75°.

From the above it is apparent that the differentiation of at least three separate species is warranted. The most important criteria appear to be: (1) the nature of the rachis, (2) the length of the pinnae and the number of them attached to the rachis per cm, and (3) the axillary angle formed by the junction of the pinnae with the rachis.

Type. — Holotype, NYSM No. 301, collected by James Hall, "from the shales of the Hamilton group". However, the label with the specimen gives the "Chemung beds" (?) at Belvidere, Allegany County, New York, as the horizon and locality of *Plumalina densa*. This specimen was figured by Hall, 1878, plate 4, figure 6.

Material. —

Figured Specimens and Localities

	Type	Locality
New York State Museum (NYSM)		
301 *P. densa*	Holotype	Chemung beds ?, Belvidere, N.Y.
302 *P. plumaria*	Holotype (mold)	Ithaca beds, Ithaca, N.Y.
United States National Museum (USNM)		
208867 *P. plumaria*	Topotype	Renwick Sh., West Hill, Ithaca, N.Y. (H.S. Williams locality XIVg)
208868 *P. densa* (?)	Homeotype	Renwick Sh., Cascadilla Creek, Ithaca, N.Y.
Alfred University (AU)		
5 *P. densa*	Homeotype	New York State Route 21, Erie-Lackawanna RR cut — opposite the Almond Dam, Steuben County, N.Y.

In addition to the above the writers had access to 12 specimens of *P. plumaria* and *P. densa* from the collection of Cornell University, through the courtesy of J. W. Wells, two of which were donated to the United States National Museum. Six of the specimens were collected before 1875 by C. F. Hartt from the Ithaca Formation (Renwick Sh.), Cascadilla Creek, Ithaca, New York. The remaining six were collected in the 1880's by H. S. Williams at his locality XIVg; Ithaca Formation (Renwick Sh.), West Hill, Ithaca, New York. One specimen *P. plumaria,* C. H. Hartt Coll., Cascadilla Creek, Ithaca, N.Y., Renwick Shale, is deposited in the Paleontological Research Institution, No. 29593.

An additional 12 specimens of *P. densa* at Alfred University were collected from an outcrop in western Steuben County, New York. The location and geologic setting is described below.

Occurrence of specimens. — Except for the Alfred specimens, the location of both figured and additionally studied material was taken from the best data available on the accompanying labels.

All the Alfred University specimens were collected from talus at the base of a 6 meter sandstone and sandy shale sequence between elevations 1320 and 1340′ AT east of the Almond Dam off New York Route 21 along the Erie-Lackawanna Railroad right-of-way; Hornell Quadrangle, New York, 7.5 Minute Series (topographic), the outcrop has coordinates of Lat. 42° 20′ 45″ N X Long. 70° 42′ 30″ W. The specimens collected at this locality (Pl. 1, figs. 1, 2) occur in one or more layers of a medium to fine-grained gray, micaceous sandstone in an alternating sequence of sandstones and shales. The specific horizon has not been located at this writing. One specimen collected by D. B. Sass at the above locality is deposited in the Paleontological Research Institution, No. 29594.

Impressions of the reticulum of *Clathrospongia* ? sp. are frequently found adjacent to those of *Plumalina densa* (Pl. 2, fig. 1); this relationship has not been reported previously. Few other fossils were noted in the blocks containing these taxa.

Geologic age. — The genus *Plumalina* seems to first appear in rocks of Middle Devonian (Hamilton) age in both North America and Europe. This impression is affirmed for the former by J. W. Wells (1974, personal communication) and the latter by the publication of Glinski (1956). The upper limit of the range of the genus may have been indicated by Schumard (1855) who described a specimen from the Louisiana (Devono-Mississippian?) limestone.

P. densa has been collected 6′ below the Tully Limestone in the Windom Shale (*fide* J. W. Wells, 1974, personal communication). The species' upper limit has yet to be established. Chadwick (1935, p. 326) cited *P. densa* as a diagnostic species of the Canadaway Group and noted that this marks its last appearance. Following Cooper, *et al.*, (1942) the New York State Route 21 outcrop would be Famennian (uppermost Devonian). Pepper's map (1954) shows this outcrop in the Canaseraga Sandstone-Caneadea Shale sequence within the Famennian. More recent investigations of the stratigraphy in Allegany County and Steuben County, New York, make exact stratigraphic placement of the exposure less certain. L. V. Rickard (1974, personal communication) placed the sequence provisionally in the Hanover Shale of the Java Group which is Frasnian (lower-Upper Devonian) in age. R. G. Sutton (1974, personal communication) believed the outcrop in question to be, "100′ above the base of the Pipe Creek Shale and stratigraphically near the Canaseraga Sandstone". If so, the stratigraphic position would be Famennian (uppermost Devonian). The matter will have to remain unresolved pending the completion of their work and its publication.

SYSTEMATIC POSITION OF PLUMALINA

Discussion. — As previously stated, little agreement has been reached concerning the systematic placement of the fossil genus *Plumalina* Hall. Vanuxem (1842) felt that the specimen was not that of a plant or crinoid because of the regularity and rigidness of the lateral appendages. *Filicites gracilis* Shumard (1855) was the only species of the genus (*Filicites*) not transferred to valid plant genera such as *Cyclopteris, Alethopteris,* and *Pecopteris* (*Filicites crispa* was transferred to the genus *Cyclopteris* as *C. crispa; F. lonchiticus* and *F. pluckeneti* were transferred to the genus *Alethopteris* as *A. lonchiticus* and *A. pluckeneti;* and *F. pennaeformis* was transferred to the genus *Pecopteris* as *P. pennaeformis* [Miller, 1877]). Hall's (1843, p. 273) tentative assignment to *Filicites* (?) was accompanied by the statement that the uniformity of both size and axillary angle of the lateral appendages along the central stem, in addition to the lack of carbonaceous material, indicated stronger affinities with crinoids or ". . . perhaps more analogous to the *Sertularia*" (an extant genus of colonial hydroids; class Hydrozoa, order Hydroida [nomenclature follows Hyman, 1940]). Later, Hall (1858) considered the genus as a member of the Graptolideae. Dawson's *Lycopodites vanuxemii* (1862), founded on Hall's *Filicites* (?) and Shumard's *F. gracilis,* was the only unqualified assignment of the fossil to the plant kingdom. Hall's establishment of *Plumalina densa* in 1878 was accompanied by placement of the genus in the family Plumularidae (class Hydrozoa, order Hydroida). Ruedemann (1916) considered *Plumalina* as an alcyonarian (class Anthozoa; Coelenterata) likely to be placed in the family Gorgoniidae. Glinski (1956) placed specimens of *P. conservata* Glinski in the Gorgonaria.

Plumalina as a plant. — We began our investigation thinking that the specimens found at the New York Rt. 21 outcrop might be those of a plant. At first sight, the appearance is that of a plant — that of a large, simple, pinnately veined leaf rather than that of a fern frond. On the other hand, the lack of a distinct margin, the densely packed condition of the supposed secondary or lateral veins, and the improbable occurrence of such a megaphyllous form in Upper Devonian strata, suggest that *Plumalina* is not a plant. Dawson's (1862) assignment of *Plumalina* to *Lycopodites* (the generic name assigned to *Lycopodium*-like or *Selaginella*-like fossils known to be homosporous; or to vegetative *Lycopodium*-like stems [Arnold, 1947]) is curious, because the general resemblance of *Plumalina* to modern species of *Lycopodium* is not obvious.

If the assumption is made that the lateral appendages seen in the fossil are simply lateral veins derived from the midvein of a simple blade (lamina) or a large pinna, then the rigidness and regularity of these structures is not a sound basis for negating the placement of *Plumalina* in the plant kingdom. Such a complex venation pattern is cause to consider such a "leaf" as a megaphyll (Foster and Gifford, 1959), a degree of complexity not common in Upper Devonian plants. Such laminar leaves did occur by Frasnian time (Banks, 1970) in the widely distributed genus *Archaeopteris* (the form-genus of leaves of the progymnosperm *Callixylon*) but the small, wedge-shaped pinnules of the plant bear little resemblance to the leaflike structure of *Plumalina.* Other contemporary plant genera (*Rhacophyton, Eospermatopteris,* and *Tetraxylopteris* for example) bore either three dimensional or planated telomes (the phylloids of Zimmermann) devoid of webbing which were simply the ultimate divisions of the aerial branching system (*i.e.* no development of a lamina or blade).

If the lateral appendages are viewed as individual pinnae or pinnules, or as separate microphylls similar to those seen in modern *Lycopodium* spp., then the rigidness and regularity seen in *Plumalina* causes one to question its plantlike nature. In addition, the pattern of branching seen in some of the specimens is apparently random and uncharacteristic of the plant kingdom. In short, the complex leaflike structure seen in *Plumalina* is simply that: leaflike, and not a structure that is in any way homologous to the photosynthetic organs of the known Upper Devonian flora.

Fossil specimens, containing some carbonized portions of the rachis, collected along Route NY 21 were bulk macerated in HF and HCL, and the remaining residue cleared in 5% sodium hypochlorite (Chlorox) and concentrated nitric acid containing approximately 5% potassium hydroxide. The latter treatment was followed by a dilute sodium hydroxide wash. Both the maceration and the clearing processes were closely monitored in an attempt to prevent total destruction of the residue. Such treatment failed to yield any recognizable plant features such as cuticular fragments, tracheary elements, or spores. This seems to indicate that the carbonized material was not that of a plant. Due to the paucity of material, no attempt could be made to analyze the chemical nature of the isolated residue. Because proteinaceous material may be reduced to a tarlike residue (Andrews, 1961), the lack of structure seen in the New York Rt. 21 fossil residue may indicate the animal nature of the specimen. What may be stated, with some certainty, is that the residue does not contain any plant material. It is interesting to note that apparently similar carbonized material ("Das schwarze Objekt. . . ") occurs on both rachis and lateral appendages of specimens of *Plumalina conservata* (Glinski, 1956; p. 53). Such material is interpreted by Glinski as possibly the remains of a chitinous endoskeleton of a Gorgonarian.

Plumalina as an animal.—We appreciate Ruedemann's (1916) consideration of *Plumalina* as an early representative of the anthozoan subclass Alcyonaria. Of the known colonial coelenterates, only some members of the class Hydrozoa and the class Anthozoa bear a resemblance to the fossils of *Plumalina*. Of the extant marine hydrozoans, members of the order Hydroida, suborder Leptomedusae (notably the genus *Plumalaria*), most closely resemble the fossil forms.

Ruedemann's statement (1916, p. 11) that ". . . the absence of any distinct thecae or cells forbids placing it with the graptolites or with the sertularians or plumularians . . ." (order Hydroida) is perhaps questionable in light of the papillae (occurring on some specimens of *Plumalina plumaria* and *P. densa*) encountered during the course of the present investigation. These surface features are not constant, but study of both coated and uncoated specimens under low magnification shows the existence of such papillae. The repeated occurrence of papillae on several specimens indicate that such structures are primary. The nearly total lack of distinct detail is not surprising considering the poor state of preservation of all of the specimens.

