INFORMATION TO USERS

This reproduction was made from a copy of a manuscript sent to us for publication and microfilming. While the most advanced technology has been used to photograph and reproduce this manuscript, the quality of the reproduction is heavily dependent upon the quality of the material submitted. Pages in any manuscript may have indistinct print. In all cases the best available copy has been filmed.

The following explanation of techniques is provided to help clarify notations which may appear on this reproduction.

1. Manuscripts may not always be complete. When it is not possible to obtain missing pages, a note appears to indicate this.

2. When copyrighted materials are removed from the manuscript, a note appears to indicate this.

3. Oversize materials (maps, drawings, and charts) are photographed by sectioning the original, beginning at the upper left hand corner and continuing from left to right in equal sections with small overlaps. Each oversize page is also filmed as one exposure and is available, for an additional charge, as a standard 35mm slide or in black and white paper format.*

4. Most photographs reproduce acceptably on positive microfilm or microfiche but lack clarity on xerographic copies made from the microfilm. For an additional charge, all photographs are available in black and white standard 35mm slide format.*

*For more information about black and white slides or enlarged paper reproductions, please contact the Dissertations Customer Services Department.

UMI Dissertation Information Service

University Microfilms International
A Bell & Howell Information Company
300 N. Zeeb Road, Ann Arbor, Michigan 48106
Hansen, Michael Christian

MICROSCOPIC CHONDRICHTHYAN REMAINS FROM PENNSYLVANIAN MARINE ROCKS OF OHIO AND ADJACENT AREAS. (VOLUMES I AND II)

The Ohio State University

University Microfilms International 300 N. Zeeb Road, Ann Arbor, MI 48106
PLEASE NOTE:

In all cases this material has been filmed in the best possible way from the available copy. Problems encountered with this document have been identified here with a check mark √.

1. Glossy photographs or pages ✓
2. Colored illustrations, paper or print ______
3. Photographs with dark background ✓
4. Illustrations are poor copy ______
5. Pages with black marks, not original copy ______
6. Print shows through as there is text on both sides of page ______
7. Indistinct, broken or small print on several pages ______
8. Print exceeds margin requirements ______
9. Tightly bound copy with print lost in spine ______
10. Computer printout pages with indistinct print ______
11. Page(s) _______ lacking when material received, and not available from school or author.
12. Page(s) _______ seem to be missing in numbering only as text follows.
13. Two pages numbered ______. Text follows.
14. Curling and wrinkled pages ______
15. Dissertation contains pages with print at a slant, filmed as received ______
16. Other

____________________________________________________

____________________________________________________

____________________________________________________

University
Microfilms
International
MICROSCOPIC CHONDRICTHYAN REMAINS FROM
PENNSSLVANIAN MARINE ROCKS OF OHIO
AND ADJACENT AREAS
VOLUME I

DISSERTATION

Presented in Partial Fulfillment of the Requirements for
the Degree Doctor of Philosophy in the Graduate
School of The Ohio State University

By

Michael C. Hansen, B.S., M.S.

* * * * *

The Ohio State University
1986

Reading Committee:
Stig M. Bergström
Ted M. Cavender
James W. Collinson
Walter C. Sweet

Approved By:
Stig M. Bergström
Adviser
Department of
Geology and Mineralogy
ACKNOWLEDGMENTS

The current document and the additional requirements for the Ph.D degree were completed principally as a part-time venture over a period of several years. These circumstances were, at times, less than ideal and I gratefully acknowledge the help, advice, understanding, and encouragement of many faculty members in the Department of Geology and Mineralogy, The Ohio State University. In particular, I am grateful to my principal adviser, Dr. Stig M. Bergstrom, and members of my committee: Dr. Walter C. Sweet, Dr. James W. Collinson, and Dr. Ted M. Cavender (Department of Biological Sciences). Dr. Bergstrom has had to long endure my periodic, but perhaps seemingly endless, requests for assistance and advice. His keen perceptions and always good nature have made my tasks more bearable.

The Department of Geology and Mineralogy supported the scanning electron microscopy through grants from the Friends of Orton Hall fund and the Appalachian Basin Industrial Associates fund. Scanning electron microscopy was carried out by Maureen Lorenz and Anthony J. Leonardi. Regina Brown and Margaret Tibbets of the Orton Memorial...
Library provided considerable assistance in locating obscure literature for this report and other projects. Charles P. Hart of the Department of Geology and Mineralogy assisted in preparation of the plates.

My interest in Carboniferous rocks, and the chondrichthyan remains within them, began while I was an undergraduate student of Dr. Myron T. Sturgeon at Ohio University. Over these many years, Dr. Sturgeon has been both a close friend and a helpful colleague. Dr. Sturgeon directly assisted in this study by providing considerable locality information for sampling of Pennsylvanian rocks and provided a number of samples through a cooperative sampling program. Dr. Richard Hoare of Bowling Green State University also provided me with chondrichthyan remains derived from his samples of Pennsylvanian rocks and with whole rock samples.

My studies of late Paleozoic chondrichthyan fishes, including the current report, have benefitted greatly over the years from discussions with a number of colleagues. Foremost in this list is Dr. Rainer Zangerl (Field Museum, retired) who has freely provided me with his considerable insight and experience on this topic. Although I was never formally a student of Dr. Zangerl's, his patient and insightful discussions have shaped my perceptions of Paleozoic chondrichthyan as only could have been
accomplished by an outstanding teacher. In addition, the following chondrichthyan workers have generously provided helpful information and discussion: Dr. Donald Baird (Princeton University); Dr. Christopher Duffin (Surrey, England); Dr. Gary D. Johnson (South Dakota Geological Survey); Dr. John G. Maisey (American Museum of Natural History); Dr. Susan Turner (Queensland Museum); Dr. Linda E. Tway (Scripps Institution of Oceanography); Dr. Michael E. Williams (Cleveland Museum of Natural History); Dr. Gavin Young (Australian Bureau of Mineral Resources); and Dr. Jiri Zidek (New Mexico Bureau of Mines).

Dr. Glen K. Merrill, University of Houston, provided locality information, samples from several units, identification of units from conodonts, and considerable insight into depositional environments of Pennsylvanian rocks in the central Appalachian Basin. Dr. Robert W. Hook, National Museum of Natural History, has similarly provided stimulating discussion on these rocks and their vertebrate faunas.

Chondrichthyan specimens and samples of Pennsylvanian rocks have been provided to me by Dr. Martin Lockley (University of Colorado), Dr. Royal H. Mapes (Ohio University), and Alan Saltsman (Pittsburgh, Pennsylvania). Several additional specimens or samples provided by other colleagues are acknowledged in the text.
Perhaps the most important contributions to the successful completion of this study were from my wife, Marsha, and my daughter, Noelle. Both have uncomplainingly endured my absence during field work, the smell of acetic acid permeating our house, and my long, and seemingly endless hours at the microscope and computer. The encouragement of my parents, John C. Hansen and Martha L. Hansen, and my wife's parents, Dr. M. K. Fugate and Eleanor C. Fugate has also been an important impetus to completion of this work. My grandmothers, Mary Hansen and Esta M. Tipton, inspired a desire for knowledge and stressed the value of an education.

As a final personal comment I take this opportunity to clearly define the record in order to avoid any future misconceptions. The current document and additional requirements for the Ph.D. degree were completed during my employment as a geologist for the Ohio Geological Survey; however, this venture was entirely at my own expense and on my personal time. Although many colleagues at the Survey gave moral support to my efforts, Horace R. Collins, Division Chief, provided no official sanction nor, more importantly, encouragement in these efforts.
VITA

February 15, 1944  Born - Columbus, Ohio
1967  B. S., Ohio University, Athens.
1972-present  Geologist - Ohio Geological Survey, Columbus.
1973  M. S., Ohio University, Athens.

Fields of Study

Major Field: Paleontology and stratigraphy.

Studies in Paleontology: Dr. Stig M. Bergstrom and Dr. Walter C. Sweet.

Studies in Stratigraphy: Dr. Stig M. Bergstrom, Dr. Walter C. Sweet, and Dr. Peter N. Webb.

Studies in Sedimentology: Dr. James W. Collinson and Dr. Kenneth O. Stanley.

Studies in Economic Geology: Professor Richard J. Anderson and Dr. J. Osborn Fuller.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACKNOWLEDGMENTS</td>
<td>ii</td>
</tr>
<tr>
<td>VITA</td>
<td>vi</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>x</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>xi</td>
</tr>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>SAMPLING AND LABORATORY PROCEDURES</td>
<td>19</td>
</tr>
<tr>
<td>STRATIGRAPHY</td>
<td>23</td>
</tr>
<tr>
<td>DEPOSITIONAL ENVIRONMENTS</td>
<td>46</td>
</tr>
<tr>
<td>TAXONOMIC PHILOSOPHY</td>
<td>64</td>
</tr>
<tr>
<td>FAUNAL COMPOSITION AND PALEOECOLOGY</td>
<td>73</td>
</tr>
<tr>
<td>BIOSTRATIGRAPHY</td>
<td>84</td>
</tr>
<tr>
<td>SYSTEMATIC PALEONTOLOGY</td>
<td>92</td>
</tr>
</tbody>
</table>

## TEETH

Class Chondrichthyes  
Subclass Elasmobranchii  
Order Xenacanthida  
   *Xenacanthus tridentatus*  
Order Euselachii  
Superfamily Ctenacanthoidea  
Family Phoebodontidae  
   *Phoebodus heslerorum*  
   *Zangerlodus williamsi*  
   122
Superfamily Hybodontidae

Family Hybodontidae

Lissodus zideki .............................................. 137
Lissodus duffini .............................................. 148
Maiseyodus johnsoni ........................................ 155
Hybodont tooth "A" ........................................... 175
Additional hybodont teeth .................................. 178

Order Symmoriida

Family Symmoriidae

Symmorium reniforme ....................................... 182
Cobelodus aculeatus ......................................... 197
Denaea saltsmani ............................................. 206

Family Stethacanthidae

Stethacanthus altonensis ..................................... 225

Order Petalodontida .......................................... 240

Order Incertae sedis

Venustodus argutus ........................................... 244

"Cohort" Neoselachii

Cooleyella peculiaris ....................................... 253

viii
Subclass Subterbranchialia
  Superorder Holocephali
  Order Bradyodontida
  Family Cochliodontidae .......... 280
  Family Psammodontida
    Lagarodus angustus .......... 282
Subclass and Order Incertae sedis
  Tooth "A" .......... 298
  Tooth "B" .......... 301
  Tooth "C" .......... 304
# LIST OF TABLES

<table>
<thead>
<tr>
<th>TABLES</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Summary of Pennsylvanian marine chondrichthyan taxa in the Appalachian basin.</td>
<td>81</td>
</tr>
<tr>
<td>2. Distribution and frequency of chondrichthyan taxa.</td>
<td>91</td>
</tr>
<tr>
<td>3. Summary of measurements of <em>Xenacanthus tridentatus</em> teeth.</td>
<td>101</td>
</tr>
<tr>
<td>4. Summary of measurements of <em>Maiseyodus johnsoni</em> teeth.</td>
<td>159</td>
</tr>
<tr>
<td>5. Summary of measurements of <em>Denaea saltsmani</em> teeth.</td>
<td>223</td>
</tr>
<tr>
<td>6. Summary of measurements of <em>Denaea meccaensis</em> teeth.</td>
<td>224</td>
</tr>
<tr>
<td>7. Summary of measurements of <em>Stethacanthus altonensis</em> teeth.</td>
<td>231</td>
</tr>
<tr>
<td>8. Summary of measurements of <em>Cooleyella peculiariis</em> teeth.</td>
<td>278</td>
</tr>
<tr>
<td>9. Numerical characteristics of <em>Lagarodus angustus</em> teeth.</td>
<td>297</td>
</tr>
<tr>
<td>FIGURES</td>
<td>PAGE</td>
</tr>
<tr>
<td>------------------------------------------------------------------------</td>
<td>------</td>
</tr>
<tr>
<td>1. Dermal dентicle terminology.</td>
<td>16</td>
</tr>
<tr>
<td>2. Distribution of Pennsylvanian rocks in the Appalachian basin</td>
<td>24</td>
</tr>
<tr>
<td>3. Distribution and lateral relationships of marine units and coal beds in the Pennsylvanian of Ohio</td>
<td>26</td>
</tr>
<tr>
<td>4. Generalized distribution of Pennsylvanian rocks in Ohio</td>
<td>28</td>
</tr>
<tr>
<td>5. Carboniferous structural features</td>
<td>50</td>
</tr>
<tr>
<td>6. Late Paleozoic collision, thrusting, and basins</td>
<td>56</td>
</tr>
<tr>
<td>7. Generalized extent of Pennsylvanian marine embayments</td>
<td>61</td>
</tr>
<tr>
<td>8. Morphological features of <em>Xenacanthus tridentatus</em></td>
<td>95</td>
</tr>
<tr>
<td>9. Holotype of <em>Xenacanthus tridentatus</em> (Harlton) 1933</td>
<td>98</td>
</tr>
<tr>
<td>10. Hypothesis of relationships of chondrichthyan taxa</td>
<td>112</td>
</tr>
<tr>
<td>11. Tooth morphology of <em>Phoebodus heslerorum</em></td>
<td>116</td>
</tr>
<tr>
<td>12. Tooth morphology of <em>Zangerlodus williamsi</em>.</td>
<td>123</td>
</tr>
<tr>
<td>13. Morphological variation of teeth of <em>Zangerlodus williamsi</em></td>
<td>130</td>
</tr>
<tr>
<td>14. Mode of articulation of teeth of <em>Zangerlodus williamsi</em></td>
<td>132</td>
</tr>
<tr>
<td>15. Tooth morphology of <em>Lissodus zideki</em></td>
<td>140</td>
</tr>
<tr>
<td>Chapter</td>
<td>Title</td>
</tr>
<tr>
<td>---------</td>
<td>----------------------------------------------------------------------</td>
</tr>
<tr>
<td>16</td>
<td>Tooth morphology of <em>Lissodus duffini</em></td>
</tr>
<tr>
<td>17</td>
<td>Postulated arrangement of teeth of <em>Lissodus duffini</em></td>
</tr>
<tr>
<td>18</td>
<td>Tooth morphology of <em>Maiseyodus johnsoni</em></td>
</tr>
<tr>
<td>19</td>
<td>Morphological variation of teeth of <em>Maiseyodus johnsoni</em></td>
</tr>
<tr>
<td>20</td>
<td>Morphology and arrangement of teeth of <em>Symmorium reniforme</em></td>
</tr>
<tr>
<td>21</td>
<td>Reconstruction of <em>Symmorium reniforme</em></td>
</tr>
<tr>
<td>22</td>
<td>Tooth morphology of <em>Cobelodus aculeatus</em></td>
</tr>
<tr>
<td>23</td>
<td>Reconstruction of <em>Cobelodus aculeatus</em></td>
</tr>
<tr>
<td>24</td>
<td>Tooth morphology of <em>Denaea saltsmani</em></td>
</tr>
<tr>
<td>25</td>
<td>Tooth morphology and variation of <em>Denaea meccaensis</em></td>
</tr>
<tr>
<td>26</td>
<td>Reconstruction of <em>Denaea meccaensis</em></td>
</tr>
<tr>
<td>27</td>
<td>Tooth morphology of <em>Stethacanthus altonensis</em></td>
</tr>
<tr>
<td>28</td>
<td>Reconstruction of <em>Stethacanthus altonensis</em></td>
</tr>
<tr>
<td>29</td>
<td>Arrangement of the dentition of <em>Petalodus ohioensis</em></td>
</tr>
<tr>
<td>30</td>
<td>Tooth morphology of <em>Venustodus argutus</em></td>
</tr>
<tr>
<td>31</td>
<td>Microscopic anatomy of a tooth of <em>Venustodus argutus</em></td>
</tr>
<tr>
<td>32</td>
<td>Holotype of <em>Cooleyella peculiaris</em> Gunnell 1933.</td>
</tr>
<tr>
<td>33</td>
<td>Tooth morphology of <em>Cooleyella peculiaris</em></td>
</tr>
<tr>
<td>34</td>
<td>Tooth morphotype II of <em>Cooleyella peculiaris</em></td>
</tr>
<tr>
<td>35</td>
<td>Microscopic anatomy of a tooth of <em>Cooleyella peculiaris</em></td>
</tr>
</tbody>
</table>
36. Tooth variation in *Cooleyella peculiaris*.

37. Frequency of tooth morphotypes of *Cooleyella peculiaris*.

38. Articulation of teeth of *Cooleyella peculiaris*.

39. Comparison of teeth of *Cooleyella peculiaris* with teeth of extant neoselachians.

40. Tooth morphology of *Lagarodus angustus*.

41. Tooth morphology of the rhomboidal morphotype of *Lagarodus angustus*.

42. Postulated arrangement of the dentition in *Lagarodus angustus*.

43. Postulated manner of occlusion in teeth of *Lagarodus angustus*.

44. Morphology of dentition tooth "A".

45. Morphology of dentition tooth "B".

46. Morphology of dentition tooth "C".
INTRODUCTION

The following report is an analysis of microscopic remains of marine chondrichthyan fishes from Pennsylvanian rocks of the Appalachian Basin, principally from Ohio. This report represents not only the first comprehensive analysis of such remains from the Appalachian Basin but also the first such analysis of microscopic chondrichthyan remains from Pennsylvanian rocks anywhere. The objectives of this study are twofold. First, the study attempted to test the hypothesis that microscopic chondrichthyan remains, consisting of teeth, scales, and other dermal elements, could be differentiated into consistent, reliable, and biologically meaningful categories using a traditional binominal system of nomenclature. The second objective was to test the potential biostratigraphic utility of these taxa. A third product, if not a primary objective, was to gain insight into the chondrichthyan community composition of Pennsylvanian seas not only to provide data on diversity of this group of fishes but also to provide comprehensive data for other workers who may be engaged in evaluating selective pressures on invertebrates brought about by predation from chondrichthyans.

Chondrichthyan fishes were the dominant marine predators during the Pennsylvanian Period, as indeed they
were throughout most of the late Paleozoic, and they occupied most of the ecological niches, in a broad sense, dominated by teleostean fishes in modern seas. From a community viewpoint, chondrichthyans probably exerted influential selective pressure on various invertebrate groups that served as prey, upon each other, and on the less dominant and less abundant osteichthyan and acanthodian fishes. The evaluation of the role of chondrichthyans in extinction events, because of intense predation on invertebrates and consequent strategies of adaptive morphology by these invertebrates in response to this predation, has only recently received much attention (Signor and Brett, 1984). However, the composition of the chondrichthyan communities of the late Paleozoic is poorly known at present and the dietary preferences of individual species can be interpreted in only a cursory fashion.

Late Paleozoic chondrichthyans are in general poorly known because of their possession of a cartilaginous skeleton that is preserved only in special depositional circumstances such as the Cleveland Shale (Upper Devonian, northern Ohio), the Bear Gulch Limestone (Upper Mississippian, Montana), and the Pennsylvanian carbonaceous black shales of the Midcontinent and Eastern Interior basins. In aerobic marine environments in which most limestones and calcareous shales were deposited (the "carbonate facies" of this report) a moribund
chondrichthyan quickly disintegrated into only its phosphatic hard parts such as teeth, denticles, dermal spines, and other specialized organs. With few exceptions, these phosphatic components of any individual chondrichthyan were widely scattered across the sea floor by currents and scavengers so that rarely, in the carbonate facies, are any of these individual skeletal elements preserved in natural assemblages that reflect in vivo associations. Unfortunately, it is unlikely that many chondrichthyan species will ever be known by more than disassociated remains such as teeth. As an example, Petalodus, a well-known petalodont first described by Agassiz (1844), is still known only from isolated teeth, although many thousands of these organs have been collected in nearly a century and a half. The point is clearly made that it is fruitless to avoid taxonomic analysis of such remains until the time when complete or at least associated remains are collected.

Considerable effort was expended during the last century to describe and name the macroscopic chondrichthyan skeletal components that are commonly encountered in Upper Paleozoic limestones and associated rocks. These lavishly illustrated reports (Newberry and Worthen, 1866; St. John and Worthen, 1875, 1883; Newberry, 1889; Smith Woodward, 1889; de Koninck, 1878; Trautschold,
1875; Davis, 1883) are, almost without exception, remarkably astute works considering the contemporaneous level of knowledge about Paleozoic chondrichthyans and the fact that nearly every skeletal element had not been previously described. Indeed, these works still constitute the principal body of knowledge about some chondrichthyan groups. Numerous species were named (many of which, in some groups, are nominal; Hansen, 1985), but few of them have received rigorous taxonomic revision. Although the number of species named in these early reports is probably much too high, it is probable, in my opinion, that the number of genera is probably too low, reflecting an early tendency to lump broadly similar teeth or spines in a common genus and then subdivide that genus into several species based, in many cases, on slight morphological variation. Owing to a lack of adequate recovery and study techniques, microscopic chondrichthyan remains were hardly considered by these early workers.

In this century there has been considerably less interest in study and description of fragmentary chondrichthyan remains for a variety of reasons. There has never been, at any particular time, more than a handful of chondrichthyan workers in the world. Most serious students of fossil sharks and sharklike fishes have been zoologically oriented vertebrate paleontologists with
interests principally in the areas of anatomy and systematics. Consequently, this small number of specialists has tended to concentrate their efforts on well-preserved individual chondrichthyan specimens. There has been considerably less interest in the initially less promising study of fragmentary shark remains such as isolated teeth or other readily preserved hard parts or in the analysis of chondrichthyan faunas composed of such remains.

Invertebrate paleontologists, most of whom have a geological orientation, have, in their studies of late Paleozoic faunas, almost totally neglected either megascopic or microscopic chondrichthyan (and other fish) remains in their collections. Faunal lists in many of these reports commonly conclude with designations such as "shark teeth", "fish teeth and scales", or more derogatory terms such as "fish debris." Such an approach cannot be realistically faulted when the complexity, lack of knowledge, and scattered literature are considered. Indeed, some chondrichthyan workers, accustomed to the luxury of relatively well-preserved specimens, are of the opinion that little can be done with isolated teeth, scales, fin spines, or other remains. This prevailing, although false, notion has provided little encouragement to potential students of isolated fossil shark remains.
It is clearly evident from the results of this report, however, that isolated teeth and other remains of chondrichthyan species can be grouped in taxonomically workable and biologically meaningful species. This fact is well illustrated by teeth of symmoriid sharks from Pennsylvanian rocks of the United States. These teeth, of cladodont design, have categorically been grouped in the generic wastebasket of "Cladodus", with little hope that they could ever be segregated into biologically meaningful species. However, the studies of Zangerl and Case (1973) and Williams (1985) on relatively well-preserved remains of symmoriid sharks from Pennsylvanian black shales of the Midcontinent and Eastern Interior basins demonstrated that cladodont teeth with significant differences were associated with sharks that were equally distinctive. The current study demonstrates that isolated teeth of cladodont design can readily and reliably be identified from microsample residues and assigned to the symmoriid species designated by the above authors.

This general dearth of studies of chondrichthyan remains from shallow-water "carbonate" communities has deprived paleoecologists from serious consideration of sharks and sharklike fishes as important and influential members of late Paleozoic communities. Without question, many of these fishes were the principal predators on a
large portion of the invertebrate constituency. Such predator-prey relationships have been documented by only a few examples (Malzahn, 1968, 1972; Hansen and Mapes, 1983; Mapes and Hansen, 1984; Hansen and Mapes, in press); however, there has been little serious investigation in this area. As noted earlier, the study of Signor and Brett (1984) on the influence of chondrichthyan predation as a factor in the extinction of certain late Paleozoic invertebrate groups, is one of the few ventures into this intriguing arena. Unfortunately, these authors were forced to use a greatly dated generic summary of chondrichthyans by Romer (1966). Consequently, this study and those of future authors who use a similar data base, will be inherently flawed. It is time to get the chondrichthyan taxonomic house in order.

**CHONDRICHTHYAN HARD PARTS**

The chondrichthyan skeleton is composed of cartilage, a tissue that readily undergoes decomposition upon the death of the individual. Certain cartilaginous skeletal elements in Paleozoic chondrichthyans had a thin, surficial layer of interlocking, calcified tesserae, however, these individual elements were rapidly dispersed upon decomposition of the underlying, noncalcified cartilage. As noted in the previous section, it is only
under special cases of anoxic bottom conditions, such as are found in black shale environments, that chondrichthyan cartilage elements are readily preserved. In the "carbonate" environments, in which perhaps most late Paleozoic benthos-feeding chondrichthyan fishes lived, only rarely are any associated chondrichthyan remains ever found. Preserved remains of sharks and sharklike fishes that lived in the carbonate environments consist, therefore, almost exclusively of isolated teeth, dermal and mucous membrane denticles, median fin spines, and certain specialized dermal elements such as clasper hooks.

Teeth.- Teeth are one of the most abundant, readily identified, and perhaps taxonomically useful types of phosphatic elements yielded by chondrichthyan fishes. These teeth consist of a tooth base, a term that is preferable to the commonly used term "root". This latter terminology implies a root in the mammalian sense, obviously quite different from that found in chondrichthyan fishes. The tooth base is covered by connective tissues during life and serves to conduct nutrient canals and nerves into the pulp cavity of the tooth and to serve as an anchor to prevent dislodgment of the tooth during feeding activities.
Vascularization of the tooth is provided by a series of canals, the openings of which are marked on the surface of the tooth by foramina. Casier (1947) introduced a series of terms for patterns of vascularization as seen in chondrichthyan teeth, from which he visualized an evolutionary pattern ranging from relatively simple vascularization in hybodonts through specialized vascular patterns in neoselachians. Anaulacorhize vascularization is the simplest condition and is typified by multiple, irregularly distributed foramina. Hemiaulacorhize vascularization is a pattern applied to teeth with a single, principal vascular canal that is partially enclosed, whereas those teeth with an open median canal are referred to as having holaulacorhize vascularization. Teeth with multiple, open vascular canals are referred to as having polyaulacorhize vascularization. These terms have never become a standard part of the descriptive vocabulary of most chondrichthyan workers, perhaps in part because the evolutionary sequence of these patterns of vascularization does not appear to have validity. An examination of the patterns of vascularization of the teeth described in the following report indicates that vascularization patterns perhaps represent common solutions to common problems, particularly the prevention of pinching of the vascular canals by teeth articulated in
a tooth file and subjected to considerable stress during prey capture. Nevertheless, patterns of vascularization in chondrichthyan teeth have received little attention by most workers. Where such features have been observed in chondrichthyan teeth most workers have simply mentioned the presence of vascular canals or foramina and perhaps noted a pattern to these features. However, few have given attention to modes of vascularization from the standpoint of functional anatomy and almost none has noted that vascular foramina and articulating bosses on teeth are mutually related features that serve to protect the nutrient vessels while maintaining proper spacing and positioning of each tooth in the tooth file.

In addition to major foramina for principal nutrient or vascular canals, many chondrichthyan teeth have numerous small foramina irregularly distributed across the surfaces of the tooth base. Little study has been directed towards these features; however, some of them undoubtedly represent an unspecialized manner of vascularization, especially in teeth that appear to lack larger, specialized foramina. In some teeth, however, these small pitlike openings appear to be loci for integumental anchoring of the tooth base. Precisely oriented thin sections of such teeth may shed light on these observations.
The tooth base of most Paleozoic chondrichthyan teeth consists of a platform upon which the cusps are set. The tooth base is anchored in and covered by the connective tissue of the jaw. In teeth of many chondrichthyans the lingual portion of the tooth base is projects lingually, more or less at a right angle to the cusps, forming a lingual torus. This structure serves as an anchoring device to prevent dislodgment of the tooth when vertical pressure is applied to the cusps during prey capture. Commonly, the oral surface of the tooth base has one or more raised, bumplike bosses that serve as pads for corresponding bosses on the basolabial margin of the succeeding tooth in the tooth file. Such structures are termed articulating bosses. The terms "basal tubercle" and "apical button" have been commonly applied to these structures, particularly in regard to teeth of xenacanths. As noted above, these articulating bosses serve not only to maintain the position and spacing of teeth in the tooth file, but also to provide passage of vascular canals from one tooth to the next in the file without crimping these vessels.

The crown of the tooth projects above the connective tissue and functions as the structure for capturing and preparing prey for swallowing. This portion of the tooth is commonly covered by a shiny layer of enameloid tissue.
Considerable variation of the crown is evident in teeth of many individual species of chondrichthysans and such variation is also evident between many species. Indeed, these variations appear to be reliable criteria for differentiation of species in these sharks and sharklike fishes. Although it is a common conception that the apparent variations in fossil chondrichthyan teeth are so great that no reliable taxonomic sense can be made of them this does not appear to be the circumstance, especially when large collections are available.

Commonly, the crown consists of individual cusps, one or more of which may be dominant in size. These cusps are termed principal or major cusps and secondary or minor cusps. Commonly, very small, bumplike cusps, or cusplets, are present along a main crown ridge. Each cusp may be ornamented with a variety of longitudinal ridges, termed cristae. A lateral carina is a more prominent ridge that divides the labial and lingual surfaces of the cusp.

Although the orientation of teeth within the mouth of a particular chondrichthyan is relatively clear to most workers, informality in terminology has led to misinterpretations of orientations in written descriptions. It is perhaps appropriate to define and clarify this generally accepted terminology. Labial refers to the portion of the tooth that faces outward, towards
the jaw margin. Lingual refers to the portion of the tooth that faces inward, towards the "tongue". These terms are preferable to anterior and posterior, respectively, because as the tooth files are traced from the jaw symphysis towards the posterior portion of the jaw they change their orientation from anterior-posterior to right angles to this orientation.

Similarly, in reference to the lateral margins of a tooth, outer and inner are imprecise terms. Johnson (1979) has suggested using anteromedial-posterolateral (am-pl) to refer to the dimension of the tooth from lateral edge to lateral edge. This term is not necessarily preferable to the term "lateral" for referring to this dimension; however, in teeth in which the lateral margin of a tooth that faced towards the anterior and/or medial portion of the jaw can be determined it permits this information to be conveyed easily.

The terms oral, referring to the crown side of the tooth, and aboral, referring to the underside of the tooth, are preferable to dorsal and ventral. Obviously, dorsal and ventral refer to opposite surfaces of teeth in the upper jaws and lower jaws, respectively. Apical and basal are commonly used interchangeably with oral and aboral and are equally acceptable terms. Figures 25 and 20, of teeth of Denaea meccaensis and Symmorium reniforme, respectively, apply these terms to chondrichthyan teeth.
Denticles.- The integument of a chondrichthyan consists of a characteristic spread of denticles and/or denticle derivatives except where they have been secondarily lost, as in the symmoriids. Denticles, some of a specialized nature, also commonly occupy the mouth cavity and the branchial arches and are referred to as mucous membrane denticles. Dermal denticles may become greatly enhanced to form spinelike denticles such as a Carboniferous form known as Listracanthus. Median fin spines, which can become quite large in some Paleozoic chondrichthians, have been interpreted to be greatly enhanced, single denticles (Zangerl, 1981). Denticles may also undergo enlargement to form specialized denticle derivatives such as clasper hooks, lateral line denticles, and head spines such as are commonly found in hybodontids. Zangerl (1981) has presented a concise summary of denticles and their derivatives.

In recent years, considerable progress has been made in the understanding of the development and differentiation of dermal denticles. Stensio (1961, 1962) advanced the concept that the simplest denticle is a lepidomorium—an enameloid-covered cone of dentine in which a single capillary loop occupied the pulp cavity. The lepidomorium was envisioned to have a single basal canal or foramen and a single, posteriorly located neck
15


It is common for individual lepidomoria to fuse into aggregates or compound scales. In some scales it is possible to recognize the individual lepidomoria, each of which bears its own basal foramen, whereas in other compound scales the fusion is such that individual lepidomorial components are undifferentiable. Such compound scales are common in Pennsylvanian marine rocks and appear to be characteristic of many chondrichthyan groups of this age. Reif (1978) illustrated excellent examples of compound scales from the Lower Carboniferous of Britain.

Placoid scales are characteristic of modern elasmobranchs and are nongrowing (Reif and Goto, 1979). Such scales are apparently shed and replaced, according to these authors. Zangerl (1981) considers placoid scales as specialized lepidomoria. Several varieties of these scales are found in Pennsylvanian marine rocks and it is unreasonable to assume that they were all derived from neoselachian sharks as only one neoselachian, Cooleyella peculiaris, has been identified on the basis of teeth in
the Pennsylvanian fauna described herein. It is possible, in my opinion, that some of the placoid scales in this fauna were derived from hybodontids.