If the specimens are those of a fossil hydroid, then the axial and lateral structures would consist of a hollow hydrocaulus, consisting of a common and continuous central coelenteronic coenosarc covered by a chitinous tubular perisarc. Each hydranth would secrete a chitinous cup or hydrotheca around itself. The hydrothecae may be tubular and elongate, in which case, such a hydrotheca could correspond to a single lateral pinna on the fossil forms. In the extant Sertulariidae and Plumulariidae, however, the hydrothecae are sessile and a number of them are fused along one surface of the periderm of the lateral branches (pinnae) of the hydrocaulus (Hyman, 1940). Such an arrangement could give the appearance of the papillae seen on the fossil specimens.

If, on the other hand, the specimens are fossil alcyonarians of the families Primnoidae or Gorgoniidae, the central stem and lateral appendages would likely be composed of a solid central horny proteinaceous axis covered by a calcified, spiculated polypiferous coenenchyme. The difference between the two families, in terms of extant members, deals largely with the thickness of the coenenchyme and thus the delicateness of the entire structure. (The Gorgoniidae have slender stems with thin coenenchyme, while the Primnoidae possess a thicker, stiffer, more heavily calcified axis with more prominent polyp bases or verrucae.)

Ruedemann (1916) suggested that both rachis and pinnae of certain fossil forms of *Plumalina plumaria* possess an inner carbonaceous axis covered by an outer "granular rind" which is only rarely preserved. He considered such carbonized material as representing a residual central axis of a horny or chitinoid nature. The granular rind was interpreted by Ruedemann as being a calcareous or chitinous skeleton encasing the central horny axis, both structures surrounded by a polypiferous coenenchyme which is not preserved in the fossils. After study of the portion of the pinnae possessing the granular rind, we consider its carbonaceous nature an indication that it represents an originally proteinaceous substance.

Surface features similar in appearance to this granular rind are seen in a photograph of *Rangea arborea* (Glaessner and Daily, 1959; pl. XLIII, fig. 2), considered to be a member of the alcyonarian order Pennatulacea. Glaessner and Daily did not mention or describe these surface features. The features do not appear to be carbonaceous in nature.

The maceration data cited previously do seem to suggest that the small amount of carbonized material associated with the main axis of the New York Rt. 21 fossils possibly are proteinaceous in nature. If, as Ruedemann suggested, this is only the central skeletal axis, and that the polypiferous sarcode (coenenchyme) is not preserved, then the structure is similar to that of a number of the soft corals, especially members of the order Gorgonacea. This order, which includes such extant members as the sea whips, sea feathers, and the sea fans, differs from the order Alcyonacea in that the gorgonians possess an axial skeleton composed of the protein gorgonin. The data of Glinski (1956) cited previously support this interpretation.

If the papillae are interpreted as poorly preserved polyp bases (either hydrothecae or verrucae), and the carbonized material associated with the rachis is proteinaceous in nature, then the genus *Plumalina* should be placed in the subclass Alcyonaria. If, on the other hand, the carbonized material represents a chitinous rind or perisarc, *Plumalina* should be placed in the order Hydroida. Unfortunately, the paucity of the residue greatly limits more precise determination of its true nature. If the papillae are casts of calcified verrucae from which leaching has removed the carbonate material, the alcyonarian placement would be appropriate. The fact that the small brachiopods noted by Ruedemann and seen on several of the specimens studied by us occur only as casts on the rachis would make this interpretation seem reasonable.

In terms of relative flexibility of structure, the hydrocauli of the hydroids would be more flexible than the stalks and branches of the alcyonarians. The rigidity seen i nthe fossils (*i.e.* the constancy of axillary angles and the total absence of bent pinnae) would tend to favor placement in the Alcyonaria.

Since the paper was submitted for publication, the authors have received a specimen of *Aglaophenia* ? collected in the waters off the Galapagos Islands by Dr. John Wells of Ithaca. Initial studies of the specimen indicate that the possible affinity of *Plumalina* with the hydroids should receive serious consideration.

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EXPLANATION OF PLATE 1

Figure

1. An overview of the Steuben County outcrop opposite the Almond Dam along New York Route 21, looking North. The bedrock exposure occurs to the East along the RR. The arrow points to the approximate location of the collection site.
2. Closeup of the alternating sandstones and sandy shales indicated by the arrow in figure 1 above. The specimens of *Plumalina* were collected in the talus at the base of the outcrop. The exposed inplace bedrock approximates 6 meters in thickness.

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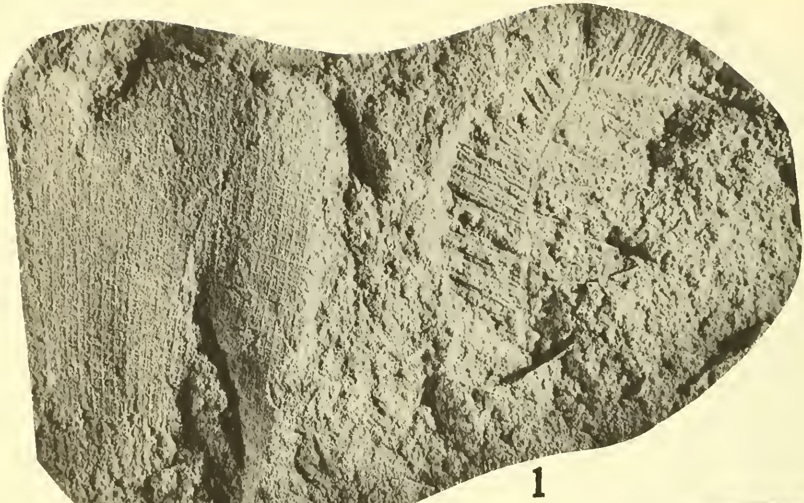

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EXPLANATION OF PLATE 2

Figure

1. **Plumalina densa** Hall, 1878

   Specimen from the outcrop opposite the Almond Dam. Natural casts of a specimen of *P. densa* to the right with *Clathrospongia* ? sp. to the left. The association is common at this outcrop. AU No. 5. Enlargement, × .987.

2. **Plumalina plumaria** Hall, 1858

   Specimen from the Renwick Shale, West Hill, Ithaca, New York. Natural casts of two overlapping specimens clearly showing the habit of the rachis and pinnae. USNM No. 208867. Enlargement, × 1.615.

3. **Plumalina densa** Hall, 1878

   Specimen from the Renwick Shale, Cascadilla Creek, Ithaca, New York. Natural cast of a single specimen showing the crowding of the pinnae which Hall used to separate this species from *P. plumaria*. USNM No. 208868. Enlargement, × 1.615.

Explanation of Plate 3

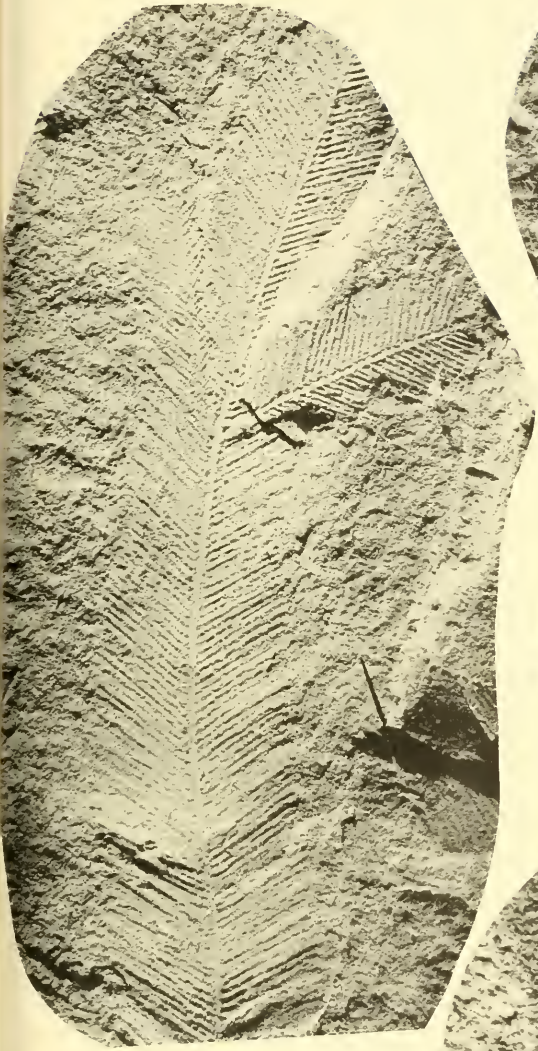
Figure

1. **Plumalina plumaria** Hall, 1858

   Specimen from the Ithaca beds, Ithaca, New York. Latex mold showing the branching of the rachis at the distal end of the stipe which Hall considered rare for this species. NYSM No. 302, latex mold of the holotype. Enlargement, × 1.405.

2, 3 **Plumalina densa** Hall, 1878

   Specimen from the Chemung beds, Belvidere, New York. 2. Natural cast, holotype, NYSM No. 301. The arrow points to an area containing some heretofore undescribed papillae. Enlargement, × .877. 3. Enlargement of area indicated by arrow above, × 8.77. The arrow points to the pinnae containing linear sequences of papillae, some of which appear to have a central pore suggesting the presence of polyp bases.



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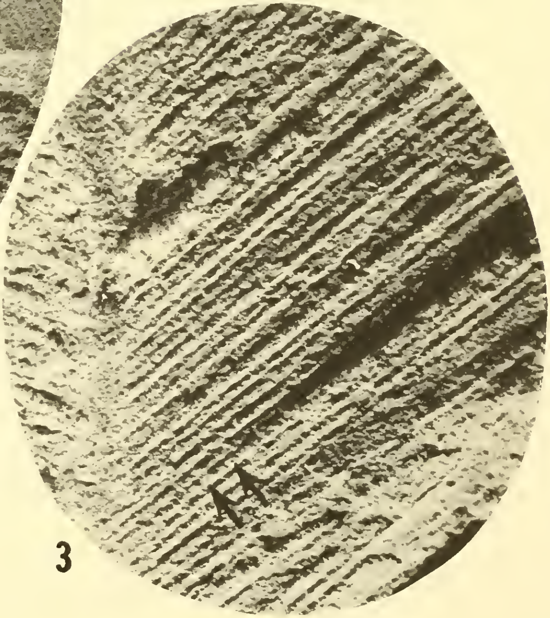

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MONOCYCLISM VS. DICYCLISM: A PRIMARY SCHISM IN CRINOID PHYLOGENY?