The following terminology (Fig. 1) is generally similar to that defined by Applegate (1967). Dermal denticles have a relatively simple morphology and can be divided into three principal parts: base, pedicel, and crown. The denticle base is commonly conical and flaring and was anchored in the integument. The underside of the base is commonly concave and has one or more comparatively large basal foramina or canal openings.

![Fig. 1.- Placoid scale of Sturgeonella quinqueloba illustrating principal parts and terminology commonly applied to dermal denticles. A, apical; B, anterior; C, lateral. Abbreviations: b, base; c, crown; l, lobe; nc, neck canal; p, pedicel; r, ridge or keel.](image-url)
The region of the denticle between the base and crown is commonly constricted and referred to as the pedicel. Most or all of the pedicel was embedded in the integument. In some denticles from Pennsylvanian rocks a pedicel is not clearly differentiable.

The crown is the portion of the denticle that was above the integument. The surface is covered by a dense, shiny tissue, probably enameloid in most cases. Dentine crowns have a variety of shapes and are the most distinctive portions of the denticle. In most cases the crown bears some form of ornamentation. Weak longitudinal ridges are termed keels. Where these ridges are more robust, with intervening sulci, I have used the term "ridge" to refer to these features. The posterior portion of the denticle crown may be divided into a series of lobes, which are differentiated as median and lateral.

Most, but not all, denticles possess clearly distinguishable anterior and posterior margins. The terms dorsal and ventral cannot be correctly applied to denticles as they may have had very different orientations in life depending upon whether or not they were derived from the back, flanks, or belly of the fish. I have used the terms apical and basal for these portions of a denticle. Figure 1 depicts principal parts of a denticle.
Denticles serve important functions on the skin of chondrichthyans, as noted by Applegate (1967). Perhaps one of the most important functions is as a barrier to the external environment; that is, the denticles prevent attacks by parasites and protect the skin from abrasion. Some denticles must have served also as a defensive mechanism by nature of a sharp, spinelike character or, in the case of massive, thick denticles, they may have discouraged attempts at predation by serving as an armor. Long, posteriorly inclined, keeled denticles are interpreted to have served a hydrodynamic function by channeling water over the body surface and reducing the coefficient of friction. Detailed study of denticles can therefore yield important paleoecological information although some care must be exercised in interpretations.
The objective of sampling for this study was to obtain samples of Pennsylvanian marine horizons from throughout all or most of their extent in the Appalachian Basin. Owing to limitations of time and logistical considerations the bulk of the sampling was done in Ohio, the platform portion of the basin where marine units are greater in number and more widespread. Some sampling was, however, carried out in adjacent states.

Many of the sampled localities (Appendix) are well known from the publications of Sturgeon and Hoare (1968) and Hoare, Sturgeon, and Kindt (1979), or earlier works such as those of Morningstar (1922) and Condit (1912). Additional sampling was done at localities described by Smyth (1957), at locations in the files of Glen K. Merrill, and at a number of previously undescribed localities, principally at recent strip mines or road cuts.

Much of the sampling was done independently; however, a portion of this task was carried out cooperatively with R. D. Hoare (Bowling Green State University) and M. T. Sturgeon (Ohio University) in conjunction with their study of Foraminifera from Pennsylvanian rocks of Ohio. A number
of samples that I collected were exchanged with these colleagues in trade for samples that they collected independently. A few samples were furnished by and exchanged with Glen K. Merrill (University of Houston). Additional samples and acetic acid residues from Pennsylvania were also furnished by Alan Saltsman of Pittsburgh. R. H. Mapes (Ohio University) also furnished picked samples of chondrichthyan remains from Pennsylvanian rocks of the Midcontinent basin.

Most Pennsylvanian marine units in Ohio and adjacent areas are less than a meter in thickness; therefore, a channel sample was taken that represents the entire thickness of the marine unit. In of thicker marine units, a top, middle, and bottom or top and bottom samples were taken in order to assess any faunal changes within the unit. It quickly became apparent after processing, picking, and analyzing some of these latter samples that no vertical changes in the chondrichthyan fauna were readily discernible.

Samples were processed using standard processing techniques for conodonts and other phosphatic microfossils. Limestone and shale samples were crushed into fragments that approximated 1-centimeter-square cubes. About 1 kilogram of crushed sample was placed in 1
gallon of acetic acid at a concentration of approximately 10 to 15 percent. Processing tanks for acid digestion were constructed from 5-gallon plastic pails with lids and handles. These containers are of the type in which joint compound for drywall construction is sold and can commonly be obtained free of charge from construction sites. Such containers are ideal processing tanks and, because of tight-fitting lids, eliminate the need for a hood or special ventilating system.

Acid was changed periodically, commonly on a weekly basis, until digestion of the sample was complete or until it became obvious that the sample would not break down using this technique. A number of samples were determined to be too siliceous for acetic acid digestion. Many shale samples required further treatment, most commonly boiling in a solution of an organic solvent such as Quaternary-0. All treated residues were washed, using a 120-mesh sieve, dried, and placed in envelopes for future picking.

Experimentation was done with magnetic separation equipment as an aid to concentrating phosphatic elements in the residues. This technique appears to work well for conodonts; however, chondrichthyan remains, perhaps because of their lesser density, do not appear to be as amenable to this process. Owing to the apparent
 unpromising future of this technique for concentrating chondrichthyan remains and to logistical problems, experimentation with magnetic separation of residues was abandoned at an early stage of this study. Heavy-liquid techniques of concentration were not employed.

Specimens were studied with a Wild M5A binocular microscope equipped with a drawing tube. This latter attachment was utilized to prepare all drawings of specimens in this report. All chondrichthyan specimens obtained in this study, including type, figured, and referred specimens, and unnumbered specimens are repositioned in Orton Museum, The Ohio State University and are referred to herein as "the collection". The numbered specimens in this collection are designated with the prefix OSU. In addition, all conodonts and remains of acanthodian and osteichthyan fishes obtained from the residues are repositioned in Orton Museum. Designations for repositories of additional specimens mentioned in this report are as follows: NMNH, National Museum of Natural History (Smithsonian Institution); PU, Princeton University (collection recently transferred to Yale University); TMM, Texas Memorial Museum, University of Texas; UM, University of Missouri.
STRATIGRAPHY

Although the title and concept of this report is the study of microscopic chondrichthyan remains from Pennsylvanian marine rocks of the Appalachian Basin, in reality the principal focus is on these remains from Pennsylvanian marine rocks of Ohio. This focus is for practical reasons of intensive sampling within a limited time frame and for obtaining a manageable number of samples that could be processed, picked, and analyzed within these temporal limitations. This apparently limited focus is philosophically justified, however, because the Ohio Pennsylvanian marine section contains the largest number of discrete marine units of any area within the basin. Such marine units are less well developed in adjacent states of Kentucky, Maryland, Pennsylvania, and West Virginia. The following discussion of stratigraphy and deposition of Pennsylvanian marine rocks in the Appalachian Basin is therefore oriented to the Ohio section, although discussion is expanded, where appropriate, to include adjacent areas. Recent comprehensive works such as those of McKee and Crosby (1975) give excellent summaries of Pennsylvanian rocks in the Appalachian basin and are useful guides to these rocks; however, this study has revealed a number of new
insights into stratigraphic problems associated with individual units and provides, perhaps, new perspectives on the deposition of these rocks in the Appalachian Basin.

Fig. 2.- Distribution of Pennsylvanian rocks, major structural features, and older and younger rocks in the Dunkard Basin and adjacent areas of the central Appalachian Basin. From Ferm (1979).

Pennsylvanian rocks in the north-central Appalachian Basin consist of a northwestward-thinning wedge of dominantly clastic rocks that accumulated in a northeast-striking synclinal feature known as the Dunkard basin (Fig. 2). In Ohio, this sequence averages 335 m (1,100 ft.) in thickness (Collins, 1979). Lithologically, these rocks are a repetitive sequence of clay, coal, limestone,
shale, and sandstone that is characterized by a lack of lateral continuity of individual beds. Owing to early economic considerations and the later emergence of the concept of cyclothem, at least 123 individual beds have received formal stratigraphic designation in Ohio. Pennsylvanian rocks in this area thus average one stratigraphic name for each 2.7 meters of rock section. Although many of these names are useful in local areas, the lack of lateral continuity of most beds (Fig. 3) renders it futile to carry such names across the basin or even across the Ohio portion of the basin. Exceptions to this observation, in part, are some marine units and coal beds.

Pennsylvanian rocks of Ohio are subdivided into four major units, originally considered as formations but later elevated to group status. These groups are, in ascending order, Pottsville, Allegheny, Conemaugh, and Monongehela. In Ohio, these groups have not been subdivided into formations although such a procedure should be an objective of future stratigraphic revision. Individual named units, including marine units under consideration here, are therefore considered as beds rather than members as stated in many reports.

Pottsville rocks average 78 m in thickness and are characterized by quartz arenites, thin beds of ironstone,
Fig. 3.- Distribution and lateral relationships of marine units and coal beds in the Pennsylvanian of Ohio. Modified from Merrill (1974).
low-sulfur coals in the lower portion of the section and several thin marine limestones and shales. Principal marine units in this group are the Lowellville (and its southern Ohio equivalent, herein referred to as "Lower Mercer"), Boggs, Lower Mercer, and Upper Mercer. All of these units are dark-gray limestones and shales that are commonly about a meter or less in thickness. Minor marine units, which are not part of this study and occur only in southern Ohio, are the Harrison ironstone, Sharon ironstone, Anthony shale, Quakertown shale, Bear Run shale, and Sand Block ironstone (Sturgeon and Hoare, 1968, p. 16). Pottsville rocks crop out in a narrow, northeast-southwest striking band across Ohio (Fig. 4).

Allegheny rocks contain 32 named beds and average 65 m in thickness. These rocks are characterized by numerous important coal beds and are dominated lithologically by dark-gray shales and micaceous sandstones. Nonmarine limestones first appear in the Pennsylvanian section near the upper part of this group of rocks. Principal marine units in the Allegheny Group are the Putnam Hill limestone, Vanport limestone, Columbiana shale, and Washingtonville shale. These rocks crop out in a narrow band that stretches from Lawrence County in the southern part of Ohio to Portage and Mahoning Counties in the northern part of the state (Fig. 4).
Fig. 4.—Generalized distribution of Pennsylvanian rocks in Ohio. From Couchot and others (1980).
Conemaugh rocks average 122 m in thickness and contain 41 named beds. These rocks are characterized by an abundance of nonmarine limestones and the first appearance of abundant red mudstones and shales. This change from dominantly gray sediments in Pottsville and Allegheny rocks to reddish ones in Conemaugh and overlying rocks has been termed the red-gray boundary (Struble and others, 1971) and suggests either a major change in depositional regime or climate, as noted recently by Donaldson and others (1985). Principal marine units in the Conemaugh are the Brush Creek limestone and shale (which is subdivided into upper and lower units in some areas), Cambridge limestone, Portersville shale and limestone, Noble limestone and shale, Ames limestone, Gaysport limestone, and Skelley limestone. The Conemaugh marks the last appearance of well-developed marine units in the Appalachian basin, although a Lingula-bearing, brackish water shale, associated with the Washington coal, is present in Belmont County, Ohio in Dunkard rocks. Sampling of this shale and ironstone concretions within it failed to produce either chondrichthyan remains or conodonts.

The Monongahela Group averages 75 m in thickness and contains 25 named beds. These rocks are characterized by mineable coals, red shales and mudstones, and nonmarine limestones. No marine or brackish units have yet been identified in these rocks.
The relative ages of Pennsylvanian marine units in the Appalachian Basin, based on their Midcontinent correlatives, have been a subject of both uncertainty and debate. Merrill (1971, 1974) has assigned approximate Midcontinent correlations to most of these marine units on the basis of conodonts. These assignments are listed below individually with discussions of each important marine unit. In summary, however, it is apparent that most of the span of the Midcontinent marine section is represented in the Appalachian Basin. Missing, apparently, are lower Morrowan rocks. The oldest Appalachian marine unit, the Lowellville and its age equivalents, is middle? Morrowan according to Merrill (1974) whereas the Ames, the last widespread and well-developed marine unit, is assigned a late Virgilian age.

PRINCIPAL MARINE UNITS

Pottsville Group

Lowellville limestone.—Middle? Morrowan. The Lowellville was named by Lamb (1910, p. 128-129) for a dark-gray, silty limestone and overlying shale exposed in the valley of Grindstone Run, near Lowellville, Poland Tp., Mahoning County, Ohio (location Mp-3). Morningstar (1922, p. 28-29) correlated the Poverty Run limestone of Stout (1918, p. 65), exposed in Muskingum County (location MUho-5), to the
Lowellville. More recently, Merrill (1974) indicated that, on the basis of conodonts, the Lower Mercer limestone of southern Ohio (Stout, 1916) is correlative to the Lowellville and not to the Lower Mercer limestone of central and northern Ohio and western Pennsylvania. The Lower Mercer of southern Ohio is thus older than the type Lower Mercer and its correlative. In this report, therefore, the southern Ohio unit is designated as "Lower Mercer" in order to distinguish it from the true Lower Mercer. Extension of the name Lowellville to this southern Ohio unit appears to be inappropriate at this time because it cannot be demonstrated that the southern Ohio body of rock is continuous with the body or bodies of rock to which the name Lowellville is now applied in central and northern Ohio. The "Lower Mercer" of southern Ohio may, therefore, require a new name.

This interpretation also has important implications for the Pottsville rocks of southern Ohio which are, by implication of the correlation of the "Lower Mercer" with the Lowellville, older than the traditional correlations with Pottsville rocks of central and northern Ohio and western Pennsylvania. This observation appears to have been confirmed by Bebel (1982) who collected plant compressions from shales above the Sharon sandstone of
southern Ohio that suggest a correlation with the New River Formation (Morrowan) of West Virginia. The southern Sharon is thus slightly older than the Sharon of northeastern Ohio (Hansen, 1984). These data have important implications for interpretation of depositional sequences of Pennsylvanian rocks in the Appalachian Basin and will be more fully developed in the section on depositional environments.

Until recently, the Lowellville of northeastern Ohio was known with certainty only at its type locality. A dark-gray, marine limestone and overlying shale exposed in the spillway below Beach City dam (location Tfr-1) in Franklin Tp., Tuscarawas County, was referred to as Boggs by Lamborn (1956) and questionably referred to this unit by Sturgeon and Hoare (1968) and Hoare, Sturgeon, and Kindt (1979). Conodonts obtained from this outcrop in this study were sent to Dr. Glen K. Merrill, who confirmed that the limestone at Beach City dam was a correlative of the Lowellville.

Thus, the oldest (middle? Morrowan), well-developed marine unit in the Pennsylvanian of Ohio is known in three areas: northeastern Ohio (Lowellville); east-central Ohio (Lowellville=Poverty Run); and southern Ohio ("Lower Mercer"). Although these beds appear to be of approximately the same age, they should not be envisioned
as a continuous body of rock nor as being deposited in a single, discrete depositional event. The Lowellville (and its equivalent, the Poverty Run) is known from only a few widely separated localities. The "Lower Mercer" of southern Ohio appears to be more widespread, or at least better exposed. Conodont-based correlations by Glen K. Merrill (personal communication, 1983) suggest that the Lowellville and its equivalents in Ohio are correlatives of the Kendrick Shale of Kentucky (Jillson, 1919, p. 96–104) and the Winifrede Limestone of Kanawha County, West Virginia (Hennen, 1941).

**Boggs limestone.**– Early Atokan. The Boggs was named by Orton (1884, p. 421–423) for a gray ironstone exposed on the Boggs farm near South Webster, Bloom Tp., Scioto County, Ohio. This apparently unfossiliferous ironstone was correlated by Stout (1916) with a fossiliferous marine chert and limestone in Muskingum County, apparently following earlier correlations of the southern Ohio unit by Orton (1884, p. 68) with a fossiliferous marine limestone and shale in Bethlehem Tp., Stark County, Ohio (location Sb–4).

There is no compelling reason to suspect that the fossiliferous limestone of Muskingum and Stark counties is correlative to the ironstone bed of Scioto and Jackson
This correlation is further suspect in view of the fact that Pottsville rocks of southern Ohio have long been miscorrelated (see discussion of Lowellville limestone). It is apparent to me, therefore, that the name Boggs should be restricted to the ironstone of southern Ohio, designated by Orton (1884). The limestone, chert, and shale of central and northern Ohio will, therefore, require a new name. It is beyond the scope of the present report to undertake this task but future efforts in this regard should include consideration of exposures along Blunt Run (location MUmu-3) or exposures along Ohio Rte. 146 (location MUf-4), both in Muskingum County, as potential type localities.