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ABSTRACT

Examination of the "law" of Wachsmuth and Springer (1885, p. 229) and the history of its treatment shows that the level of crinoid classification at which the "law" is useful has long been debated. Data gathered from the literature and personal examination of crinoids are found to support this "law" in a modified sense: 1) Crinoids with infrabasals and interradial column pentameres are dicyclic whereas crinoids with infrabasals and radial pentameres are pseudodicyclic (phylogenetically monocyclic); crinoids lacking infrabasals and with radial pentameres are monocyclic, whereas crinoids lacking intrabasals and with interradial pentameres are pseudomonocyclic (phylogenetically dicyclic); and 2) column angles commonly correspond to pentameres, whereas lumen angles and cirri commonly correlate with interpentameric sutures. Evolution of true dicyclic crinoids to true monocyclic crinoids (and *vice versa*) requires more than loss (or addition) of infrabasals. Such evolution also requires rotation of the calyx 36° relative to the column — a difficult, and unsupported, proposition. Monocyclism (with pseudodicyclism) versus dicyclism (with pseudomonocyclism) may represent a primary schism in crinoid phylogeny, as Bather (1899; 1900) suggested, and, if shown to be the case, will necessitate extensive rearrangement of crinoid taxa in classification and phylogeny.

HISTORICAL SUMMARY

Until 1878, plates forming the proximal (lowermost) circlet in the dorsal cup of both monocyclic and dicyclic crinoids were called basals. Plates of the overlying circlet in dicyclic crinoids were then called subradials or parabasals. In 1878, P. H. Carpenter (pp. 358-371) suggested that plates of the second circlet (subradials or parabasals in the older terminology) in dicyclic crinoids are really homologues of basals in monocyclic crinoids, for these plates are interradial in both. Carpenter termed the most proximal circlet of plates in dicyclic crinoids underbasals, for which Zittel (1879, pp. 326-327) substituted the term infrabasals.

In 1885 (p. 229), Wachsmuth and Springer proposed what has come to be known as the "law" of Wachsmuth and Springer:

> 1. In species with underbasals [infrabasals], whenever the column is pentangular, its longitudinal angles are directed interradially, the sides and columnar cirrhi [cirri] radially; on the contrary, in species with basals only, those angles are radial, the sides of the column and the cirrhi [cirri] interradial.
>
> 2. When there are underbasals [infrabasals] and the column is pentapartite, the five sections of the column are radial [this is a *lapsus*; it should read interradial], the longitudinal sutures interradial [should read radial], the radiation along the axial canal radial, but the opposite is the case when basals only exist.

That is, monocyclic crinoids with pentagonal, pentapartite columns have radial pentameres and column angles and interradial cirri (if the column possesses cirri) and extensions of the axial canal, whereas dicyclic crinoids with pentagonal, pentapartite columns have interradial pentameres and column angles and radial cirri and extensions of the axial canal. Wachsmuth and Springer reported that they knew of no exception among all Palaeocrinoidea — Paleozoic crinoids now belonging to the subclasses Inadunata, Flexibilia, and Camerata — and the Neocrinoidea — post-Paleozoic crinoids now belonging to the subclass Articulata.

In a review of Wachsmuth and Springer (1885), Carpenter (1886a, pp. 285-288) criticized wording of rule 2 of Wachsmuth and Springer's "law" and objected to their conclusion (1885, p. 71) that the dominantly monocyclic Neocrinoidea, after having the "law" applied to them, appear to be built on a dicyclic, rather than a monocyclic, plan.

Wachsmuth and Springer (1886, p. 218) corrected wording of rule 2 of their law and discussed the nature of the base of the calyx in the Neocrinoidea. Although Wachsmuth and Springer (1885; 1886) admitted that the presence or absence of infrabasals is important in crinoid classification, they used this only as a familial (and lower) taxobasis, and then inconsistently — Table 1. Wachsmuth and Springer included seven monocyclic families, two dicyclic families, and one family with both 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.

Carpenter (1886b) reviewed Wachsmuth and Springer (1886) and again (p. 410) disagreed with the view that neocrinoids are really dicyclic crinoids — some with obsolescent infrabasals.

Bury (1888) discovered infrabasals in an early larval stage of *Antedon rosacea* Carpenter, 1866 (= *A. mediterranea* (Lamarck), 1816 — *fide* Clark, 1915, p. 315), and Wachsmuth and Springer's dicyclic neocrinoid view began to gain acceptance. These infrabasals later fuse with the most proximal columnal of the pentacrinoid larva to form the centrodorsal plate and give *Antedon* a monocyclic appearance.

Table 1. Monocyclic-dicyclic evaluation of the classification of Wachsmuth and Springer (1885; 1886). M denotes monocyclic; D denotes dicyclic.

Class Pelmatozoa Leuckart, 1848	
Subclass Crinoidea Miller, 1821	
Order Palaeocrinoidea Wachsmuth and Springer, 1879	
Suborder Camerata Wachsmuth and Springer, 1885	
Family Reteocrinidae	M,D
" Rhodocrinidae	D
" Glyptasteridae	D
" Melocrinidae	M
" Actinocrinidae	M
" Platycrinidae	M
" Hexacrinidae	M
" Acrocrinidae	M
" Barrandeocrinidae	M
" Eucalyptocrinidae	M
Suborder Articulata Wachsmuth and Springer, 1885	
Family Ichthyocrinidae	D
" Crotalocrinidae	D
Suborder Inadunata Wachsmuth and Springer, 1885	
Branch Larviformia Wachsmuth and Springer, 1886	
Family Haplocrinidae	M
" Symbathocrinidae	M
" Cupressocrinidae	D
" Gasterocomidae	D
Branch Fistulata Wachsmuth and Springer, 1886	
Family Hybocrinidae	M
" Heterocrinidae	M
" Anomalocrinidae	M
" Belemnocrinidae	M
" Cyathocrinidae	D
" Poteriocrinidae	D
" Encrinidae	D
" Astylocrinidae	M,D
" Catillocrinidae	M
" Calceocrinidae	M

Bather (1890, pp. 316-318) instituted use of the term pseudomonocyclic for monocyclic crinoids demonstrably derived from dicyclic crinoids by loss of infrabasals.

Oehlert (1891, pp. 850-851) used the "law" of Wachsmuth and Springer to show that his new genus *Diamenocrinus,* even though lacking infrabasals, is really a dicyclic (or pseudomonocyclic, in Bather's terminology) crinoid. The pentapartite column of *Diamenocrinus* has pentameres that are disposed interradially (*i.e.,* that directly underlie the basals) in contrast to truly monocyclic crinoids with radial pentameres (*i.e.,* pentameres that alternate with the overlying basals). Oehlert inferred that the infrabasals are hidden beneath the basals, but the same relationship of column pentameres and dorsal cup plates would be true for crinoids that have lost infrabasals altogether.

Wachsmuth and Springer (1897, pp. 52-68) included an historical summary of the debate caused by application of their "law" before citing additional evidence for their "law's" validity.

Bather (1900, pp. 104-105), using information mainly from studies of living crinoids, 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 interradial. 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 infrabasals, 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, if not phylogenetic relationship, by including in each of his two subclasses an order Inadunata and an order Camerata (Table 2).

Table 2. Monocyclic-dicyclic evaluation of the classification of Bather (1899; 1900). M denotes monocyclic; D denotes dicyclic.

- Class Crinoidea Miller, 1821
  - Subclass Monocyclica Bather, 1899 .... M
    - Order Inadunata
    - " Adunata
    - " Camerata
      - Suborder Melocrinoidea
      - " Batocrinoidea
      - " Actinocrinoidea
  - Subclass Dicyclica Bather, 1899 .... D
    - Order Inadunata
      - Suborder Cyathocrinoidea
      - " Dendrocrinoidea
    - Order Flexibilia
      - Grade Impinnata
      - " Pinnata
    - Order Camerata

Clark (1915, p. 314) supported Wachsmuth and Springer's (1885, p. 71; 1886; 1897, pp. 52-68) view that extant crinoids (now placed in the Articulata), although appearing to be nearly exclusively monocyclic, are fundamentally dicyclic (*i.e.,* are pseudomonocyclic) — a view also supported by Hyman (1955, pp. 53 and 91).

Jaekel (1918 — Table 3 herein) and Moore and Laudon (1943 — Table 4 herein) arrived at classificatory positions intermediate between Wachsmuth and Springer's (1885; 1886) and Bather's 1899; 1900) by using monocyclism versus dicyclism 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 (= Monobathrida) and the dicyclic Diplobathra (= Diplobathrida). According to Moore and Laudon (1943, pp. 7-9) Bather's view of a primary monocyclic-dicyclic crinoid schism seemed to be supported by several 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 cup stability. But evidence for a primary schism along monocyclic-dicyclic lines was balanced, in the view of Moore and Laudon (1943, pp. 7-9), by evidence for numerous examples of derivation of monocyclism from dicyclism (and possibly *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 groups (this is especially true, in the opinion of Moore and Laudon, 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 infrabasals to a point of disappearance, and 3) dicyclic camerates seem to represent offshoots from a number of different monocyclic camerate lines. Moore and Laudon suggested that the camerate type of calyx, with its rigid vault of tegminal plates concealing the mouth, is a feature that deserves higher status in classification than does monocyclism-dicyclism. In fact, they sug-

Table 3. Monocyclic-dicyclic evaluation of the classification of Jaekel (1918). M denotes monocyclic; D denotes dicyclic.

Class Crinoidea Miller, 1821	
Subclass Eocrinoidea	
Subclass Cladocrinoidea Jaekel, 1894	
Order Monocyclica	M
Suborder Tetramera	
" Disjuncta	
" Pentamera	
" Miomera	
Order Dicyclica	D
Suborder Tetramera	
" Pentamera	
Subclass Pentacrinoidea Jaekel, 1894	
Order Fistulata Wachsmuth and Springer, 1886	D
Suborder Cyathocrinites	
" Dendrocrinites	
" Merocrinites	
" Barycrinites	
" Rhenocrinites	
" Poteriocrinites	
Order Articulata	
Suborder Typica	D
" Libera	M,D
" Compacta	D
Order Articulosa Jaekel, 1894	D
Suborder Taxocrinites	
" Calpiocrinites	
" Lecanocrinites	
" Ichthyocrinites	
Order Reducta	D
Order Turbata	M
Suborder Heterocrinites	
" Calceocrinites	
" Triacrinites	
" Symbathocrinites	
Order Costata	M
Suborder Hybocrinites	
" Hyocrinites	

Table 4. Monocyclic-dicyclic evaluation of the classification of Moore and Laudon (1943). M denotes monocyclic; D denotes dicyclic.

Class Crinoidea Miller, 1821	
Subclass Inadunata Wachsmuth and Springer, 1885	
Order Disparata	M
" Cladoidea	D
Suborder Cyathocrinoidea Bather, 1899	
" Dendrocrinoidea Bather, 1899	
Subclass Flexibilia Zittel, 1879	D
Order Taxocrinoidea Springer, 1913	
" Sagenocrinoidea Springer, 1913	
Subclass Camerata Wachsmuth and Springer, 1885	
Order Diplobathra	D
" Monobathra	M

gested that diminution of infrabasals in Ordovican diplobathrid camerates illustrates that dicyclic camerates gave rise to monocyclic camerates.

Yakovlov (1930) showed that in the crinoid *Petschoracrinus* Yakovlov, 1928, from the Russian Permian, infrabasals are lost during ontogeny, so that *Petschoracrinus* passes from a dicyclic to a monocyclic (really pseudomonocyclic) condition.

Ubaghs (1953, pp. 666-671) discussed the base of the crinoid dorsal cup and illustrated phylogenetic potentialities (evolution of monocyclism to dicyclism, or *vice versa*) with a number of examples drawn from his and others' experience (Bather, 1900; Beyrich, 1871; Kirk, 1937; Springer, 1920; Wachsmuth and Springer, 1897; Wilson, 1916; and Yakovlov, 1930).

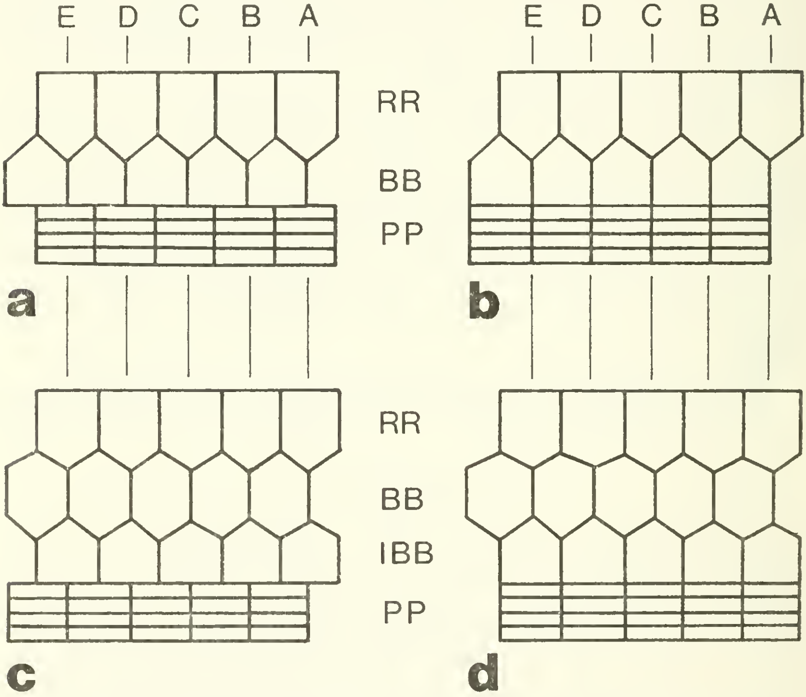
Perusal of crinoid literature shows that Bather's (1899; 1900) view that monocyclism versus dicyclism represents an early divergence in crinoid evolution has been held, and is held today, in low esteem. Modern crinoid specialists are of the opinion that evolution of dicyclism to monocyclism (and perhaps monocyclism to dicyclism) has occurred at least three times in the history of crinoids, and probably more. For example, Moore and Laudon (1943, p. 8) opined:

> There is evidence that evolutionary change within each order produced monocyclic crinoids out of dicyclic stocks and that some dicyclic crinoids may have monocyclic ancestors.

DISCUSSION

Wachsmuth and Springer's "law" is apparently valid in part. Early in the history of crinoid study it was recognized that plates of the dorsal cup lie in alternate circlets. Radials are the fundamental cup plates of crinoids (Philip, 1965, p. 146) and by definition are radially disposed; basals in both monocyclic and dicyclic crinoids are interradial; and infrabasals, limited to dicyclic crinoids, are radial. Not until 1885 (Wachsmuth and Springer, p. 229) was it learned, however, that pentameres of the column are also alternate in position — that pentameres alternate with the overlying basals in monocyclic crinoids and with the overlying infrabasals in dicyclic crinoids. That is, the column pentameres are interradial in dicyclic crinoids (Text-fig. 1c) and radial in monocyclic crinoids (Text-fig.

1a). If a dicyclic crinoid loses infrabasals, it becomes pseudomonocyclic. By observing that the adjacent basals and pentameres of an apparent monocyclic crinoid are interradial, one can discover that radial elements (infrabasals) have been lost between the two adjacent interradial elements (Text-fig. 1b). In other words, one can determine that the crinoid in such a case is phylogenetically dicyclic (*i.e.*, pseudomonocyclic). The same would hold true for recognition of a pseudodicyclic crinoid, in which the radial disposition of adjacent infrabasals and pentameres (Text-fig. 1d) would show that



Text-figure 1. 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 infrabasals (pseudomonocyclic and pseudodicyclic — b and d) have column pentameres directly underlying the lowest circlet of cup plates.

radial elements (infrabasals) had been added between the radial pentameres and interradial basals.

It is evident that evolution of the true dicyclic to the true monocyclic condition (or *vice versa*) requires more than loss (or addition) of infrabasals. Such evolution requires rotation of the calyx 36° (relative to the column) to bring the pentameres of the proximal columnal into alternate position with the overlying circlet of plates (basals or infrabasals) of the dorsal cup. Nothing short of rotation of the pentameres of a pentapartite column and plates of the calyx in relation to one another (*e.g.*, rotation of the chambered organ or the five major columnar nerve strands) would suffice.

It is unlikely that loss or addition of infrabasals in crinoid evolution was accompanied by rotation of the calyx and column relative to one another. No known cases showing loss or reduction of infrabasals exhibit concommitant rotation of column or calyx. *Petschoracrinus, Promachocrinus kerguelensis* Carpenter, 1879, and a number of species of *Antedon* de Freminville, 1811, lose infrabasals during ontogeny without apparent rotation. As well, in no crinoid exhibiting diminution (but not complete loss) of infrabasals (many Ordovician diplobathrid camerates, *Decadocrinus hughwingi* Kesling, 1964, *Dunnicrinus mississippiensis* Moore, 1967, *Metacrinus* Carpenter, 1884, and *Uintacrinus* Grinnell, 1876) is there evidence for rotation — Table 5. Further, a reason (*i.e.,* selection pressure) for rotation is not evident.

Table 5. Known disposition of pentameres, column angles, lumen angles, and cirri in crinoid genera and species.

R denotes a radial distribution, while I denotes an interradial disposition. A blank space represents information completely unknown (*e.g.,* the author has been unable to determine not only the disposition of pentameres in *Belemnocrinus* White, 1862, but even whether or not *Belemnocrinus* has a column composed of pentameres). A dash (—) denotes inapplicable heading (*e.g., Anomalocrinus* Meek and Worthen, 1865, has a round column and no cirri). A solitary question mark (?) means that the heading is applicable but that disposition is unknown (*e.g., Botryocrinus cylindricus* (Hall), 1852, has a pentagonal lumen, but the author has been unable to discover disposition of the angles). Type of crinoid (column labelled TYPE) represents the author's application of Bather's (1890) terminology (M = monocyclic; D = dicyclic; PM = pseudomonocyclic). Sources of information are listed in the far right column (numbers correspond to works below).

[1] Columnals of *Ectenocrinus simplex* are made up of trimeres disposed as follows: 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 DE interray. Although *E. simplex* has trimeres, its axial canal has five lobes, all directed interradially (Text-fig. 3).

[2] *Heterocrinus heterodactylus* Hall, 1847, (type species of *Heterocrinus* Hall, 1847) has been determined to be unrecognizable. This discovery necessitates new names for a number of taxa. These new names will be supplied in future publications.

[3] *Decadocrinus hughwingi* has five infrabasals that, according to Kesling (1971, p. 193), form a thin, inconspicuous ring scarcely exceeding the diameter of the largest columnals.

[4] Yakovlov (1930) showed that *Petschoracrinus* loses infrabasals during ontogeny.

[5] *Xenocrinus* Miller, 1881, apparently has a quadrangular column with two of the four angles directed interradially and two directed radially.

[6] According to Moore (1967, p. 14), tiny remnants of infrabasals are present in only a few specimens.

[7] In *Metacrinus,* the infrabasals form a tiny ring hidden inside the basal circlet.

[8] Infrabasals are present in early larval stages but are lost later in ontogeny.

[9] Infrabasals are usually absent but are occasionally found hidden beneath the basals.

[10] Non-stalked crinoids, as a homologue of the crinoid column, have a single plate (the centrodorsal) just below the calyx. Apparently (what we know of crinoid embryology comes mainly from studies of *Antedon*), during development, the top columnal of the larval column enlarges and fuses with the calyx; the rest of the column is autotomized, and the infrabasals are either fused to this columnal, now centrodorsal, or are resorbed. While the centrodorsal represents the ancestral column, it is of little value in determining the nature of the base of non-stalked crinoids, because: 1) abundant, and usually equally distributed, cirri are given off from the centrodorsal; and 2) while many non-stalked crinoids have pentagonal centrodorsals with interradial angles, the angles of this ossicle might represent secondary pentamerism for alternation with the adjacently overlying, pentagonal radial circlet (in most non-stalked crinoids the basals are greatly reduced and lie inside the radial circlet, so that the radials and centrodorsal are in direct contact). The pseudomonocyclic nature of existing non-stalked crinoids is inferred from the embryology of a few species that lose infrabasals during ontogeny.