The name Boggs, as used in this report, is understood to refer to the marine limestone, shale, and chert in central and northern Ohio. The Boggs is best developed in Muskingum County where it undergoes rapid lateral changes from chert to interbedded chert and limestone to well-developed limestone and shale. An exposure in Stark County (location Sb-4) is the only well-known outcrop of this unit in northern Ohio. An exposure of dark-gray limestone in southern Hocking County (location Hwa-1), thought to be Lower Mercer, has been identified as Boggs by Glen K. Merrill on the basis of conodonts. This exposure represents the southernmost known exposure of marine Boggs limestone.
Lower Mercer limestone.—Middle Atokan. The Lower Mercer limestone and shale was named by H. D. Rogers (1858, p. 476) from exposures in Mercer County, Pennsylvania. This unit is commonly a dark-gray limestone that is overlain by dark-gray, fossiliferous shale. Stout (1944) indicated an average thickness of about 0.6 m (2 ft.) for this unit in Ohio. The Lower Mercer is widespread and known from numerous outcrops in western Pennsylvania, northeastern Ohio and southward through Muskingum County to Hocking County. True Lower Mercer is unknown from southern Ohio. Merrill (personal communication, 1983) indicates that, on the basis of conodonts, the type Lower Mercer is similar in age to the Magoffin marine zone (Morse, 1931) of Kentucky.

The Lower Mercer is perhaps the most reliable stratigraphic unit in Pottsville rocks of Ohio and has been widely used for correlation purposes. Misidentifications of this unit, such as that of Stout (1916) in southern Ohio (see discussion of Lowellville limestone), have created difficulties in proper correlation of beds above and below the Lower Mercer.

Upper Mercer limestone.—Late Atokan. The Upper Mercer limestone was named by I. C. White (1878, p.36) for a limestone above the Lower Mercer limestone in Mercer
County, Pennsylvania. Rogers (1858, p. 489) had previously used the name Mahoning limestone for this unit. Orton (1878, p. 898–903) used the name Gore limestone for a unit in Hocking and Vinton counties; however, in 1884 (p. 13–14) he adopted White's name of Upper Mercer for this unit. Owing to uncertainties of correlation noted in this report, it is questionable if Orton’s Gore limestone is indeed Upper Mercer.

The Upper Mercer is a well-developed limestone in northern Ohio but becomes increasingly cherty to the south in central Ohio. Stout indicated an average thickness of 0.5 m (1 ft. 8 in.) for this unit in Ohio. The occurrence of the Upper Mercer in southern Ohio is a matter of some uncertainty. Stout (1916) indicated that an ironstone occurs at the position of the Upper Mercer in southern Ohio. Merrill (1974; personal communication, 1984) has obtained conodonts from a marine bed in Lawrence County that suggests Upper Mercer. No outcrops of Upper Mercer could be located in southern Ohio during the field portion of this study. It is apparent that the Upper Mercer is poorly developed in southern Ohio and it does not appear to be continuous with the Upper Mercer in central and northern Ohio.
Allegheny Group

Putnam Hill limestone.—Early Desmoinesian. The Putnam Hill was named by Andrews (1870, p. 84-85) for exposures of this unit at Putnam Hill in the town of Zanesville, Muskingum County, Ohio (location MUsp-1). The Putnam Hill is a bluish-gray limestone that locally contains chert nodules. This unit, which commonly directly overlies the Brookville (No. 4) coal, also consists of overlying fossiliferous shale. The Putnam Hill averages 1.2 m (4 ft.) in thickness but ranges from a few centimeters to nearly 4 m (Lamborn, 1951, p. 25).

The Putnam Hill is best developed in central and northern Ohio. To the northeast, this unit extends only as far as Stark County. In southern Ohio the Putnam Hill becomes a thin limestone and shale. In Vinton County, which includes the southernmost extension of this unit, the Putnam Hill was interpreted to be a separate marine unit, termed the McArthur limestone, by Morningstar (1922, p. 116-129). The Zaleski flint of Stout (1927, p. 176, 183), interpreted to be a separate marine unit of limited distribution in southern Ohio, has now been interpreted to be a siliceous shoreline facies of the Putnam Hill (Cavaroc and Ferm, 1968).
Vanport limestone.—Early Desmoinesian. The Vanport limestone was named by I. C. White (1878, p. 60-66) from exposures near Vanport, Beaver County, Pennsylvania. Rogers (1858, p. 491) had earlier used the term Ferriferous limestone in reference to the ironstone that is commonly at the top of this unit. The name Ferriferous was widely used in Ohio, particularly in the southern portion of the state where this iron ore was important in the charcoal iron industry of the Hanging Rock district.

The Vanport is present in three separate bodies of rock (Merrill, 1974). The type area in northwestern Pennsylvania is characterized by an east-west oriented body of limestone that reaches a thickness of 6 m (20 ft.) or more. The second body of Vanport is thinner and ranges from Stark and Tuscarawas counties southward to Muskingum County. Commonly, the Vanport is siliceous in this area. In Tuscarawas County the interval between the Putnam Hill and Vanport is entirely marine (Merrill, 1974). The third body of Vanport crops out in southern Ohio in Jackson, Lawrence, Scioto, and Vinton counties and continues southward into northeastern Kentucky. The Vanport in this area is extremely pure and is characterized by its variable thickness within a very short distance. Merrill (1974) indicated that, on the basis of conodonts, the southern Vanport is slightly older than the northern bodies of rock.
Columbiana shale.—Middle Desmoinesian. The Columbiana shale was originally named Hamden by Stout (1918, p. 173-174) for an ironstone exposed near Hamden Furnace in Vinton County. Sturgeon (1943) recognized that the marine shale and limestone nodules overlying the Lower Kittanning coal (No. 5) in central and northeastern Ohio was not the same unit as the Hamden of southern Ohio and named this unit the Columbiana for exposures in Perry Tp., Columbiana County.

The common lithology of the Columbiana is a dark-gray shale with a few scattered nodules of fossiliferous limestone. In Hopewell Tp., Muskingum County, the Columbiana is a well-developed, buff-colored limestone that lies within a body of clay termed Oak Hill by Stout (1918). The Columbiana is unknown from southern Ohio and appears to have a southern limit in the Muskingum-Perry County area. Couchot and others (1980) have defined the southern subsurface limit of the Columbiana on the basis of drill cores.

Washingtonville shale.—Late Desmoinesian. The Washingtonville shale was named by Stout and Lamborn (1924, p. 175-181) from exposures in Green Tp., Mahoning County, Ohio. This dark-gray shale with a few limestone nodules is very irregular in its distribution and
thickness. Stout (1944) gave an average thickness of 1.2 m (4 ft.) for this unit. The Washingtonville is well developed in northeastern Ohio where it is abundantly fossiliferous in some areas. It is exposed as far south as northern Perry County, which is about as far south as it can be expected according to subsurface data presented by Couchot and others (1980). The Washingtonville is unknown from southern Ohio.

Conemaugh Group

Brush Creek limestone.—Early Missourian. The Brush Creek limestone and accompanying shale were defined by I. C. White (1878, p. 34) from exposures in Butler County, Pennsylvania. The Brush Creek ranges from a relatively pure limestone to a dark-gray shale with carbonate nodules. Stout (1944) gave an average thickness of 6 m (20 ft) for the Brush Creek; however, this figure is more typical of the shale than the limestone, which is typically much thinner. In northeastern Ohio the Brush Creek is commonly a dark gray shale with limestone nodules. In central Ohio this unit is typically a dark-gray shale overlain by an impure limestone. In southern Ohio, particularly Athens County, the Brush Creek exhibits a twofold development of limestone beds, which have been
termed the Lower Brush Creek and Upper Brush Creek. Commonly, 6 to 9 m of shale separates these two limestone beds. Morris (1967) has demonstrated that the twofold development of this unit in southern Ohio is because of a clastic wedge that divides them. The Brush Creek has been studied more recently by Norton (1975).

Cambridge limestone.—Middle to Late Missourian. The Cambridge limestone was named by Andrews (1873, p. 262) from exposures in the vicinity of Cambridge, Guernsey County, Ohio. In western Pennsylvania the Cambridge has also been termed Upper Cambridge and Pine Creek limestone. Stout (1944) indicated an average thickness of this unit in Ohio of 1.2 m (4 ft). The Cambridge is highly variable in both lithology and distribution, details of which have been given by Carothers (1976). This unit is thickest in Muskingum and Guernsey counties where 4 m of siliceous limestone are present. The Cambridge is best developed in southern Ohio in Gallia and Lawrence counties.

Portersville shale. Late Missourian. The Portersville was named by Condit (1912, p. 41-42) from exposures in Bearfield Tp., Perry County, Ohio (location Pb-1). The Portersville has been termed Friendsville Shale in
Maryland and Woods Run Shale in Pennsylvania. Sturgeon (1958) has noted that the name Woods Run (Raymond, 1910, p. 187) is older than the name Portersville; however, the former name has been applied to both the Cambridge and Portersville.

Stout (1944) gave an average thickness of the Portersville in Ohio of 0.6 m (2 ft). Commonly, the Portersville consists of a dark-gray shale with a thin limestone bed or limestone nodules near the top of the unit. The Portersville is irregular in distribution and is not present in many areas. Best development of the Portersville is in Athens, Guernsey, Morgan, Muskingum, and Noble counties. Blake (1952) interpreted a sandy unit in Gallia County to represent the Portersville; however, considerable uncertainty surrounds this assignment. Recent studies of the Portersville include those of Hansen (1973) and Baker (1975).

Noble limestone.—Early to Middle Virgilian. The Noble was named by Murphy and Picking (1967) for a meter-thick, gray-green shale that is interbedded with a light-colored, waxy appearing, nodular limestone exposed in Buffalo Tp., Noble County (location Nbu-1). Additional work by Murphy (1973) extended the known distribution of the Noble from
Noble County into southern Guernsey County. This unit has been identified only in its type area. Although the Noble has a limited distribution, it has a well-developed marine fauna.

**Ames limestone.** Late Virgilian. The Ames was named by Andrews (1873, p. 235) for exposures near Amesville, Athens County, Ohio. Sturgeon (1958, p. 134-140) designated the type locality for this unit (location Aam-19). The Ames was known as the Crinoidal limestone in early reports of the Ohio Geological Survey and has been characterized as the most persistent marine unit in the Pennsylvanian of Ohio and adjacent areas. Although the Ames is perhaps the most reliable and persistent marine unit in this area, it is missing in some portions of southern Ohio.

The Ames is a gray to greenish-gray to reddish limestone that averages from 0.3 to 0.6 m (1 to 2 ft) in thickness. Commonly, a gray fossiliferous shale, a meter or more thick, is associated with this characteristic limestone. The Ames has been depicted as occurring as far east as the anthracite belt of Pennsylvania (the Mill Creek limestone of Chow, 1955). Merrill and Wentland (in ms) recently collected conodonts from this unit and suggested that the Mill Creek is slightly older than the
Ames, perhaps corresponding in age to the Noble limestone. Recent studies of the Ames include those of Al-Qayum (1983), Saltsman (1986), and Merrill (in ms).

**Gaysport limestone.** Late Virgilian. The Gaysport was named by Stout (1918, p. 258-259) for exposures of a thin marine limestone near Gaysport, Blue Rock Tp., Muskingum County, Ohio. No type locality has been specified for this unit. The Gaysport is typically an impure limestone or calcareous sandstone associated with fossiliferous shale and averaging less than 0.3 m in thickness. This unit is very irregular in distribution and is best known from Muskingum and Athens counties. It is probable that the Gaysport and the overlying Skelley were associated with the Ames transgression.

**Skelley limestone.** Late Virgilian. The Skelley limestone was named by Condit (1912, p. 27) from exposures near Skelley Station, Jefferson County, Ohio. This limestone and accompanying shale is commonly only a few tens of centimeters thick and highly variable in distribution, although it is recognized from its type area in northeastern Ohio to Athens County in southeastern Ohio. Sturgeon (1958) has suggested that the Skelley and the
Gaysport may be identical units and that the Birmingham shale of western Pennsylvania may represent the Skelley. The Skelley is the youngest marine unit known in the Appalachian Basin.
DEPOSITIONAL ENVIRONMENTS

Although Pennsylvanian rocks in the north-central Appalachian Basin have been the subject of serious study for more than a century and a half, it has only been during the last two decades that serious and detailed interpretations of depositional environments have begun to emerge. A voluminous literature on this topic has accumulated in this relatively short span and it is far beyond the intent of the present discussion to cite and discuss more than a small fraction of it. Perhaps the seminal studies of John C. Ferm (Ferm and Cavaroc, 1968, 1969; Ferm, 1970; Ferm and others, 1971, Ferm, 1974) on Allegheny rocks in the upper Ohio valley and later on Mississippian and Lower Pennsylvanian rocks in northeastern Kentucky were the catalysts needed for launching detailed investigations and re-evaluations of traditional interpretations. Basinwide analyses of the entire Pennsylvanian sequence have been given by Arkle (1969, 1972) and Donaldson and Shumaker (1981) and Donaldson and others (1985).

A pattern of progressive refinement can be discerned in these studies and others and many nagging questions are now seemingly being answered by plausible interpretations. However, many questions remain, particularly in regard to
distributions, correlations, and depositional patterns of marine units and the influence and control exerted by geologic structures on the deposition of late Paleozoic rocks in the north-central Appalachian Basin. The role of structure and tectonics has received only minimal consideration in most studies. Recently, the influence of climate on the deposition of Pennsylvanian rocks has received detailed attention (Cecil and others, 1985; Donaldson and others, 1985).

Structure and Tectonics

It has become increasingly apparent in recent years that patterns of sediment distribution during the late Paleozoic in the north-central Appalachian basin were markedly influenced by pre-existing structure and concurrent tectonics. These controls have been less than apparent in Ohio, on the western platform of the basin, where the long-existing perception has been of relatively flat-lying rocks dipping gently (southeast) into the Appalachian Basin with only minor perturbations such as gentle anticlines and synclines. Recently, however, publication of relatively detailed aeromagnetic and gravity maps of the state (Hildenbrand and Kucks, 1984a, 1984b) has revealed an unexpected complexity to basement rocks. Although interpretations of these complexities are
in the beginning stages, it is apparent that the basement of Ohio and adjacent areas consists of highly fractured terrane within which basement faults have been periodically reactivated within the contemporaneous stress field. Certainly, during the Carboniferous, with continental collision occurring along the southeast margin of the North American plate, stresses were such that many faults and basement structures of late Precambrian age were reactivated and exerted significant influence on near-sea level deposition of sediments.

The preserved clastic wedge of Pennsylvanian sediments in the north-central Appalachian Basin is bounded on the east and southeast by tectonic lands of the Appalachian Mountains and on the west and northwest by the Ohio-Indiana platform (Cincinnati Arch) and its northeastward extension, the Findlay Arch. These later structures, which may be most accurately viewed as positive areas around which basins subsided, were positive features during the Carboniferous and were probably never, or only rarely, crossed by Pennsylvanian seas. Although the western limit of preserved Pennsylvanian rocks is well east of the Ohio-Indiana platform, restricted marine invertebrate faunas (Sturgeon and Hoare, 1968; Hoare, Sturgeon and Kindt, 1979; Sturgeon and others, in ms) and somewhat restricted marine vertebrate
faunas (this report) in the Appalachians suggest that the Cincinnati positive area was emergent and restricted migration of midcontinent faunas. Marine transgression, therefore, was confined in the Appalachian Basin between the low, positive Cincinnati Arch on the west and the Appalachian Mountains and their clastic wedges on the east and southeast (Fig. 5).