Information sources:

11 personal observation
12 Lane (1970)
13 Wachsmuth and Springer (1885)
14 Regnell (1948)
15 Ubaghs (1969)
16 Philip and Strimple (1971)
17 Goldring (1948)
18 Kesling (1971)
19 Sigler *et al.* (1971)
20 Ubaghs (1972)
21 Yakovlov (1930)
22 Kesling (1969)
23 Oehlert (1891)
24 Carpenter (1884)
25 Moore (1967)
26 Clark (1915)
27 Seelinger (*fide* Clark, 1915)
28 Bury (1888)
29 Clark (1921)
30 Clark (1931)
31 Carpenter (1888)
32 Hyman (1955)

	IBB evident	pentameres	column angles	lumen angles	cirri	type	source
DISPARIDA							
Anomalocrinus	no	R	—	I	—	M	11
Atopocrinus	no	R	—		—	M	12
Belemnocrinus	no		R	I	I	M	13
Daedalocrinus	no	R	R	I	—	M	11
Dystactocrinus	no	R	R	I	—	M	11
Ectenocrinus simplex	no	[1]	—	I	—	M	11
E. geniculatus	no		—	I	—	M	11
Heterocrinus heterodactylus[2]	no	R	R	I	—	M	11
H. pentagonus	no	R	R	I	—	M	11
Homocrinus	no		—	I	—	M	11
Hoplocrinus dalecarlicus	no			I		M	14
Ibexocrinus	no	R	—		—	M	12
Iocrinus	no	R	R	I	—	M	11
Isotomocrinus	no	R	R	I	—	M	11
Ohiocrinus laxus	no	R	R	I	—	M	11
O. brauni	no	R	R	I	—	M	11
Sygcaulocrinus	no			?I		?M	11
Synbathocrinus	no			I		M	13
CLADIDA							
Aethocrinus moorei	yes	I	I	I	—	D	15,16
Barycrinus	yes	I	I	R	—	D	13
Botryocrinus cylindricus	yes	I	I	?	—	D	17
Cyathocrinites	yes		I	R	R	D	13
Decadocrinus hughwingi	[3]		I	R	—	D/PM	18
Logocrinus brandoni	yes		I		—	D	19
Merocrinus	yes	I	—	R	—	D	11
Ottawacrinus	yes	I	I		—	D	20
Petschoracrinus	[4]			R		PM	21
Poteriocrinites	yes		I	R	R	D	13
P. duluki	yes		I	R		D	22
Zeacrinites	yes			R	—	D	13
MONOBATHRIDA							
Actinocrinites	no			I	—	M	13
Batocrinus	no			I	—	M	13
Dolatocrinus	no			I	—	M	13
Eucalyptocrinites	no			I	—	M	13
Glyptocrinus	no	R	—	I	—	M	11
Melocrinites	no			I	—	M	13
Xenocrinus	no		[5]	I	—	M	13
DIPLOBATHRIDA							
Diamenocrinus	no	I				PM	23
Reteocrinus	yes		I	R	—	D	13
Rhodocrinites	yes			R	—	D	13

ARTICULATA (stalked)							
Bathycrinus	no		—	?R	—	?PM	24
Dunnicrinus mississippiensis	[6]			—	—	PM	25
Hyocrinus bethellianus	no		—	?R	—	?PM	24
Metacrinus	[7]		I		R	D/PM	26
M. angulatus	no		I	R	R	PM	24
M. cingulatus	no		I	R	R	PM	24
M. moseleyi	no		I	R	R	PM	24
M. murrayi	no		I	R	R	PM	24
M. nobilis	no		I	R	R	PM	24
M. wyvillii	no	I	I	R	R	PM	24
Neocrinus	no		I			PM	24
Pentacrinites	no		I		R	PM	13
P. alternicirrus	no		I	I	R	PM	24
P. asteria	no		I	I	R	PM	24
P. blakei	no		I	R	R	PM	24
P. decorus	no		I	I	R	PM	24
P. naresianus	no	I	I	I	R	PM	24
P. wyvillethomsoni	no	I	I	I	R	PM	24
Proisocrinus ruberrimus	no		I			PM	26
Teliocrinus springeri	no		I		R	PM	26
ARTICULATA (non-stalked)[10]							
Actinometra	no		I			PM	24
Antedon adriatica	[8]		I			PM	26,27
A. mediterranea	[8]		I			PM	26,28
A. microdiscus	no		I			PM	24
A. parvicirra	no		I			PM	24
Capillaster macrobrachius	no		I			PM	30
C. multiradiata	no		I			PM	29
C. sentosa	no		I			PM	29
C. tenuicirra	no		I			PM	30
Comantheria alternans	no		I			PM	29
C. briareus	no		I			PM	30
C. polycnemis	no		I			PM	30
Comanthina schlegelii	no		I		I	PM	26,30,31
Comanthus	no		I			PM	26
C. annulata	no		I			PM	26
C. parvicirra	no		I		I	PM	26
C. solaster	no		I			PM	26
C. timorensis	no		I			PM	26
C. trichoptera	no		I			PM	30
C. wahlbergh	no		I		I	PM	26
Comaster gracilis	no		I			PM	30
C. minima	no		I			PM	29,30
C. multifida	no		I			PM	30
Comatella stelligera	no		I			PM	30
Comatula micraster	no		I			PM	30
C. pectinata	no		I			PM	29
C. purpurea	no		I		I	PM	26,30
C. rotalaria	no		I		I	PM	26,30
Comatulides decameros	no		I			PM	26
Comissia brevicirra	no		I			PM	30
C. gracilipes	no		I			PM	30
C. hartmeyeri	no		I			PM	30

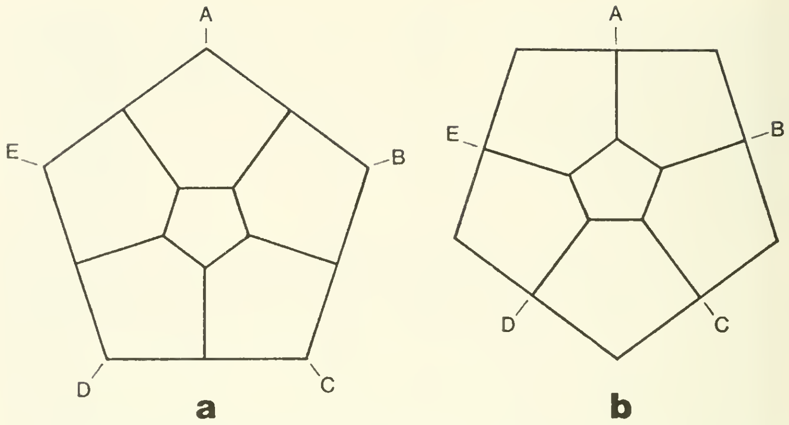
Heliometra glacialis	no		R	PM	26
Marsupites	yes			D	26
Nemaster rubiginosa	no	I		PM	29
Parametra orion	no	I		PM	29
Promachocrinus kerguelensis	[8]			PM	26
Psathyrometra fragilis	no	I		PM	29
Strotometra ornatissima	no	I		PM	26
Stylometra spinifera	no	I		PM	29
Uintacrinus	[9]			PM	26
Zenometra columnaris	no	I	R	PM	26,29

If loss or addition of infrabasals has never been accompanied by rotation of the column or calyx, then the class Crinoidea may be diphyletic, as Bather (1899; 1900) suggested and should be divided into Bather's two subclasses, Monocyclica (to include monocyclic and pseudodicyclic crinoids) and Dicyclica (to include dicyclic and pseudomonocyclic crinoids) — Table 6. The subclass Monocyclica would include disparids and true monocyclic monobathrids (apparently there exist some pseudomonocyclic monobathrids). The subclass Dicyclica would include cladids, pseudomonocyclic monobathrids, diplobathrids, flexibles, and articulates (most of which are pseudomonocyclic).

Table 6. A diphyletic classification of the class Crinoidea.

Subclass Monocyclica Bather, 1899
    Order Disparida Moore and Laudon, 1943 (*nomen corregendum* Moore, 1952, *ex* Disparata Moore and Laudon, 1943)
    Order Monobathrida Moore and Laudon, 1943 (*nom. correg.* Moore, 1952, *ex* Monobathra Moore and Laudon, 1943)
Subclass Dicyclica Bather, 1899
    Order Cladida Moore and Laudon, 1943 (*nom. correg.* Moore, 1952, *ex* Cladoidea Moore and Laudon, 1943)
    Order Diplobathrida Moore and Laudon, 1943 (*nom. correg.* Moore, 1952, *ex* Diplobathra Moore and Laudon, 1943) — this group would include the pseudomonocyclic forms placed by Moore and Laudon, 1943, in the order Monobathrida
    Order Flexibilia Zittel, 1879
    Order Articulata Miller, 1821 (aside from a few true dicyclic members, the group is apparently made up of pseudomonocyclic forms)

The force of this argument must be tempered, however, by some complications to the "law". Discerning monocyclism, dicyclism, pseudomonocyclism, and pseudodicyclism is a relatively easy matter in the many early Paleozoic crinoids in which the pentapartite nature of the column manifests itself. Late Paleozoic and post-Paleozoic crinoids, in which fusion of pentameres has progressed so far that relict sutures between pentameres are seldom observable, present a problem. However, this problem may not be without solution.



Text-figure 2. Disposition of pentameres, interpentameric sutures, column angles, and lumen angles in crinoids. a) monocyclic and pseudodicyclic (with radial pentameres and column angles and interradial sutures and lumen angles) and b) dicyclic and pseudomonocyclic (with interradial pentameres and column angles and radial sutures and lumen angles). Rays are lettered A, B, C, D, and E.

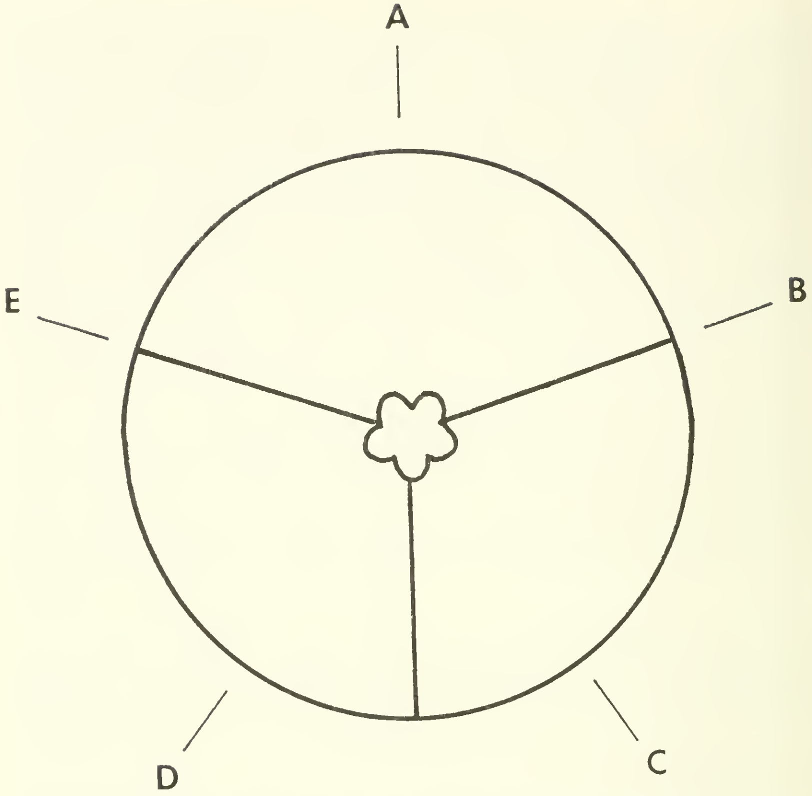
Since Wachsmuth and Springer's (1885, p. 229) proposal of their "law", relationships of column angles, cirri, and extensions of the lumen with column pentameres have become known. Although these relationships do not allow one to suggest the disposition of undetected pentameres with complete certainty, these relationships are consistent enough to allow one to suggest pentamere distribution with relative confidence. In pentagonal (in transverse section) crinoid columns, the angles commonly represent the pentameres (Text-fig. 2). If a crinoid column has a pentagonal or star-shaped lumen, the five angles (which carry five extensions of the nervous system down the column) correspond to the interpentameric sutures (Text-fig. 2). Further, if cirri are present, they commonly lie at the outer ends of the interpentameric sutures, for they are innervated by the five axial nerve strands. Thus, column angles commonly represent pentameres, whereas lumen angles and cirri commonly correspond to interpentameric sutures.

Another complication is sparsity of evidence. Crinoid works often include description of column shape, contain mention of lumen shape or possession of cirri, and include allusion to the existence of pentameres. But these features are rarely correlated with the dorsal cup. Thus, information on the disposition of pentameres, column angles, lumen angles, and cirri in various crinoids is sparse. Table 5 is a compilation of information from crinoid literature, to which the author has added information from personal examination of crinoids.

The data in Table 5 support the "law" of Wachsmuth and Springer with a number of exceptions. One exception which is known to the first part of rule 2 of that "law" (having to do with pentamere distribution), is *Ectenocrinus simplex* (Hall), 1847 (Text-fig. 3) which has trimeres. Specimens that possess quadrangular columns, which perhaps represent quadrameric conditions, may be additional complexities and certainly pose problems for rule 1 of the "law" (having to do with disposition of column angles). However, the author knows of no exception among crinoids with pentagonal columns.

That part of the law pertaining to lumen angle distribution is contradicted by *Aethocrinus moorei* Ubaghs, 1969, and five species of *Pentacrinites* Blumenbach, 1804. Ubaghs (1969) described *A. moorei* as having radial pentameres directly underlying the radial infrabasals and radials alternate in position with the overlying brachials. Philip and Strimple (1971) reinterpreted *A. moorei,* in the author's opinion correctly, as having radials in line with the brachials and infrabasals alternate in position with the underlying interradial pentameres (what Ubaghs, 1969, called infrabasals Philip and Strimple, 1971, interpreted as pentameres of the most proximal columnal). In this case, the dicyclic *A. moorei* has a lumen with interradial angles. In Table 5, five of the six species of *Pentacrinites,* interpreted as pseudomonocyclic, also have lumina with interradial extensions, although disposition of pentameres, column angles, and cirri is as it should be in pseudomonocyclic crinoids.

With respect to distribution of cirri, five extant non-stalked species [*Comanthina schlegelii* (Carpenter), 1881, *Comanthus parvicirra* (Müller), 1841, *C. wahlbergh* (Müller), 1843, *Comatula purpurea* (Müller), 1843, and *C. rotalaria* (Lamarck), 1816] present exceptions. Distribution of cirri (as well as disposition of angles) in the centrodorsal of non-stalked crinoids, however, is hardly trustworthy (see footnote 10 of Table 5 explanation).



Text-figure 3. 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.

MORAL OF THE STORY

The "law" of Wachsmuth and Springer is useful in segregating crinoids into two apparent phyletic groups; however, more attention must be given by crinoid specialists to disposition of pentameres, column angles, lumen angles, and cirri before reclassification can be attempted.

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The author wishes to thank James C. Brower, Richard A. Davis, and N. Gary Lane for critically reviewing the manuscript. Their help in no way necessarily signifies that they agree with any of the views expressed here. Greatest thanks, however, are due Kenneth E. Caster, who initiated and supervised the author's paleontologic study, while the author was a student at the University of Cincinnati. Perhaps Professor Caster's encouragement to question basic paleontologic beliefs is manifest in this paper.

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THE SEXUAL DIMORPHISM AND ONTOGENY OF *CERATOPSIS CHAMBERSI* (MILLER) (OSTRACODA, PALAEOCOPIDA) FROM THE UPPER ORDOVICIAN OF SOUTHWESTERN OHIO AND NORTHERN KENTUCKY

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ABSTRACT

Critical reexamination of *Beyrichia chambersi* Miller (1874), the type species of *Ceratopsis* Ulrich (1894), has shown that this species exhibits velar dimorphism. The occurrence of dimorphic traits necessitates the removal of *Ceratopsis* from the non-dimorphic Quadrijugatoridae Kesling and Hussey (1953) to the Ctenonotellidae Schmidt (1941). As yet sexual dimorphism has not been reported for other members of the genus.

Ontogenetic studies reveal that *C. chambersi* is trilobate in the adult-5 instar (the earliest instar thus far recovered) and attains the quadrilobed condition in the adult-4. Coupled with the intensification and addition of lobes is a continuous change in the lateral outline of the valves from subelliptical and strongly preplete in the early growth stages to subquadrate and amplete in the later ones. Both of these factors may reflect the manner in which appendages were added during ontogeny. Morphologic changes also can be observed in the development of the lateral surfaces of the valves. These areas display a gentle convexity in the early instars but develop into a sharp lateromarginal bend in the adult-1 and into a lateromarginal flange in the adult.

This marks the first report of the family Ctenonotellidae in North America, an Ordovician taxon heretofore restricted to the Baltoscandian faunal realm.

INTRODUCTION

In 1953 Kesling and Hussey proposed the family Quadrijugatoridae for non-dimorphic, quadrilobed palaeocopids. Included in the family were four genera, *Quadrijugator* Kesling and Hussey, *Glossopsis* Hessland, *Ogmoopsis* Hessland, and *Ceratopsis* Ulrich, all of which were restricted to the Middle and Upper Ordovician of either Baltoscandia or the Midwestern United States. Additional genera were added to, and some deleted from, the family by Jaanusson (1957) and Kesling (1961b), both of whom emended the family concept to include sexual dimorphism in several of the genera. However, Schallreuter (1966), in his review of the family Ctenonotellidae Schmidt, 1941, removed all of the dimorphic forms from the Quadrijugatoridae and placed them in the Ctenonotellidae subfamilies Ctenonotellinae Schmidt, 1941, and Steusloffiinae Schallreuter, 1966. *Ceratopsis,* because of its supposed lack of dimorphic traits, remained in the Quadrijugatoridae, even though it otherwise displayed great similarity to several ctenonotellids. The present recognition of velar dimorphism in *Ceratopsis chambersi* (Miller), 1874, the type species of *Ceratopsis,* necessitates the removal of the genus from the Quadrijugatoridae and assignment to the ctenonotellid subfamily

Ctenonotellinae, along with *Kiesowia* Ulrich and Bassler, *Tallinella* Öpik, *Ctenonotella* Öpik, *Tetrada* Neckaja, and *Quadrita* Schallreuter. This marks the first assignment of a North American genus to the family Ctenonotellidae, a Lower through Upper Ordovician taxon heretofore restricted to Baltoscandia.

Most of the extraordinary specimens that serve as a basis for this report were collected from a bed of Edenian age mudstone (Kope Formation) on the bank of West Fork Creek, 150 ft. (45.7 m) northwest of the intersection of Diehl Road and West Fork Road in the Mt. Airy Forest of Cincinnati (U.S.G.S. 7.5′ Cincinnati West Quadrangle, Hamilton County, Ohio; N39°09′45″, W84°34′20″). Stratigraphically, the bed occurs within the lower third of the Kope Formation, 198 ft. (60.4 m) below the Maysvillian age Fairview Formation. Associated with *Ceratopsis chambersi* are several other ostracodes, as well as brachiopods, trilobites, crinoids, and bryozoans. Several thousand other specimens (mostly as isolated spines) of *C. chambersi* were collected from an 1,100 square mile area of southwestern Ohio and northern Kentucky, where this species is a common Upper Ordovician faunal element (Warshauer, 1972). All of the specimens preserving the critical ventrolateral features were examined and support the morphologic data supplied by the West Fork Creek material.

All figured and measured specimens have been deposited in the University of Cincinnati Geological Museum (U.C.G.M.).

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SYSTEMATIC PALEONTOLOGY

Superfamily **HOLLINACEA** Swartz, 1936

Family **CTENONOTELLIDAE** Schmidt, 1941

Subfamily **CTENONOTELLINAE** Schmidt, 1941

Genus **CERATOPSIS** Ulrich, 1894

Type species: *Beyrichia chambersi* Miller, 1874, by original designation, Ulrich, 1894, page 676.

Diagnosis.—A subquadrate quadrilobed palaeocopid with L1 modified into a dorsally directed fimbriate spine; infravelar antral dimorphism present, tecnomorph with a narrow concave frill, heteromorphs with a wide convex frill.

Ceratopsis chambersi (Miller) Pls. 1-3

1874. *Beyrichia chambersi* Miller, p. 234, text-fig. 27.
1875. *Non Beyrichia chambersi* Miller, Hall and Whitfield, p. 104, pl. 4, figs. 11-12.
1894. *Non Ceratopsis chambersi* (Miller), Ulrich, p. 676, pl. 46, figs. 19-22, 1897 (advanced edition, 1894, *fide* Bassler and Kellett, 1934).
1951. *Ceratopsis chambersi* (Miller), Keenan, p. 564, pl. 78, fig. 7.

Diagnosis.—*Ceratopsis* with elongate, subconical and serrated L1; lateromarginal flange developed in adults but not in juveniles.

Description of adult tecnomorphs.—Valves equal in size and subelliptical in lateral view. Greatest length slightly dorsal to mid-length and greatest height slightly dorsal to mid-height. Greatest thickness coincident with the central portion of the lateromarginal flange. Hingeline slightly convex and approximately 85% of the greatest length. Ventral margin strongly convex and grades into convex anterior and posterior margins. Anterior more bluntly rounded than posterior. Cardinal angles obtuse and subequal, approximately 130°. Velate frill narrow and concave, present on the anterior and ventral portions of valve but lacking on the posterior. Velar frill and marginal rim sub-parallel around entire free margin and coalesce at antero-dorsal and postero-dorsal cardinal corners. Wide prominent canaliculus developed around the entire free margin between velar frill and marginal rim. In lateral view marginal rim concealed by velar frill around the entire margin. L1 is prominent and modified into a large sub-conical spine (speral process, Jaanusson, 1957, p. 190). Edge of the process is serrated into comblike teeth. Distally speral process sharp and directed postero-dorsally. L2 short, narrow, inclined posteriorly, and does not reach dorsal margin. Most dorsal portion of L2 separated from rest of lobe by a shallow horizontal sulcus. Separated portion consists of small hemispherical node of translucent calcite and may represent an eyespot. L2 inclined posteriorly and separated from L1 by narrow shallow sulcus (S1) and from L3 by wide deep sulcus (S2). L3 long, narrow and extends to dorsal margin. L3 curved, with concave side facing anteriorally, and separated from L2 by wide deep sulcus. L3 and L4 are separated by wide extremely shallow sulcus. L4 wide, not well defined, and grades into posterior and postero-dorsal margins. All of the lobes are connected ventrally by lateral connecting lobe. Crest of connecting lobe sharply defined and sags ventrally, creating a lateromarginal flange. Hemi-conical channel formed beneath lateromarginal flange in supra-velar position. Lateromarginal flange parallel to velar frill around anterior and anteroventral margins but coalesces with velar frill on the posterior margin. S1 narrow, shallow and joins S2 dorsally. S2 wide, deep and extends approximately 75% of the way to the ventral margin. S2 curved with concave side facing anterior. S3 extremely shallow and poorly defined. Entire surface of valves, including the velum, finely reticulate. No hingement was observed.