Perhaps one of the more intriguing features to emerge from preliminary interpretations of aeromagnetic and gravity data from basement rocks of Ohio and adjacent states is a north-south oriented zone of fracturing and intrusion in west-central Ohio that has been interpreted as a Keweenawan rift zone (Keller and others, 1982). This 50 km-wide zone can be traced from Tennessee northward across Kentucky to Ohio, where it enters the southern part of the state, with a western boundary on the east edge of the Ohio-Indiana platform and an eastern boundary in Scioto County along the axis of the Waverly Arch of Woodward (1961). Studies in northeastern Kentucky (Ettensohn, 1980; Haney, 1979) have demonstrated that the Waverly Arch was a positive structure in mid-Carboniferous time. Larsen (1984) has confirmed the existence of the Waverly Arch in southern Ohio on the basis of subsurface structure mapping and gravity data. In addition, the Olive
Figure 5
CARBONIFEROUS STRUCTURAL FEATURES

- CRATON
- Oriskany Dome
- Tyrone-Mt. Union lineament
- Transylvania fault
- Burning Springs Anticline
- Cambridge Arch
- Wavenly Arch
- Basement Fracture Zone
- Rome Trough Basin
- Tectonic Lands

Legend: 0 mi 100
0 km 100
Hill flint clay of Kentucky and its presumed equivalent in Ohio, the Sciotoville clay, are confined to the postulated axis of the Waverly Arch, which suggests that this structure was positive during the Early Pennsylvanian. In addition, the chain of islands in the Maxville sea (late Mississippian), postulated by Uttley (1974) as emergent hills of Logan Formation that were not covered by Maxville carbonates, follow the axis of the Waverly arch, again suggesting that this feature was positive during the Late Mississippian.

Additional pre-Pennsylvanian structural features that appear to have influenced deposition of Pennsylvanian sediments on the platform portion of the basin include the Rome Trough, a northeasterly oriented zone of basement fracturing (Fig. 5) that is thought to have originated in the Cambrian (Donaldson and others, 1985). Arkle (1969, 1974) noted that earliest Pennsylvanian sedimentation, including continuous sedimentation across the Mississippian-Pennsylvanian boundary, appears to have been confined to areas south of the Rome trough.

Northeastern Ohio and western Pennsylvania also exhibit structural features that appear to have influenced Pennsylvanian sedimentation. Williams and Bragonier (1974) and Rodgers and Anderson (1984) noted the existence of
structural controls in western Pennsylvania including the Tyrone-Mt. Union lineament, which the latter authors interpreted as an uplift boundary that defines a basement fracture zone. South of this lineament and more or less parallel to it (northwest-southeast) is the Transylvania fault of Root and Hoskins (1974). Gray (1983) mapped a series of high-angle, down-to-the-south faults in northeastern Ohio that are oriented similarly to the above-named features of western Pennsylvania and lie between them (Fig. 5). Hook (1985) has demonstrated that deposition of the Upper Freeport coal in the area of the famous Linton vertebrate site in northern Jefferson County, Ohio was controlled by the Highlandtown Fault of Gray (1983), which was apparently active during the Middle Pennsylvanian.

All of the above structural features appear to be related to basement control. There are, however, several structural features that appear to be products of thin-skinned, contemporaneous tectonism. Perhaps the most prominent structural feature in Pennsylvanian rocks of Ohio is the Cambridge Arch, which can be traced from northern Washington County, Ohio, northward through Noble and Guernsey counties (Collins and Smith, 1979). This structure, which has been interpreted to represent a
series of tear faults coinciding with the eastern pinchout of the Salina salt (Clifford and Collins, 1974), appears to have been active during the Pennsylvanian. It coincides with the axis of a subsurface body of Sharon sandstone (Majchszak, 1984; Hansen, 1984) and the Ames limestone appears to be represented by a shoal facies along the axis of the arch (Alan Saltsman, personnel communication, 1984). In addition, relatively thick coals (Struble and others, 1971) coincide with this axis. The Burning Springs anticline of northern West Virginia has been postulated to be a southern extension of the Cambridge Arch; however, Collins and Smith (1979) demonstrated that these two features are separate; the Burning Springs anticline extends only into southern Washington County. It is of interest to note that the Ames limestone is exposed just north of the Ohio River (location Wn-1) along the axis of the burning Springs anticline.

The Huntington-Pittsburgh synclinorium coincides with the axis of the Rome Trough and appears to have been an area of subsidence during the Pennsylvanian. Merrill (in ms) has noted a relationship between the Ames limestone and this feature.
**Mississippian-Pennsylvanian Boundary**

The boundary between Mississippian and Pennsylvanian rocks has traditionally been interpreted to be disconformable throughout the central Appalachian Basin; however, Ferm and others (1971) introduced the controversial interpretation that these two systems are conformable and represent progressive offshore to onshore facies. In this interpretation, late Mississippian carbonates (Maxville Limestone of Ohio, Greenbrier Limestone of West Virginia, Newman Limestone of Kentucky, Loyalhanna Limestone of Pennsylvania) represent offshore carbonate facies, quartz arenites (Sharon sandstone of Ohio and Pennsylvania, Lee Formation of Kentucky) represent barrier bars, and Lower Pennsylvanian coals and associated rocks represent lagoonal and lower delta plain facies.

In Ohio, which is located on the distal portion of the platform, the Mississippian-Pennsylvanian boundary does indeed appear to be marked by disconformity; however, as noted by Hansen (1984) the data base, particularly in regard to the lateral relationships of boundary rocks, is inadequate for detailed evaluation of depositional models. It is worthy of note here that the Maxville Limestone of Meramecian and Chesterian age is preserved as isolated
outliers and apparently dissected re-entrants in the southeastern quadrant of the state. Two "fairways" between Maxville outliers, one in southern Ohio and one in eastern Ohio, are filled with Sharon sandstone, a Lower Pennsylvanian unit that marks the traditional base of the Pennsylvanian System. Although a fluvial or a barrier origin of the Sharon is a topic of continuing controversy (Hansen, 1984), a large body of evidence suggests that the Mississippian-Pennsylvanian boundary in Ohio is disconformable. Sedimentation was, however, continuous across this boundary in the Pocahontas basin of southern West Virginia and Virginia (England, 1974; Donaldson and others, 1985).

The fact that sedimentation was continuous across the Mississippian-Pennsylvanian boundary in some portions of the basin whereas in other portions of the basin this boundary is marked by significant disconformity can be explained by a collision-tectonics model. The model of plate collision for the Appalachians (Oliver, 1986) postulates subsidence in the foredeep portion of the foreland basin as the collision-generated thrust sheets overrode the basin (Fig. 6). In the central Appalachians, this basin would correspond to the Pocahontas basin and sedimentation would have been continuous across the boundary. The more distal (platform) portion of the
foreland basin, corresponding to the Dunkard Basin of the central Appalachians, was marked by a domed forebulge (Fig. 6) that would have raised Mississippian rocks above base level and subjected them to considerable weathering and dissection. The oldest Pennsylvanian marine unit in Ohio (Lowellville limestone) appears to be no older than Middle Morrowan (Merrill, 1974) and suggests that Early Morrowan time on the platform did not witness extensive sedimentation.

![Diagram of late Paleozoic collision and thrusting](image)

**Fig. 6.-** Schematic block diagram of late Paleozoic collision and thrusting with consequent subsidence (Pocahontas Basin) and an orogenic forebulge in the platform portion of the north-central Appalachian Basin. The disconformable Mississippian–Pennsylvanian boundary in Ohio is postulated to represent the onset of plate collision and orogenic (pre-orogenic) forebulging on the platform. Redrawn and modified from Oliver (1986).

The Mississippian–Pennsylvanian disconformity has also been interpreted to represent a worldwide eustatic lowering of sea level (Donaldson and others, 1985; Saunders and Ramsbottom, 1986), known as the mid-
Carboniferous eustatic event. Although Saunders and Ramsbottom (1986) cite volcanism as the likely cause of this event, it is more likely, in my opinion, that this disconformity in portions of the Appalachian Basin records the onset of collision between the North American and African plates.

Basins, Sub-basins, and Marine Transgressions

Detailed distributions of individual Pennsylvanian marine units in Ohio and adjacent areas are incompletely known at present, particularly in regard to their subsurface distributions. However, available distributional data, and particularly identification and correlation of units by conodonts (Merrill, 1974; Merrill, personal communication, 1982-1986), presents sufficient data to offer preliminary interpretations of patterns of marine transgression in the Appalachian basin.

Generalized distributions of each important marine unit in Ohio are given in the section on stratigraphy and need not be repeated here. Of importance, however, is the pattern of distribution of Pennsylvanian marine rocks, through time, in Ohio and adjacent areas.

Pottsville marine units in particular exhibit distributional patterns that appear to have been influenced by localized structural and/or topographic
features. The Lowellville limestone of northern and central Ohio appears to be distributed discontinuously from central Ohio (Muskingum County) through northeastern Ohio to the type area in Mahoning County. The Lowellville equivalent in southern Ohio, referred to herein as the "Lower Mercer" limestone, is not physically connected to the Lowellville and appears to represent a separate depositional sub-basin in southern Ohio. A similar depositional pattern can be noted for the Vanport limestone. The Vanport in southern Ohio is a separate body of rock (slightly older than the northern Vanport, according to Merrill, 1974) and is not physically connected to the Vanport of northern Ohio and western Pennsylvania.

This postulated southern Ohio sub-basin, incorporating parts of Jackson, Scioto, and Vinton counties, is also characterized by numerous, local, marine ironstones that are not present in central and northern Ohio. Of particular note are the Harrison and Sharon ironstones. Hansen (1984) indicated that the marine Harrison ironstone is not present at the base of the Sharon sandstone, as is commonly stated in many reports (i.e., Stout, 1947). In general, the Pottsville and Allegheny rocks in southern Ohio are dissimilar lithologically to their supposed
equivalents in central and northern Ohio. It appears, therefore, that marine transgression during the Pottsville and perhaps the Allegheny also, had a locus in southern Ohio and another locus in northern Ohio and western Pennsylvania. Central Ohio, from Muskingum County southward, may have been a topographic high created by outliers of Maxville Limestone that were, perhaps, on the apex of the forebulge.

The most prominent area of marine influence during the Pennsylvanian was in northeastern Ohio, from Muskingum County northward, and into western Pennsylvania. Marine units in this area occur in greater frequency and tend to be thicker and more fossiliferous. For example, Merrill (1974) has noted that the interval between the Putnam Hill limestone and Vanport limestone in northern Tuscarawas County (location Tg-1) is entirely marine, indicating continued marine presence in this area. Such marine persistence, although somewhat subdued, continues into western Pennsylvania.

Northeastern Ohio and western Pennsylvania are characterized by an east-west oriented embayment, herein referred to as the northern embayment, in which marine influence was persistent throughout most of the Pennsylvanian. Apparently, brackish waters persisted in
this area until at least mid-Dunkard time because the Washington coal in Belmont County, the northernmost preserved limit of these rocks, contains a split with Lingula and bivalves.

Morris (1967) noted a similarly configured embayment during Conemaugh time and Ferm and others (1974) portray such an embayment during Allegheny time. Donaldson and Shumaker (1981) and Donaldson and others (1985) noted a similar embayment during much of Pennsylvanian time.

The major pattern of Pennsylvanian marine transgression in the north-central Appalachian Basin appears to follow a well-defined and persistent path. It is likely that the midcontinent sea entered southern Ohio between the Ohio-Indiana platform on the west and an ill-defined eastern border, perhaps represented by the Waverly arch.

This point of entry of the sea into Ohio coincides with the postulated Keeweenawan rift zone (Keller and others, 1982), which may have undergone subsidence in response to continental collision. The embayment then swung eastward (Fig. 7) across northern Ohio into western Pennsylvania. This east-west orientation of the northern embayment appears to be confined by the Tyrone-Mt. Union lineament on the north and the Transylvania fault on the
south (Fig. 7), suggesting possible subsidence of a crustal block as the primary mechanism for apparent persistent focus of the northern embayment. The southeast quadrant of Ohio, and adjacent areas in Pennsylvania and West Virginia, appears to have experienced only occasional marine influence, particularly during the Conemaugh when marine units were most extensive.

A minor marine embayment (Pocahontas Basin) was present in western West Virginia during Early and Middle Pennsylvanian time. This embayment appears to coincide, in general, with the axis of the Rome trough and probably represents the foreland foredeep of the basin.

Gondwana glaciations have long been considered as a possible mechanism for eustatic changes in sea level that were responsible for multiple marine transgressions and regressions during the Pennsylvanian (see Crowell, 1973, for a recent discussion). It is possible, perhaps, that such glaciations contributed to some transgressive-regressive sequences. However, collision tectonics has not received adequate consideration as perhaps the principal mechanism for control of marine transgression and regression in the Appalachian Basin. It is probable that marine intervals record relatively quiescent episodes of tectonism when sediment influx into the basin was minimal. A renewed episode of tectonism would spawn a clastic
wedgè. Certainly, of course, there are overprints of individual delta-lobe abandonments and subsidence which led to localized transgressions, but such mechanisms appear to be inadequate to explain all changes in shoreline position because many transgressions (such as the Ames, for example) covered an area of the basin that is greatly in excess of that which could influenced by changes in a delta lobe.

Unquestionably, some of the above interpretations are speculative and may require considerable revision as new data are acquired. Much of the currently existing data base is inadequate for detailed basinwide analysis, although surface mapping of Pennsylvanian rocks is beginning to make progress and an increasing number of subsurface core records is becoming available. In addition, the acquisition of data from basement rocks has increased at a significant rate in recent years and new perspectives on basement structure and tectonic history of the basin are beginning to emerge.
TAXONOMIC PHILOSOPHY

The majority of chondrichthyans that lived during the Pennsylvanian, and indeed throughout geologic time, are known only from isolated phosphatic remains--teeth, denticles, median fin spines, and other specialized elements. Although articulated remains of some of these fishes turn up from time to time, it is unlikely that the majority, perhaps the vast majority, of chondrichthyans will ever be known from more than isolated hard parts. As noted previously, a moribund chondrichthyan disintegrates rapidly in aerobic environments and many individuals, particularly most of those from the "carbonate facies" described herein, have little chance of being preserved as nearly complete specimens as are typical of anaerobic environments such as black shales. It is evident, therefore, that the top trophic levels of Paleozoic marine faunas will always be incompletely known.

In general, modern vertebrate paleontologists have had considerable reluctance to use standard binominal nomenclature as a means of reference to these isolated chondrichthyan remains. This attitude has been brought about, perhaps, by fears of repeating errors of the last century when species were commonly defined on the basis of minor morphological variations, resulting in a host of nominal species. Unfortunately, most of these century-old
taxonomic enigmas have yet to be resolved, principally because little effort has been expended towards this goal. And perhaps more unfortunately, some workers have regarded these long-existing taxonomic enigmas as proof that the problems are unsolvable. It is evident to me, however, from study of isolated teeth of the Order Petalodontida (Hansen, 1985) that isolated chondrichthyan remains can be organized into taxonomically workable and biologically meaningful species.

Microscopic chondrichthyan remains are similar to macroscopic ones; however, they have received far less attention—most studies that have dealt with such remains have treated only small faunas or certain groups. The earliest serious attempts to describe isolated microscopic chondrichthyan remains from Pennsylvanian rocks were those of Gunnell (1931, 1933), Harris and Hollingsworth (1933), and Harlton (1933). These remains, consisting of isolated scales and a few teeth, were treated along with mutually occurring conodont faunas in a similar taxonomic manner. Species were based on minor morphological variations, thus yielding little biologic data and a greatly confusing perspective on workable taxonomic schemes. Little attempt was made, apparently, to examine variation of teeth and denticles in modern chondrichthyan and apply a scheme of morphological variation and transition to fossil chondrichthyan remains.
The seemingly endless variety of isolated chondrichthyan remains, and indeed remains of other so-called "fragmentary fossils", led Croneis (1938) to propose an artificial taxonomic system based on the divisions of the Roman army (*Ordo militaris*). Although pronouncements such as those of Arkell and Moy Thomas (1940), that erection of genera and species based on isolated remains of fishes is valueless, apparently carried great weight in discouraging the use of standard binominal nomenclature. Systems like that proposed by Croneis (1938), however, have never received enthusiastic support. In part, perhaps, this is because such schemes are complicated and unfamiliar to most workers. In short, artificial, biologically meaningless systems seem to yield so little useful information that they have not been worth the effort. Brilliant organizational schemes are not the substitute for poor biology.

Wells (1944), in a pioneering study of isolated chondrichthyan and other fish remains from bone beds in the Columbus Limestone (Middle Devonian) succinctly noted that Linnean species are "convenient tabs for recognizable units" and function consistently better than artificial schemes such as those of Croneis (1938). To this statement may be added the observation that current knowledge of
Paleozoic chondrichthyan is such that "convenient tabs" may be, in most cases, upgraded to biologically meaningful units.