Description of heteromorphs. — Heteromorphs like adult tecnomorphs in every way except in development of the velar frill. The frill is wide, convex and distally recurved, thereby forming an elongate dolonal antrum. In addition, faint radiating ribs present on lateral surface of frill. Examination of the one nearly complete carapace indicates that the right and left frill borders do not meet, thereby creating a gap around the entire ventral margin.

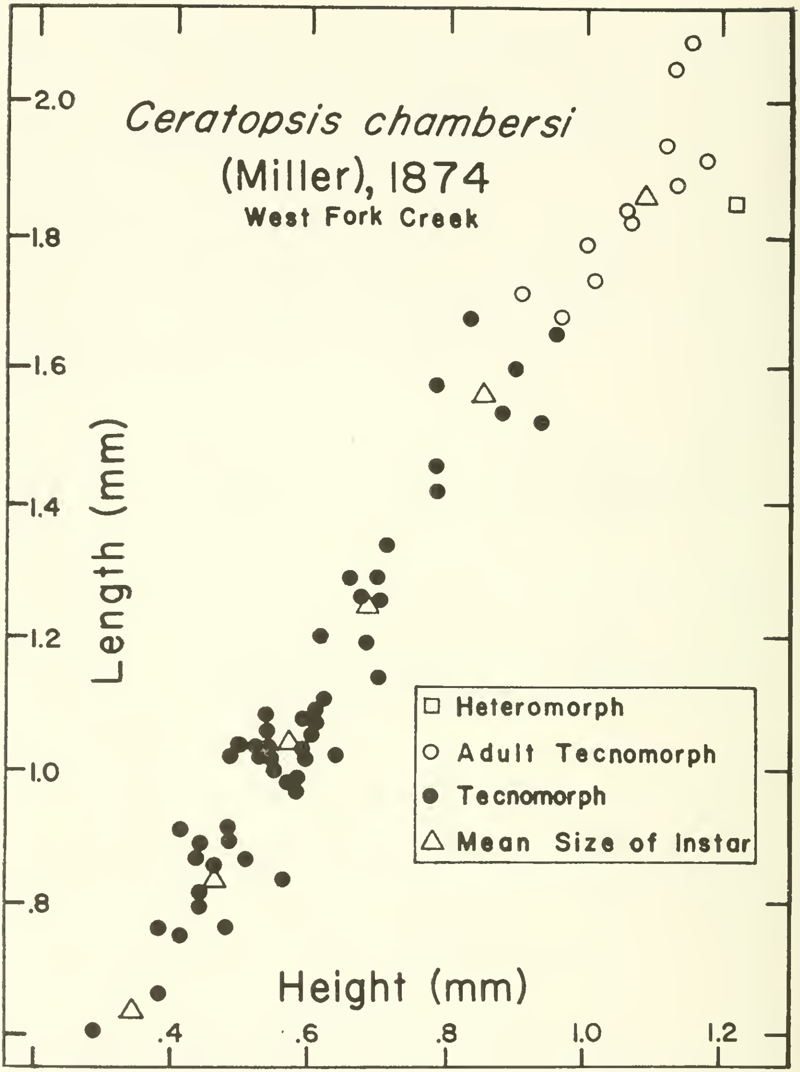
Measurements. — See Table 1 for statistical summary of the specimens from West Fork Creek.

Ontogeny. — On first examination, the discrimination of instar clusters on the size-dispersion diagram (Text-fig. 1) met with little success. However, empirical examination makes it apparent that the diagram consists of four instar clusters in the 0.6-1.4 mm (length) range and one elongate cluster in the 1.4-2.1 mm (length) range. A binary subdivision of the elongate cluster may be further accomplished on morphologic grounds. In this way, six growth stages,

Table 1 — Statistical summary of measurements (in mm) of 63 specimens of *Ceratopsis chambersi* from West Fork Creek.

Statistic	Adult	Adult-1	Adult-2	Adult-3	Adult-4	Adult-5
N L	12	8	8	20	13	2
$\bar{x}$ L	1.863	1.558	1.248	1.037	.841	.637
R L	1.678-2.100	1.420-1.681	1.141-1.340	.975-1.105	.752-.911	.630-.655
s^2L	.017	.008	.004	.001	.003	—
s L	.129	.091	.065	.037	.057	—
N H	12	8	8	20	13	2
$\bar{x}$ H	1.083	.857	.679	.567	.456	.335
R H	.910-1.219	.779-.961	.610-.715	.480-.639	.381-.563	.290-.380
s^2H	.009	.005	.001	.002	.002	—
s H	.095	.074	.033	.042	.047	—
N H/L	12	8	8	20	13	2
$\bar{x}$ H/L	.581	.546	.546	.546	.543	.523
R H/L	.528-.659	.493-.618	.508-.613	.472-.628	.450-.674	.475-.571
s^2H/L	.001	.002	.001	.002	.003	—
s H/L	.035	.043	.034	.041	.058	—

N = number of specimens
$\bar{x}$ = mean
R = range
s^2 = variance
s = standard deviation
L = length
H = height
H/L = height/length ratio



Text-figure 1.—Size dispersion diagram for 63 specimens of *Ceratopsis chambersi.* Comparative growth of the length (L) × height (H) approaches linearity as indicated by the allometric equation ($y = bx^a$), $L = 1.73H^{.887}$. A least squares fit of these points to the above equation indicates a high degree of correlation, $r^2 = .945$.

the adult, adult-1, adult-2, adult-3, adult-4 and the adult-5 are recognized. Smaller instars may exist also as living ostracodes have 6-9 instars (Kesling, 1961a) and some palaeocopids have been reported to have as many as 11 (Spjeldnaes, 1951). The earliest stage of *C. chambersi* so far recovered, the adult-5, is trilobate, with the most posterior lobe (L3 or L4) being much wider than L1 or L2, and without a lateromarginal bend or flange. The lateromarginal surface of the valves is convex, and as in the adults, finely reticulate. The velar structure is limited to a low ridge on the adventral surface. A strong marginal ridge is parallel to the entire free margin and is not concealed by the velar ridge. There is also an ontogenetic change in the lateral outline of the valves. In the adult-5 the greatest height is located in an extreme anterior position. During the rest of ontogeny the greatest height moves progressively away from the anterior border until, in the adult, it is just anterior to the mid-length. The adult-4 is quadrilobed and has a velar ridge developed on both the anterior and ventral borders. These conditions also occur in the adult-3 and the adult-2, although they do show a steady increase in the intensity of lobal inflation and sulcal impression. An extremely close similarity exists between the adult and the adult-1, the most obvious difference being the occurrence of the lateromarginal flange in the adult but not in the adult-1. The occurrence of the lateromarginal flange is the unique criterion used to differentiate the adult from the adult-1 on the size dispersion diagram (Text-fig. 1). The adult-1, however, has a sharp lateromarginal bend, a factor that allows the differentiation of the adult-1 from the earlier instars (Text-fig. 2).

Discussion. — Identification of the present specimens as *Ceratopsis chambersi* was made difficult as the whereabouts of the type specimen is unknown. However, Miller (1874), in his original abbreviated description of the species, reported the following:

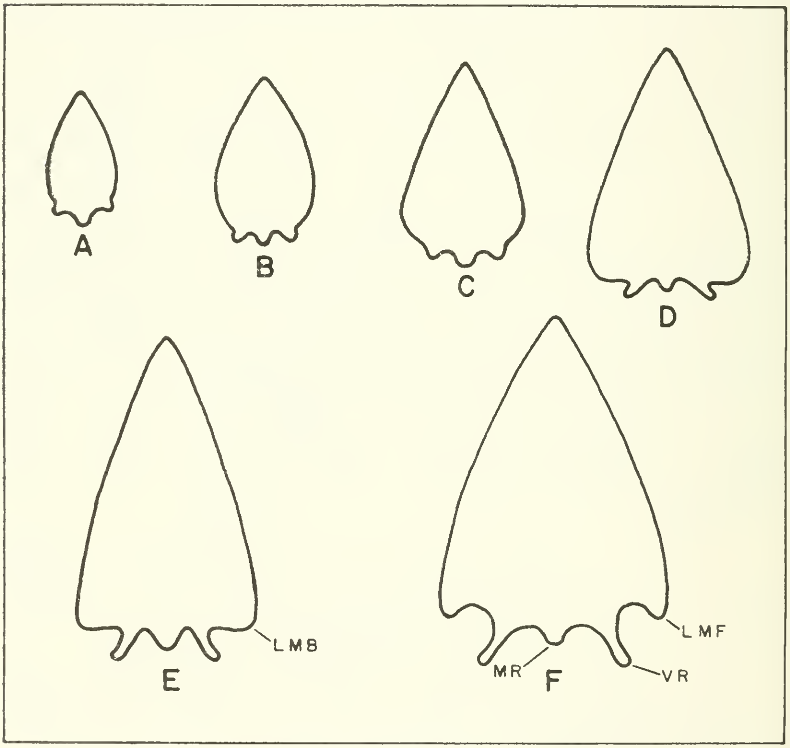
> "I first found it in the excavation for Columbia Ave., in Cincinnati, about 150 feet above low water mark [of the Ohio River]; (p. 234)."

This would fix the original occurrence as being within the (Kope Formation) of the type Edenian Stage (at Cincinnati the Edenian

Stage and the lithostratigraphically defined Kope Formation are coincident). Miller further wrote:

> "Subsequently I found it at Richmond, Indiana in the upper part of the Cincinnati Group (p. 234)."

A cursory examination of specimens of *Ceratopsis* (several hundred specimens from different intervals throughout the Richmondian; collected by W. Shideler and now in the Miami University collections) from the Richmondian Stage of Indiana reveals differences from the Edenian specimens of at least a specific nature.



Text-figure 2. — Schematic transverse sections through carapaces of *Ceratopsis chambersi* illustrating the ontogenetic development of the lateromarginal flange. A. Adult-5; B. Adult-4; C. Adult 3; D. Adult-2; E. Adult-1; F. Adult Tecnomorph; LMB = Lateromarginal Bend; LMF = Lateromarginal Flange; MR = Marginal Ridge; VR = Velar Ridge (in this case, the frill).

Therefore, I am reserving the name *Ceratopsis chambersi* for forms identical to the Edenian specimens herein described. This restriction is felt to be imperative as no other species of *Ceratopsis,* with the exception of several specimens of *C. intermedia,* a form without the large, elongate speral process described by Miller, have been recovered during the present extensive sampling of the Edenian Stage in its type area. In fact, the two poorly preserved specimens of *C. intermedia* were collected from the base of the Kope Formation and may represent material that has been reworked from the underlying Pt. Pleasant Formation. Accordingly, the identification of the specimens described and poorly figured by Hall and Whitfield (1875) from the Richmondian near Waynesville, Ohio, have been questioned in the synonymy. In 1894, Ulrich reported and figured *C. chambersi* from the Middle Ordovician Decorah Shale of Minneapolis and Cannon Falls, Minnesota. Examination of topotype material (approximately 100 specimens collected from the Decorah Shale at Cannon Falls by L. G. Henbest and now in the possession of J. Berdan of the U.S.G.S.) reveals that this species is also distinct from *C. chambersi sensu strictu.* As far as can yet be ascertained, the Trentonian and Richmondian specimens previously assigned to *C. chambersi* are distinct and separate entities, differing from *C. chambersi* in the development of the subvelar field and the disposition of the speral process. Further information as to the nature of these specimens must await future investigation.

Examination of the holotype (U.S.N.M. 41335) of *C. robusta* Ulrich, from the Richmondian of Minnesota, reveals a great similarity between that specimen and the adult-1 of *C. chambersi.* In particular, both forms have a lateromarginal bend but no lateromarginal flange. Whether or not the holotype of *C. robusta* represents an adult of a paedomorphic derivative of *C. chambersi,* the juvenile of a distinct Richmondian species or a juvenile of *C. chambersi,* remains to be investigated. Therefore, I do not agree with the synonymy for the poorly known *C. robusta* put forth by Bassler and Kellett (1934) and have reevaluated each citation on its own merit.

Ceratopsis chambersi differs from the other described Cincinnatian members of the genus, *C. intermedia* and *C. oculifera,* by the extreme development of the speral process. In *C. intermedia,* the process is short and subtriangular while in *C. oculifera,* it is short and circular. More importantly, however, *C. chambersi* exhibits velar dimorphism. Thus far no sexual dimorphism has been reported for *C. intermedia, C. oculifera* or any other described member of the genus. Admittedly though, the heteromorphs of *C. chambersi* are rare and fragile, thereby making them unknown until the present study. This delicate nature of the valves could also explain the lack of heteromorphic valves for the other described species of *Ceratopsis.*

Keenan (1951) figured but did not describe *C. chambersi* from the base of the Edenian at Cincinnati. This was the first adequate photograph of the species ever to be published and for that reason, was included in the synonymy. Most previous figures were based on Ulrich's 1894 illustration and were merely inaccurate generalized drawings.

For a synonymy that includes all citations of *C. chambersi,* including those that simply repeat the original description, see Bassler and Kellett, 1934.

Occurrence. — In addition to its occurrence throughout the Kope Formation of the Cincinnati area, *C. chambersi* has also been reported from the Richmondian Liberty Formation at Richmond and Versailles, Indiana (Cummings, 1908), the Upper Ordovician Indian Ladder beds of Albany County, New York (Ruedemann, 1912), the Eden division of the Martinsburg Shale of Pennsylvania and Maryland (Bassler, 1919), the Middle to Upper Ordovician Utica and Lorraine Formations of New York (Ruedemann, 1926), and the Martinsburg Shale of Virginia (Butts, 1940).

Figured specimens. — U.C.G.M. 40171, U.C.G.M. 40812, U.C.G.M. 40816, U.C.G.M. 40817, U.C.G.M. 40818, U.C.G.M. 40819, U.C.G.M. 40820, U.C.G.M. 40813, UCGM 40813a.

Measured specimens. — U.C.G.M. 40814 (47 specimens on one slide), U.C.G.M. 40815 (9 specimens on one slide).

CONCLUSIONS

1. *Ceratopsis chambersi* is definitely dimorphic, as suggested by Henningsmoen (1965, p. 345). The dimorphism makes itself manifest in the development of an infravelar antrum, a type of structure that has been interpreted (Henningsmoen, 1965) as being an adaption for egg brooding in the heteromorph.

2. The occurrence of sexual dimorphism in *C. chambersi* makes it necessary to remove the genus *Ceratopsis* from the non-dimorphic Quadrijugatoridae and place it in a dimorphic family. As presently understood, *C. chambersi* most closely resembles the genera of the Ctenonotellidae, subfamily Ctenonotellinae, and has thus been placed in that group.

3. The developmental changes in lateral outline and lobal morphology are most probably related to a posterior addition of appendages throughout ontogeny (Henningsmoen, 1965, pp. 366-370). At each succeeding ecdysis more appendages were added and thus the posterior portion of the carapace had to be expanded to accommodate them.

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EXPLANATION OF PLATE 1

All specimens, unless otherwise indicated, are from West Fork Creek.

Figure

1-7. **Ceratopsis chambersi** (Miller)

1. Lateral view of the left valve of an adult tecnomorph; 30.7×. Newport, Kentucky. U.C.G.M. 40171. 2. Lateral view of the right valve of an adult heteromorph; 30.7×. U.C.G.M. 40812. 3. Lateral view of the right valve of an adult-1 carapace; 39.5×. U.C.G.M. 40820. 4. Lateral view of the right valve of an adult-2 carapace; 39.5×. U.C.G.M. 40819. 5. Lateral view of the left valve of an adult-3 carapace; 39.5×. U.C.G.M. 40818. 6. Lateral view of the left valve of an adult-4 carapace; 39.5×. U.C.G.M. 40817. 7. Lateral view of the left valve of an adult-5 carapace; 39.5×. U.C.G.M. 40816.


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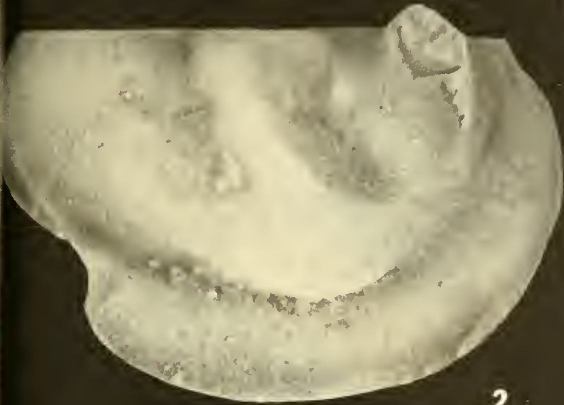
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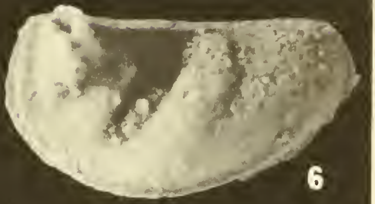
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EXPLANATION OF PLATE 2

All figures are scanning electron micrographs of specimen U.C.G.M. 40813, an adult tecnomorphic carapace from West Fork Creek. Figures are not oriented in conventional manner, with anterior towards top of page, but instead are oriented in manner that original scanning micrographs were taken; 43.8×.

Figure

1-5. **Ceratopsis chambersi** (Miller)

1. Ventral view, anterior towards bottom of plate; 20° tilt. 2. Antero-ventral view, anterior towards bottom of plate; 57° tilt. 3. Dorso-ventral view, posterior towards top of page; 57° tilt. 4. Oblique view, ventral surface up; 45° tilt. 5. Oblique view, ventral surface up; 45° tilt.

EXPLANATION OF PLATE 3

All figures are scanning electron micrographs of specimens from West Fork Creek.

Figure

1-6. **Ceratopsis chambersi** (Miller)

1. Oblique dorso-ventral view of heteromorphic frill and reticulation. Distal edge of frill of opposite valve is visible in bottom portion of figure. U.C.G.M. 40812; 66° tilt; 85.7×. 2. Oblique view of lateral surface of right valve, showing development of lateromarginal flange on an adult heteromorph. U.C.G.M. 40812; 84° tilt; 85.7×. 3. Lateral view of a heteromorphic right valve, clearly displaying the radiating ribs on the frill. U.C.G.M. 40812; 10° tilt; 42.8×. 4. Oblique interior view of valve. Material on interior of valve consists mostly of bryozoan fragments. U.C.G.M. 40813A; 45° tilt. 42.8×. 5. Detailed view of reticulation along edge of heteromorphic frill. Notice the differential rate of weathering of reticulation. U.C.G.M. 40812; 72° tilt; 500×. 6. Detailed view of reticulation on either side of marginal rim on an adult tecnomorph. U.C.G.M. 40813; 20° tilt; 428×.

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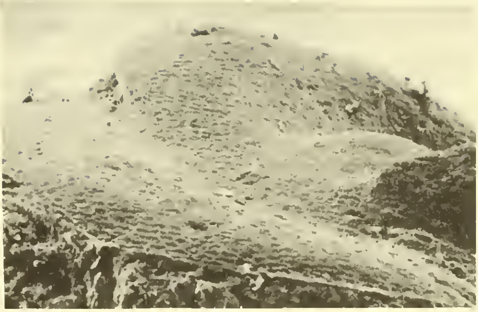

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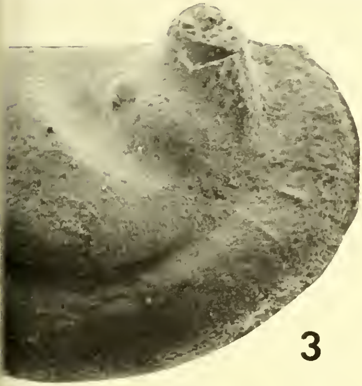

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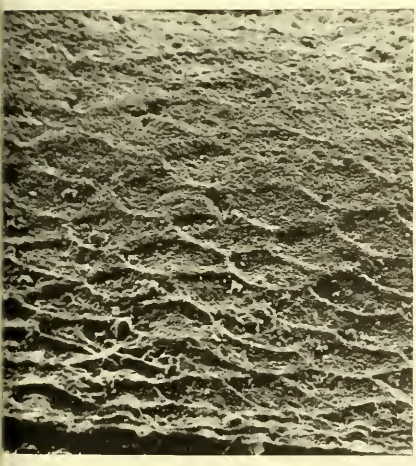

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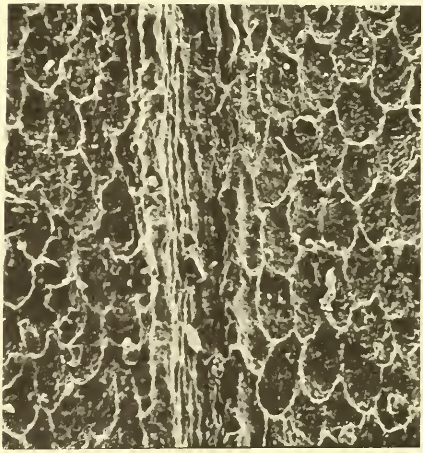

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