More recently, an attempt has been made to establish another artificial taxonomic system for dealing with isolated remains of fishes. This approach, known as the Scripps system for the institution at which it was developed, was first applied by Helms and Riedel (1971) and further developed by Doyle, Kennedy, and Reidel (1974). This system, applied by these authors to isolated fish remains from deep-sea cores of Mesozoic and Cenozoic age, uses a series of letters and numbers as descriptors of morphology. As an aid to these long, cumbersome series of descriptors, colloquial names have been developed for individual teeth and denticles. These authors refer to microscopic fish remains, collectively, as "ichthyoliths" and have coined the term "stratignathy" for the study of the stratigraphic distribution of these fossils. Both terms are, in my opinion, abhorrent and should be avoided by serious workers. We are certainly capable, in most cases, of recognizing and differentiating teeth, denticles, scales, and other hard parts of fishes and should refer to them by their proper designation. The term "biostratigraphy" is well known, long established and is
applied to any fossil group. There is certainly little need to develop a separate term for the study of the stratigraphic distribution of each group of fossils.

Recently, Tway (1979a, 1979b, 1984) and Tway and Zidek (1982, 1983a, 1983b) have applied the Scripps system of artificial taxonomy to Pennnsylvanian microscopic fish remains. The present study clearly points out the limitations and shortcomings of the Scripps system, at least as applied to Pennsylvanian microscopic chondrichthyan remains. Obviously, the Scripps system provides virtually no biological insight on these fossils. No interpretations of systematic placement, with consequent evolutionary implications, are possible with this system. In addition, interpretations of functional morphology and faunal diversity and composition are lacking. It is also quite obvious from perusal of the systematic paleontology section of the present study that minor variations in morphology of a particular element type require variations in the descriptor code of the Scripps system. Obvious morphological transition series are therefore designated by several descriptor codes and subtypes.

Although the Scripps system is highly computer compatible and has biostratigraphic utility, it has limitations in addition to those noted above. Tway (1979)
noted that the descriptor codes are long and cumbersome and can easily be inaccurately transcribed. This system is unlikely to be widely accepted by paleoichthyologists and has been rejected by one already (Schultze, 1985).

That such systems as the Ordo militaris of Croneis (1938) or the Scripps system would be seriously considered as an alternative to a classic Linnean system is indicative of the lack of study and understanding of the fossil record, particularly that portrayed by Paleozoic chondrichthyans. Unfortunately, there has been a common concept that isolated chondrichthyan remains exhibit unlimited variation and that describing teeth and particularly scales would be a task similar to describing the grains of sand on a beach. The current study clearly demonstrates the fallacy of such speculations and also demonstrates that application of basic biological principles of morphological variation and the concept of morphological transition series is sufficient to delineate workable species.

In part, the difficulties experienced by many paleontologists in dealing with isolated parts of an organism stem from a desire for perfection in the fossil record, or at least perfection in the descriptions of a particular organism. However, as pointed out by Jeppsson and Merrill (1982) many species in paleontology and
neontology are form species, that is, recognized solely on the basis of morphology without recourse to phylogenetic relationships.

As noted previously, the nature of the chondrichthyan skeleton is such that only under special circumstances of preservation will articulated skeletal remains be preserved. Consequently, the majority of chondrichthyans that ever lived will be known only from isolated teeth, scales, and such. Consequently, we are faced with the decision to regard the situation as taxonomically hopeless and disregard such remains for their biostratigraphic, paleoecologic, and evolutionary potential or to apply serious study to them with the hope of solving these puzzles.

All of these isolated chondrichthyan remains are properly considered as organ taxa and it is intuitively obvious that a species based on teeth is probably synonymous with other species based on scales, median fin spines, or other organs. This fact has, in itself, been discouraging to some workers who fear the "sin" of coining a name that will ultimately become a junior synonym. Obviously, due care must be exercised in the naming process and large collections are recommended, if not necessary, in order to assess morphological variation in a species.
Paleoichthyologists need only be familiar with the studies of conodonts in order to obtain an excellent example of methodology and procedures to follow in working with isolated remains of organisms. The current practice of multielement taxonomy, introduced and developed by Bergstrom and Sweet (1966) and Sweet and Bergstrom (1972), has permitted the consolidation of numerous "form" species based on single conodont elements, into an organ species based on the concept of an apparatus.

Isolated chondrichthyan remains are philosophically no different than are remains of conodonts except, perhaps, chondrichthyan remains are more complex in their degree of variation. Chondrichthyan workers have a distinct advantage in knowing a great deal about the biology of their study organisms from both Recent and fossil specimens. There will always be difficulties with a certain proportion of chondrichthyan remains. Certainly, some dentitions will never be properly associated with the denticles that graced the skin of the same chondrichthyan and perhaps many denticles will not be properly associated with other dentine varieties from the same fish. Nevertheless, it is likely that many fossil chondrichthyans will eventually be known from their teeth, scales and other elements, as one species, although none of these elements will ever be found in anatomic articulation. Although the current study has not been
overwhelmingly successful in associating such isolated remains, it should be kept in mind that this is an initial first step. Additional sampling and larger collections will probably establish such associations through mutual occurrence data.

Nevertheless, this study has demonstrated that what initially appeared to be a tremendous variety of remains could be divided into a finite number of species, most of which are probably reliable for both biostratigraphic and paleoecologic studies. In my opinion, this study also clearly demonstrates the utility of a traditional binominal system, in contrast to an artificial one, at least for the chondrichthyan remains considered here.
Although the principal focus of this report is on the chondrichthyan microfauna from Pennsylvanian marine rocks of the Appalachian Basin, understanding of both paleoecologic and biostratigraphic aspects of this fauna must include information on the chondrichthyan macrofauna. This macrofauna includes larger specimens of teeth and fin or dermal spines that have been collected on the outcrop, commonly as isolated specimens. Fortunately, a very large collection of these remains has been assembled over the years, principally by Dr. Myron T. Sturgeon and his students at Ohio University. Important additions to this collection have been made by William J. Hlavin, the late Lloyd J. Millhorn, James L. Murphy, Alan L. Saltsman, and the author. This collection is reposited at Orton Museum, The Ohio State University. Another significant collection, although smaller than the Orton collection, was made by the late John J. Burke and is reposited at the Cleveland Museum of Natural History. These macroscopic specimens will be the basis of a future report.

Although macroscopic teeth and spines in the collections mentioned above are not part of the systematic portion of this report, I have studied most of them in some detail and can provide reasonably accurate
identifications. An assessment of both the macrofauna and microfauna is necessary in order to evaluate the paleoecological composition of the chondrichthyan fauna and to assess the biostratigraphic and systematic aspects of this collection. It is obvious that many dermal denticles in the collection were derived from chondrichthyans known by teeth in the macrofauna. In addition, the median fin spines and dermal spines in the collection were probably derived from chondrichthyans known from teeth in either the macrofauna or microfauna. It is quite obvious that the number of taxa in the fauna is too high when teeth, denticles, and spines are considered as individual species. The most accurate assessment of the faunal composition is therefore based on species defined by teeth.

Table 1 lists all defined chondrichthyan taxa from both the macroscopic and microscopic collections. Twenty-nine taxa are based on teeth; 17 of these are known only from the microfauna. Most of these taxa are well documented by numerous specimens and appear to represent distinct members of the chondrichthyan fauna. It is probable that additional collecting in Pennsylvanian marine limestones of Ohio and adjacent areas of the Appalachian Basin will yield teeth representing a few additional species. Although comprehensive modern studies
of the chondrichthyan fauna of the "carbonate facies" in Pennsylvanian rocks of other areas of the United States have not been carried out, older faunal reports, such as those of St. John and Worthen (1875, 1883) and Eastman (1903), do not suggest that more than a few species based on teeth will be added to the fauna. Tway and Zidek's (1982, 1983) illustrations of "carbonate facies" microfauna from the Midcontinent Basin indicate only one species based on teeth (Xenacanthus nebraskensis) that has not been found in the Appalachian Basin. It is probable, therefore, that the list of taxa in Table 1 is a relatively accurate and nearly complete census of the chondrichthyan fauna of the "carbonate facies" of the Appalachian basin.

Table 1 also lists the probable function of teeth in prey capture and the probable size of the prey. Three categories of prey capture can be distinguished. Piercing or stabbing teeth consist of several spikelike, elongated cusps that served to stab and immobilize prey and prevent the prey from escaping. Teeth of xenacanthids, ctenacanthids, and symmoriids are in this category. It is probable that chondrichthyans with this tooth form preyed upon nektic organisms including other chondrichthyans, paleoniscoids, acanthodians, and perhaps nektic invertebrates such as crustaceans. Prey size, either small
or large, is based on the size of the teeth with the assumption that small teeth, in the microscopic range, were used to capture and subdue relatively small prey. Chondrichthians such as *Symmorium reniforme* grew perhaps two meters or more in length, and possessed correspondingly large teeth. Obviously, larger individuals of this species were capable of capturing and ingesting large prey; indeed, it may be speculated that any other creature in Pennsylvanian seas was fair game for this shark. Smaller individuals of this species, documented by teeth in the microfauna, preyed upon smaller nekton. A total of six species in the fauna are interpreted to have had teeth of the piercing/stabbing type.

A second, and perhaps more ambiguous category of tooth function, includes teeth that have a crown margin with a sharp, laterally elongate cutting edge. Teeth of this morphology are interpreted to have functioned in nipping, cutting or shearing of prey. At least five species possess this tooth form, including four petalodonts and one hybodont. Four of these five forms are interpreted to have utilized large prey, based on the size of the teeth. It is probable that this group of teeth was utilized for slightly different functions and different prey. *Janassa*, one of the genera known from teeth in the macrofauna, is also known by nearly complete specimens from the Upper
Permian of Germany that have stomach contents consisting of brachiopods, crustaceans, and foraminifers. A straight cephalopod from Pennsylvanian rocks is interpreted by Hansen and Mapes (in press) to have been bitten by the petalodont, *Petalodus*. Teeth of the shearing/nipping variety probably were used to crush a variety of benthic organisms including both hard-shelled and soft-shelled forms. In addition, teeth such as those of *Petalodus* could have functioned in slicing nektic prey such as other fishes.

A final category of tooth function includes those teeth clearly adapted for crushing prey, most probably hard-shelled invertebrates. Seventeen species based on teeth are included in this category; six were capable of crushing relatively large prey such as larger brachiopods, bivalves, cephalopods, and gastropods. Those species distinguished by relatively small teeth probably preyed upon small molluscs, foraminifers, crustaceans, and soft-bodied invertebrates. Cochliodontids and hybodontids were groups dominated by these tooth forms. Collectively, those forms with crushing teeth and probably some of the species characterized by teeth of the nipping/cutting category were major predators on the benthic community of the "carbonate facies". As suggested by Signor and Brett (1984), such predation may have been influential in extinction events among several invertebrate groups.
The fauna of the "carbonate facies" of Pennsylvanian rocks of the Appalachian basin, as noted above, appears to be typical of rocks of similar age and lithology throughout the United States. This fauna differs, however, in many respects from the chondrichthyan fauna of sheety black shales of the Eastern Interior and Midcontinent basins, described in recent years by Zangerl (1976, 1981), Zangerl and Case (1973), and Williams (1985). These shales bear in common with rocks in the Appalachian basin such forms as Cobelodus aculeatus, Stethacanthus altonensis, Symmorium reniforme, and Phoebodus heslerorum. A symmoriid, Denaea meccaensis, is absent in the Appalachian Basin although another species of this genus, D. saltsmani is present. Absent from the black shales are petalodontids, hybodontids, cochliodontids, psammodontids, xenacanthids, and neoselachians, all of which are interpreted probably to have fed on benthic invertebrates.

The black shales, on the other hand, contain a chondrichthyan fauna that includes, in addition to the forms listed above, representatives of a number of species or groups that are absent in the Appalachian Basin. These include iniopterygians (several genera and species), Calopodus apicalis, Edestus heinrichsi, Ornithoprion hertwigi, and most species of eugeneodontids. It is well
established that these black shales were deposited in environments with anoxic bottom conditions that excluded benthic organisms and, consequently, benthic-feeding fishes. The absence of a particular species of chondrichthyan from the black shale fauna suggests, therefore, that its principal diet consisted of benthos. Symmoriids, interpreted as stabbers of nektic prey, were apparently not limited by bottom conditions and could move freely between the black shale and carbonate environments as their prey was in the oxygenated surface waters common to both environments.

Although a diligent search was carried out during the course of this study, black shales of the variety found in the Eastern Interior and Midcontinent basins were not encountered in the Appalachian Basin, even though exposures of marine rocks in this area are interpreted to range from shoreline to at least several tens of kilometers offshore. The origin of the sheety black shales has been the subject of much debate in recent years with a shallow-water origin proposed by Zangerl and Richardson (1963) and a deep-water origin proposed by Heckel (1977). A detailed discussion of this debate is beyond the scope of the present report; however, it is important to note these differences in the chondrichthyan faunas of the
black shale and carbonate environments. Such information has not been considered previously in published debate on alternative depositional models for these black shales.
Table 1.—Summary of Pennsylvanian marine chondrichthyan taxa from the Appalachian basin. Categories indicate functional mode of teeth and probable prey size, respectively, occurrence in macrofauna (M) or microfauna (m), and relative abundance (C=common; A=abundant; R=rare).

<table>
<thead>
<tr>
<th>Teeth</th>
<th>Function</th>
<th>Prey Size</th>
<th>Occurrence</th>
<th>Relative Abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Xenacanthus tridentatus</td>
<td>Stabbing</td>
<td>Small</td>
<td>M</td>
<td>R</td>
</tr>
<tr>
<td>Phoebodus heslerorum</td>
<td>Stabbing</td>
<td>Small</td>
<td>M</td>
<td>R</td>
</tr>
<tr>
<td>Zangerlodus williamsi</td>
<td>Stabbing</td>
<td>Small</td>
<td>A</td>
<td></td>
</tr>
<tr>
<td>Cobelodus aculeatus</td>
<td>Stabbing</td>
<td>Small</td>
<td>M</td>
<td>R</td>
</tr>
<tr>
<td>Denaea saltsmani</td>
<td>Stabbing</td>
<td>Small</td>
<td>R</td>
<td></td>
</tr>
<tr>
<td>Stethacanthus altonensis</td>
<td>Stabbing</td>
<td>Small</td>
<td>R</td>
<td></td>
</tr>
<tr>
<td>Symmorium reniforme</td>
<td>Stabbing</td>
<td>Small to Large</td>
<td>M, M, C</td>
<td></td>
</tr>
<tr>
<td>Hybodont tooth &quot;A&quot;</td>
<td>Crushing</td>
<td>Small</td>
<td>M</td>
<td>R</td>
</tr>
<tr>
<td>Lissodus duffini</td>
<td>Crushing</td>
<td>Small</td>
<td>R</td>
<td></td>
</tr>
<tr>
<td>Lissodus zideki</td>
<td>Nipping/Slicing</td>
<td>Small</td>
<td>M</td>
<td>A</td>
</tr>
<tr>
<td>Maisodus johnsoni</td>
<td>Crushing</td>
<td>Small</td>
<td>A</td>
<td></td>
</tr>
<tr>
<td>Uncertain hybodonts</td>
<td>Crushing</td>
<td>Small</td>
<td>R</td>
<td></td>
</tr>
<tr>
<td>Orodus sp.</td>
<td>Crushing</td>
<td>Large</td>
<td>M, R</td>
<td></td>
</tr>
<tr>
<td>Agassizodus variabilis</td>
<td>Crushing</td>
<td>Large</td>
<td>M, R</td>
<td></td>
</tr>
<tr>
<td>Lagarodus angustus</td>
<td>Crushing</td>
<td>Small to Large</td>
<td>M, M, R</td>
<td></td>
</tr>
</tbody>
</table>
### Table 1.—Continued.

**PETALODONTIDS**

<table>
<thead>
<tr>
<th>Species</th>
<th>Type</th>
<th>Size</th>
<th>Gender</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cholodus inaequalis</td>
<td>nipping</td>
<td>large</td>
<td>M, C</td>
<td></td>
</tr>
<tr>
<td>Janassa sp.</td>
<td>nipping</td>
<td>large</td>
<td>M, A</td>
<td></td>
</tr>
<tr>
<td>Peripristis semicircularis</td>
<td>nipping</td>
<td>large</td>
<td>M, C</td>
<td></td>
</tr>
<tr>
<td>Petalodus ohioensis</td>
<td>nipping</td>
<td>large</td>
<td>M, A</td>
<td></td>
</tr>
<tr>
<td>Polyrhizodus carbonarius</td>
<td>crushing</td>
<td>large</td>
<td>M, R</td>
<td></td>
</tr>
</tbody>
</table>

**COCHLIODONTIDS**

<table>
<thead>
<tr>
<th>Species</th>
<th>Type</th>
<th>Size</th>
<th>Gender</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cochliodus sp.</td>
<td>crushing</td>
<td>large</td>
<td>M, R</td>
<td></td>
</tr>
<tr>
<td>Deltodus angularis (includes Sandalodus carbonarius)</td>
<td>crushing, large</td>
<td>M, A</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deltodus cf. D. propinquus</td>
<td>crushing</td>
<td>large</td>
<td>M, R</td>
<td></td>
</tr>
</tbody>
</table>

**NEOSELACHIANS**

<table>
<thead>
<tr>
<th>Species</th>
<th>Type</th>
<th>Size</th>
<th>Gender</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cooleyella peculiaris</td>
<td>crushing</td>
<td>small</td>
<td>m, A</td>
<td></td>
</tr>
</tbody>
</table>

**UNCERTAIN HIGHER TAXON**

<table>
<thead>
<tr>
<th>Species</th>
<th>Type</th>
<th>Size</th>
<th>Gender</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Venustodus argutus</td>
<td>crushing</td>
<td>small</td>
<td>m, R</td>
<td></td>
</tr>
<tr>
<td>Dentition tooth &quot;A&quot;</td>
<td>crushing</td>
<td>small</td>
<td>m, R</td>
<td></td>
</tr>
<tr>
<td>Dentition tooth &quot;B&quot;</td>
<td>crushing</td>
<td>small</td>
<td>m, R</td>
<td></td>
</tr>
<tr>
<td>Dentition tooth &quot;C&quot;</td>
<td>crushing</td>
<td>small</td>
<td>m, R</td>
<td></td>
</tr>
</tbody>
</table>

**ICHTHYODORULITES**

<table>
<thead>
<tr>
<th>Species</th>
<th>Type</th>
<th>Size</th>
<th>Gender</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acondylacanthus nuperus</td>
<td>M, R</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ctenacanthus lamborni</td>
<td>M, R</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;Harpacanthus&quot; sp.</td>
<td>M, R</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Listracanthus sp.</td>
<td>M, R</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Physonemus acinaciformis</td>
<td>M, R</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sphenacanthus marshi</td>
<td>M, R</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**DENTICLES**

<table>
<thead>
<tr>
<th>Species</th>
<th>Type</th>
<th>Size</th>
<th>Gender</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cooperella striata</td>
<td>m, R</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cooperella typicalis</td>
<td>R</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dermal dentine &quot;A&quot;</td>
<td>m, R</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dermal dentine &quot;B&quot;</td>
<td>m, R</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dermal dentine &quot;C&quot;</td>
<td>m, R</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dermal dentine &quot;D&quot;</td>
<td>m, R</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dermal dentine &quot;E&quot;</td>
<td>m, R</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dermal dentine &quot;F&quot;</td>
<td>m, R</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kirkella typicalis</td>
<td>m, C</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 1.- Continued.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>Locality</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Moreylla typicalis</em></td>
<td>m, C</td>
<td></td>
</tr>
<tr>
<td>Mucous membrane denticle &quot;A&quot;</td>
<td>m, R</td>
<td></td>
</tr>
<tr>
<td><em>Nebraskella ossiani</em></td>
<td>m, R</td>
<td></td>
</tr>
<tr>
<td><em>Ohioella merrilli</em></td>
<td>m, C</td>
<td></td>
</tr>
<tr>
<td><em>Petrodus sp.</em></td>
<td>M, R</td>
<td></td>
</tr>
<tr>
<td><em>Sturgeonella quinqueloba</em></td>
<td>m, A</td>
<td></td>
</tr>
<tr>
<td>Symmoriid mucous membrane denticle</td>
<td>m, A</td>
<td></td>
</tr>
<tr>
<td><em>Tawavella zideki</em></td>
<td>m, C</td>
<td></td>
</tr>
<tr>
<td><em>Williamsella striata</em></td>
<td>m, C</td>
<td></td>
</tr>
<tr>
<td><em>Williamsella typicalism</em></td>
<td>R</td>
<td></td>
</tr>
</tbody>
</table>
BIOSTRATIGRAPHY

A principal objective of this study was to test the utility of using chondrichthyan remains for biostratigraphic analysis. Little previous investigation of this potential has been carried out for late Paleozoic chondrichthyans, principally because many species have been so poorly defined that any such investigation would require extensive taxonomic revision of a particular fauna.

The studies of Tway (1982) and Tway and Zidek (1982, 1983) suggested biostratigraphic potential for some chondrichthyan remains that are identical to some of those described herein. However, the use of an artificial taxonomic system in these studies presents difficulties with biostratigraphic analysis because many distinct subtypes in this system represent morphological punctuations within a transition series. In addition to this serious limitation, in my opinion, Tway and Zidek's analyses dealt with chondrichthyan remains from rocks of Virgilian age, perhaps a much too limited interval to assess properly the stratigraphic ranges of many species.

It is apparent to even the casual observer of late Paleozoic chondrichthyan faunas that many genera have long ranges. Even on the species level, some taxa appear to
have persisted for a considerable period of time. For example, teeth of *Stethacanthus altonensis* appear to remain unchanged from Late Devonian through Pennsylvanian. However, on the other hand, detailed study of isolated teeth that superficially appear to be similar, if not identical, commonly reveals distinct species that may have more limited stratigraphic ranges.

In part, the results of this study, from a biostratigraphic perspective, are disappointing although not necessarily surprising. Only ten taxa from the microfauna appear to have limited stratigraphic ranges within the Pennsylvanian sequence, although all but of few of these are so rare in the Appalachian fauna that their utility as index fossils is seriously limited. Teeth and other elements from the macrofauna appear to be even less useful at this stage of investigation. However, it should be kept in mind that this study is an initial first step into this line of investigation and it is quite possible that additional sampling and study will improve the biostratigraphic potential of Pennsylvanian chondrichthyan remains.

It should be noted at this point that Pennsylvanian rocks may not be the optimum sequence in which to test the biostratigraphic utility of isolated, late Paleozoic
chondrichthyan remains. Although the existing literature does not document the chondrichthyan record from Lower Carboniferous rocks very well, my studies (unpublished) of these faunas indicate a considerably higher diversity of species and apparently more limited stratigraphic ranges. The Mississippian, particularly the Chesterian, was a time of rapid diversification of the chondrichthyan fauna. By the beginning of the Pennsylvanian, however, many species were extinct, leaving a depauperate chondrichthyan fauna that was relatively stable until at least the Early Permian. Reasons for these changes are uncertain and unexplored at this time but the diversity, stratigraphic distributions, and evolution of late Paleozoic chondrichthyan, based on teeth and other isolated elements, are subjects for worthwhile future research.

The following list notes the ten taxa in the microfauna of Pennsylvanian marine rocks of the Appalachian Basin that exhibit limited stratigraphic ranges. The stratigraphic distributions for the entire fauna, both microfauna and macrofauna, are given in Table 2. This table also lists frequency data for the microfauna. In addition, discussions of stratigraphic distributions for each species are given in the Discussion sections of the systematic portion of this report.
Microscopic chondrichthyan remains with limited distributions

Tooth "A" - Upper Allegheny
Dermal dentine "A" - Conemaugh
Dermal dentine "D" - Conemaugh
Lagarodus angustus - Lower Allegheny
Lissodus duffini - Upper Conemaugh
Lissodus zideki - Upper Conemaugh
Mucous membrane dentine "A" - Conemaugh
Nebraskella ossiani - Conemaugh
Twayella zideki - Conemaugh
Xenacanthus tridentatus - Pottsville and Allegheny

No chondrichthyan elements in the fauna appear to be restricted to a particular unit. Those elements that are restricted to one bed or perhaps to two adjacent beds occur in such low frequency, perhaps only one or two specimens, that they have limited biostratigraphic value. Indeed, higher frequencies may indicate a broader distribution. Several teeth or denticles that occur in higher frequencies appear to be restricted to a particular group or groups of rocks.

Teeth of Xenacanthus tridentatus appear to define Pottsville and Allegheny rocks, although these teeth occur in relatively low frequencies. This apparently limited distribution is reinforced by the fact that these teeth did not occur in the relatively abundant microfaunas from Conemaugh rocks and by the fact that teeth of this species apparently did not occur in Tway and Zidek's (1982, 1983) samples from Virgilian rocks of the Midcontinent basin.
The absence of *X. tridentatus* teeth in Midcontinent rocks of Virgilian age is not likely to be attributable to paleogeographic variances because the holotype of this species was derived from Morrowan rocks of Oklahoma.

Dermal denticles assigned to *Twayella zideki* also appear to have biostratigraphic value. These denticles are confined to Conemaugh rocks above the Brush Creek and appear to occur in a high enough frequency to expect their occurrence with some regularity, although the data (Table 2) suggest that they cannot be expected in every sample. No specimens were derived from the oldest Conemaugh marine unit, the Brush Creek, although nine productive samples from this horizon yielded an average of 27 chondrichthyan elements per sample. Until demonstrated to the contrary, the absence of *Twayella zideki* denticles from this unit must be regarded as genuine.

The teeth of a psammodont, *Lagarodus angustus*, appear to be confined to the Putnam Hill and Vanport of the lower Allegheny Group, although these teeth occur in very low frequency. This stratigraphic distribution is generally consistent with occurrences of teeth of this species in the Minturn Formation of Colorado, although the Minturn specimens are larger and part of the macrofauna. *Lagarodus*
angustus teeth also appear to be more abundant in the Minturn than in the Appalachian units. It is probable that L. angustus teeth will eventually be found in older Pennsylvanian rocks and perhaps also in upper Allegheny marine units. Their absence in Conemaugh rocks appears to be genuine, as both microfaunas and macrofaunas are abundant at these horizons.

The 2,281 chondrichthyan elements from 106 localities occurred at an average frequency of 21.5 elements per sample. The Conemaugh Group yielded the greatest number of elements, 1,840, and the highest frequency per sample, 32.9. The Noble limestone yielded the highest frequency of chondrichthyan elements with 51.5 per sample. The Portersville (34.5) and Ames (30.1) were next highest in frequency. Allegheny units were the least frequently sampled (26) and yielded the smallest number of elements (5.5). The highest frequency in this group of rocks was in the Putnam Hill with an average of 7.7 elements per sample. Pottsville rocks averaged 11.4 elements per sample with the highest frequency in the Lowellville ("Lower Mercer") with an average of 21.7 elements per sample. It can be noted (Table 2) that some elements that range through all or most of the Pennsylvanian sequence
have higher frequencies in Conemaugh units. It may be possible at some point to utilize these frequency data in determining individual units or at least groups of rocks.

Although it appears that chondrichthyan skeletal elements may be considerably less useful than conodonts or fusulinids for biostratigraphic studies of Pennsylvanian rocks, it must be noted that they have not been subjected to nearly the intensity of study as have these latter groups. Indeed, the present study is the first attempt to define species among a total Pennsylvanian chondrichthyan microfauna. It is obvious that improvements will be made upon this taxonomic scheme and new species may be added to the fauna. Such additions and refinements may improve considerably upon the biostratigraphic perceptions presented here. Certainly, the eventual linking of teeth and denticles of the same chondrichthyan species will generate improvements in the biostratigraphic scheme. It certainly may be possible eventually to delineate range zones based on chondrichthyan taxa.
Table 2.- Stratigraphic distribution of the marine chondrichthyan fauna in the Appalachian Basin. Frequency data given for microfauna. Presence (+)/absence (-) noted for macrofauna. Abbreviations for stratigraphic units: LM=Lowellville and "Lower Mercer"; BB=Boggs; UM=Upper Mercer; PH=Putnam Hill; VP=Vampour; CW=Columbiana; WA=Washingtonville; BC=Brush Creek; CA=Canonsburg; P=Portersville; N=Noble; A=Ameos; G=Gaysport; S=Skelley. The Gaysport (G) yielded no microscopic chondrichthyan remains and is therefore not listed under this section of the table.

**MICROFAUNA**

| TAxON               | L | B | LN | UN | PH | VP | CO | WA | BC | CA | P | N | S |
|---------------------|---|---|----|----|----|----|----|----|----|----|----|---|---|---|
| Cobelodus aculeatus |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Cochliodons         |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Coolerellodespeciars | 2 | 3 | 9  | 9  | 3  |    | 3  | 8  | 13 | 21 | 16 | 61| 5 |
| Deniceaeelasmidae   |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Dentition tooth "A" |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Dentition tooth "B" |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Dentition tooth "C" |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Hybodont tooth "A"  |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Lemnascodon angustus |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Lissodus dentifloris |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Lissodus zideki      |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Maimaxodon johnsoni |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Petalodon           |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Pholusae eae尤其herorum |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Stere. aitonensis   |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Troamiae raniformes |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Tenusodae aeginae   |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Tencan. tridentatus  |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Zangerlodon williamsi | 4 | 1 | 2  | 2  |    |    |    |    |    |    |    |   |   |   |
| Cooperella striata  |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Cooperella typicales |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Dermal denticle "A" |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Dermal denticle "B" |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Dermal denticle "C" |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Dermal denticle "D" |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Dermal denticle "E" |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Kirkella typicales  |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Mooreella typicales |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Mucoa. mes. dent. A |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Nebeskella ossiani  |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Cheliodus serruleus |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Pterog. echinodermi |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Pant. quinquelebs  | 74 | 5 | 38 | 24 | 19 |    |    |    |    |    |    |   |   |   |
| Symm. sec. dent.   | 21 | 3 | 3  | 5  | 6  | 1  | 2  | 65 | 48 | 69 | 28 | 138| 16 |
| Tavella zideki      |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Williama striata   |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| Williama typicales |   |   |     |    |    |    |    |    |    |    |    |   |   |   |
| No. of localities  | 7 | 2 | 13 | 6  | 9  | 10 | 5  | 2  | 9  | 12 | 6  | 2  | 24 | 3 |
| No. of elements     | 152|17|52|97|69|59|8|8|246|351|208|103|722|210 |
| Elements per locality|22|9|4|16|8|6|2|4|27|29|35|52|30|70 |

**MACROFAUNA**

| TAxON               | L | B | LN | UN | PH | VP | CO | WA | BC | CA | P | N | A | G | S |
|---------------------|---|---|----|----|----|----|----|----|----|----|----|---|---|---|---|---|
| Acanthias variabilis |   |   |     |    |    |    |    |    |    |    |    |   |   |   |   |   |
| Acanthias aculeatus |   |   |     |    |    |    |    |    |    |    |    |   |   |   |   |   |
| Cheliodus inaequalis |   |   |     |    |    |    |    |    |    |    |    |   |   |   |   |   |
| Cobelodus sp.       |   |   |     |    |    |    |    |    |    |    |    |   |   |   |   |   |
| Ctenacanthus laboresi |   |   |     |    |    |    |    |    |    |    |    |   |   |   |   |   |
| Delitodus angolarius |   |   |     |    |    |    |    |    |    |    |    |   |   |   |   |   |
| L. cf. X. propinquus |   |   |     |    |    |    |    |    |    |    |    |   |   |   |   |   |
| Harpocanthus sp.    |   |   |     |    |    |    |    |    |    |    |    |   |   |   |   |   |
| Janaceae sp.        |   |   |     |    |    |    |    |    |    |    |    |   |   |   |   |   |
| Orodus sp.          |   |   |     |    |    |    |    |    |    |    |    |   |   |   |   |   |
| Perigi. semicircularis |   |   |     |    |    |    |    |    |    |    |    |   |   |   |   |   |
| Petalodon echinodes |   |   |     |    |    |    |    |    |    |    |    |   |   |   |   |   |
| Thalassem. scinciformis |   |   |     |    |    |    |    |    |    |    |    |   |   |   |   |   |
| Poliroleboid. carbonarius |   |   |     |    |    |    |    |    |    |    |    |   |   |   |   |   |
| Sphenacanthus maraibus |   |   |     |    |    |    |    |    |    |    |    |   |   |   |   |   |
| Sphenacanthus raniformes |   |   |     |    |    |    |    |    |    |    |    |   |   |   |   |   |
SYSTEMATIC PALEONTOLOGY

- TEETH
Class Chondrichthyes Huxley 1880
Subclass Elasmobranchii Bonaparte 1838
Order Xenacanthida Glickman 1964
Genus Xenacanthus Beyrich 1848

**Characterization.**- Elasmobranchs possessing xenacanthid teeth in which the lateral cusps are circular to subcircular in cross section and possess cristae on their labial margin.

*Xenacanthus tridentatus* (Harlton) 1933

*Plate I, Figs. 1-16*

**Bransonella tridentata** Harlton, 1933, p. 14, Pl. 3, figs. 9a-c.

**Dittodus tridentata**, Zidek, 1972, p. 176; 1973, p. 97, fig. 3c,d.

**Thrinacodus (Bransonella) tridentata**, Johnson, 1984, p. 183-185, figs. 15a-c.

**Holotype.**- NMNH 85529.

**Referred Specimens.**- See Table 3 and Occurrence.

**Distribution.**- Chesterian of Kentucky, Pottsville and Allegheny of the Appalachian Basin, Lower Pennsylvanian of the Midcontinent Basin, and Montana.

**Characterization.**- Xenacanth teeth with tooth base slightly longer in labiolingual dimension than in anteromedial dimension, relatively thin, concave basally,
with prominent lingual notch and lacking a lingual foramen. Principal nutrient foramen in central portion of concave aboral surface of tooth base. Apical button prominent, overhanging labially, distinct lingually, not in contact with principal cusps. Basal tubercle half-moon shaped, prominent, and raised above aboral surface. Cristae of cusps descend to base of tooth on labial surface with a definite spiral pattern in which cristae appear to pass from one cusp to the next. Medial cusp less than one half the height of principal cusps.

**Description.**—The following observations are based on 20 specimens from Mississippian and Pennsylvanian rocks of Ohio, Kentucky, Montana, and Oklahoma and comparisons with descriptions and figures of the holotype. Morphological designations generally follow Johnson (1979, 1984) with some minor exceptions (Fig. 8).

Tooth bases tend to be slightly longer in the labiolingual dimension than in the anteromedial-posterolateral dimension (1-l/am-pl = 1.06) and are relatively thin in the aboral-oral dimension. The apical button (apical articulating boss) is prominent and raised, with a shape that is nearly circular on small specimens to nearly triangular, narrowing labially between the cusps, to somewhat elliptical, tapering both labially and lingually. Commonly, the apical button has a slight
overhang on its labial margin and is very close to, but not in contact with, the principal cusps. The apical button may, however, touch the lingual edge of the intermediate cusp in some specimens. Lingually, the apical button may descend sharply onto the lingual edge of the tooth base or it may show a distinct overhang. In all available specimens, however, the apical button is distinct lingually from the tooth base. The apical button commonly has a roughened, punctate surface.

Figure 8. Morphological features of Xenacanthus tridentatus teeth. A, labial; B, lateral; C, aboral; D, oral. Abbreviations: ab, apical button; am-pl, anteromedial-posterolateral; bt, basal tubercle; cr, cristae; g, groove for nutrient canal; lc, lateral cusps; l-l, labiolingual; ln, lingual notch; mc, medial cusp; mf, minor foramina; mta, major transverse axis.

The basal tubercle (basolabial articulating boss) is a prominent lunate structure on the basolabial portion of the tooth base. The aboral surface of the basal tubercle is slightly concave and distinct lingually from the tooth base.
The aboral surface of the tooth base is slightly concave in the central portion and penetrated by several small, irregularly distributed foramina. Most specimens exhibit a single, comparatively large, foramen in the central portion of the aboral surface which is connected by a shallow groove to the lingual notch in the tooth base.

The lingual margin of the tooth base is marked by a prominent notch or cleft. In one specimen (OSU 35354, unfortunately lost during removal from a stub for scanning electron microscopy) lingual edges of the notch are in contact and form a tubelike canal that opens to the aboral surface of the tooth base. Although this feature on this specimen appears superficially to be a prominent lingual foramen, it is not connected directly to the internal portion of the tooth (see Discussion).

The principal cusps diverge laterally at about a 30-degree angle, taper distally, and recurve lingually. Proximally, the principal cusps are compressed but appear to become nearly circular distally. Proximally, the long cross-sectional axis (major transverse axis=mta) of each cusp is parallel to or at a slight angle with the labial margin of the tooth base. Approximately six relatively coarse cristae are present on the labial side of the principal cusps. These cristae become finer and more numerous, owing to bifurcation, as they descend in an
inclined, spiral-like pattern to the base of the tooth. The crista are truncated at the base of the tooth by a faint indentation or groove.

A medial cusp is almost always present; however, one specimen in the collection (OSU 35356, Pl. I, figs. 11-13) lacks this cusp. The medial cusp is narrow and compressed in the anteromedial-posterolateral (am-pl) dimension and is half or less the height of the principal cusps. Very fine crista, up to five in number, are present on this cusp.

DISCUSSION

Until very recently, the teeth of xenacanth sharks have not received adequate and comprehensive treatment, with the result that reliable and meaningful identifications and comparisons were impossible. The significant works of Johnson (1979, 1980, 1984), based on large samples of teeth from North America, have demonstrated the taxonomic integrity of xenacanth shark species based partially or solely on isolated teeth. As a consequence of these studies, the stratigraphic record, geographic distribution, and taxonomic diversity of xenacanths is beginning to become known in greater detail. The large and diverse European xenacanth fauna is greatly in need of restudy and cannot be adequately considered here.
The xenacanth teeth described in this study are referred to a species first reported and named by Harlton (1933), based on a single specimen (NMNH 85529) from the Lower Pennsylvanian (pre-Johns Valley Shale, possibly the Wapanucka Limestone or Goddard Shale according to Zidek [1973]) of southern Oklahoma. Harlton named the specimen (Fig. 9) *Bransonella tridentata* and considered it to be assignable to the conodonts.

![Figure 9. Holotype (NMNH 85529) of *Xenacanthus tridentatus* (Harlton) 1933, from the Lower Pennsylvanian of Oklahoma. A - oral; B - labial; C - lateral. Bar scale represents 0.5 mm. Redrawn from Johnson (1984).](image-url)

Zidek (1973) re-examined Harlton's holotype, recognized that it was the tooth of a xenacanthid shark, and assigned it to *Dittodus* (unavailable) of Hay (1899).
Johnson (1979, 1984) restudied the holotype as part of his larger work on xenacanthid shark teeth and concluded that it was closely related to, but distinct from, his new species, *Xenacanthus nebraskensis*. Johnson (1984) suggested that this species be assigned, questionably, to *Thrinacodus* St. John and Worthen 1875 because the apical button is not in contact with the intermediate cusp; however, in a note added in proof, Johnson (1984) indicated that the rediscovery, by Susan Turner, in the collections of the U. S. National Museum, of St. John and Worthen's missing specimens of *Thrinacodus* confirms that these teeth are not assignable to *Xenacanthus* and may not even be teeth of xenacanth sharks. On the basis of this evidence, therefore, *X. ? nebraskensis* should be assigned unquestionably to *Xenacanthus* as should Harlton's holotype of *Bransonella tridentata*.

Johnson (1984) indicated that the distinctions between *Xenacanthus nebraskensis* and *X. tridentatus*, based on his study of the holotype of the latter, include the position of the apical button, attitudes of the proximal major transverse axes of the principal cusps (mta), and possibly the lingual margins of the tooth base. The additional specimens of *X. tridentatus* available for this study further define and clarify these morphological
differences, although in most cases these differences are not glaringly sharp. In addition, the stratigraphic and geographic distributions of these species must be considered.

The apical button of *Xenacanthus* *tridentatus* is more prominent than in *X. nebraskensis* and, on its lingual margin, is distinct from the remainder of the tooth base. In *X. nebraskensis* the tooth base is also thicker and more massive than in *X. tridentatus*. The tooth bases of *X. tridentatus* are generally longer in the labiolingual (1-1) than in the anteromedial-posterolateral (am-pl) dimension, with an average ratio of 1.06. In contrast, the teeth of *X. nebraskensis* average 0.92 for the 1-1/am-pl ratio (Johnson, 1984). This morphological distinction was confused, perhaps, when the holotype was the only known specimen of *X. tridentatus* because it has an 1-1/am-pl ratio of 0.84, approximating that of *X. nebraskensis*. Several other specimens in the *X. tridentatus* sample (Table 3) have ratios close to that of the holotype. These relatively wide teeth may represent specimens derived from certain specialized tooth families in the dentition of *X. tridentatus*. Both of these species of *Xenacanthus* appear to have relatively homodont dentitions; however, there may be slight differences in the proportions of teeth within any individual dentition. Perhaps the wider teeth (such as
the holotype) in each species represent specialized tooth families. Their comparative rarity in my sample would tend to support that conclusion.

Table 3.- Summary of labiolingual (1-1), anteromedial-posterolateral (am-pl), and 1-1/am-pl ratios for *Xenacanthus tridensatus*. This ratio for *X. tridensatus* averages 1.06. According to Johnson (1979) the ratio for *X. nebraskensis* is 0.92, for *X. luedersensis* is 1.17, and for *X. moorei* is 1.48. Measurements are in millimeters.

<table>
<thead>
<tr>
<th>SPECIMEN NO.</th>
<th>UNIT</th>
<th>STATE</th>
<th>L-L</th>
<th>AM-PL</th>
<th>RATIO</th>
</tr>
</thead>
<tbody>
<tr>
<td>NMNH 85529</td>
<td>Wapanucka?</td>
<td>OK</td>
<td>1.52</td>
<td>1.80</td>
<td>0.84</td>
</tr>
<tr>
<td>OSU 35354</td>
<td>U. Mercer</td>
<td>OH</td>
<td>0.52</td>
<td>0.40</td>
<td>1.30</td>
</tr>
<tr>
<td>OSU 35355</td>
<td>U. Mercer</td>
<td>OH</td>
<td>1.20</td>
<td>1.24</td>
<td>0.97</td>
</tr>
<tr>
<td>OSU 35356</td>
<td>L. Mercer</td>
<td>OH</td>
<td>1.12</td>
<td>1.08</td>
<td>1.04</td>
</tr>
<tr>
<td>OSU 35357</td>
<td>L. Mercer</td>
<td>OH</td>
<td>1.12</td>
<td>1.08</td>
<td>1.04</td>
</tr>
<tr>
<td>OSU 35358</td>
<td>Boggs</td>
<td>OH</td>
<td>0.92</td>
<td>0.88</td>
<td>1.05</td>
</tr>
<tr>
<td>OSU 35367</td>
<td>Heath?</td>
<td>MT</td>
<td>0.30</td>
<td>0.40</td>
<td>0.75</td>
</tr>
<tr>
<td>OSU 35370</td>
<td>Vanport</td>
<td>OH</td>
<td>1.60</td>
<td>1.60</td>
<td>1.00</td>
</tr>
<tr>
<td>OSU 35371a</td>
<td>Wewoka</td>
<td>OK</td>
<td>1.40</td>
<td>1.24</td>
<td>1.13</td>
</tr>
<tr>
<td>OSU 35371b</td>
<td>Wewoka</td>
<td>OK</td>
<td>1.60</td>
<td>1.44</td>
<td>1.11</td>
</tr>
<tr>
<td>OSU 35371c</td>
<td>Wewoka</td>
<td>OK</td>
<td>1.52</td>
<td>1.44</td>
<td>1.06</td>
</tr>
<tr>
<td>OSU 35371d</td>
<td>Wewoka</td>
<td>OK</td>
<td>1.80</td>
<td>1.96</td>
<td>0.92</td>
</tr>
<tr>
<td>OSU 35371e</td>
<td>Wewoka</td>
<td>OK</td>
<td>1.56</td>
<td>1.36</td>
<td>1.15</td>
</tr>
<tr>
<td>OSU 35374</td>
<td>L. Mercer</td>
<td>OH</td>
<td>1.12</td>
<td>0.96</td>
<td>1.17</td>
</tr>
<tr>
<td>OSU 35375</td>
<td>Pennington</td>
<td>KY</td>
<td>1.56</td>
<td>1.32</td>
<td>1.18</td>
</tr>
<tr>
<td>OSU 35376</td>
<td>L. Mercer</td>
<td>OH</td>
<td>1.05</td>
<td>0.90</td>
<td>1.17</td>
</tr>
<tr>
<td>OSU 35377</td>
<td>Vanport</td>
<td>OH</td>
<td>1.68</td>
<td>1.52</td>
<td>1.11</td>
</tr>
<tr>
<td>OSU 35378a</td>
<td>L. Mercer</td>
<td>OH</td>
<td>1.20</td>
<td>1.36</td>
<td>0.88</td>
</tr>
<tr>
<td>OSU 35379</td>
<td>Columbiana</td>
<td>OH</td>
<td>0.80</td>
<td>0.80</td>
<td>1.00</td>
</tr>
</tbody>
</table>

Johnson (1984) indicated that virtually all of his specimens of *Xenacanthus. nebraskensis* teeth have a comparatively large foramen at the lingual base of the apical button and in association with the lingual notch.
None of the specimens of *X. tridensatus* possesses such a foramen, although the lingual notch is a prominent feature of these teeth. One specimen of *X. tridensatus* (OSU 35354) appears to have this lingual foramen. Close inspection of the specimen, however, reveals that this feature is a "tube", created by contact of the distal ends of the lingual notch, that has no internal connection with the tooth. This "tube" was simply a conduit for the principal nutrient canal to pass from soft tissue covering the jaw to the principal foramen on the aboral surface of the tooth. The lingual notch serves a similar function in other *X. tridensatus* teeth. The lingual notch permits passage of the nutrient canal along the aboral surface of articulated tooth families without danger of pinching of the canal of any particular tooth in the file, should it shift position slightly during prey capture or other vigorous activities. A functionally similar, although morphologically different, method of passage of the nutrient canal between teeth in a tooth file is exhibited among ctenacanthid and cladodontid teeth (see discussion of *Zangerlodus williamsi*).

The position of the principal nutrient foramen at the lingual edge of the apical button in *Xenacanthus nebraskensis* is interpreted to be an apomorphous character and derived from the plesiomorphous character state in *X.*
tridentatus. Functionally, entrance of the principal nutrient canal through the lingual foramen in X. nebraskensis reduces the length of this canal and provides additional protection for this delicate vessel.

**Paleoecology.**—Xenacanth sharks have commonly been regarded as freshwater fishes (Zangerl, 1981), principally because of the large number of well-preserved specimens described in the last century from Carboniferous and Permian rocks of Britain, Czechoslovakia, and the United States. Most of these specimens are referable to either Orthacanthus or Xenacanthus and are indeed, and in most cases without question, freshwater sharks. Additionally, teeth assigned to these genera have commonly been reported from nonmarine deposits in association with tetrapod remains (e.g., Berman, 1970; Olson, 1946, 1956).

There is little doubt, however, that Xenacanthus tridentatus was a marine xenacanth. All specimens considered in this report, including the holotype, occurred in marine rocks in association with a normal marine fauna and in probable offshore facies. It is highly improbable that these specimens were derived from floating carcasses carried offshore from rivers debouching into the sea.
Specimens of *Xenacanthus nebraskensis* have not been reported from as many localities as have those of *X. tridentatus*; however, available evidence suggests that this species was also a marine xenacanth. Johnson's (1979, 1984) specimens, originally reported by Ossian (1974), are from a sandstone within the Towle Shale Formation (Upper Pennsylvanian) of Nebraska. The diverse vertebrate fauna of this locality contains both marine (petalodonts, cochliodonts, eugeneodonts, cladodonts) and nonmarine (*Orthacanthus*, tetrapods) elements. In addition, marine invertebrates including crinoids, brachiopods, trilobites, cephalopods, and probable marine gastropods and bivalves have been recovered from this bone-bed concentration. This occurrence represents an undoubted thanatacoense; however, *X. nebraskensis* could be interpreted as either marine or nonmarine on this evidence alone.

A specimen of *Xenacanthus nebraskensis* illustrated by Tway and Zidek (1983, figs. 52a–e; their subtype number 173) is from the marine Bell Limestone of Kansas. In addition, Tway (1982) has recorded this species from the Heebner Shale and the Plattsmouth Limestone, both of which are marine units. These occurrences strongly suggest that *X. nebraskensis* is a marine xenacanth and that the specimens described by Johnson (1984) from the Towle Shale of Nebraska are part of the marine fauna represented at that locality.
The diminutive teeth (less than 2 mm in maximum dimension) of *Xenacanthus tridentatus* suggest that these were small fishes. There is no direct evidence of dietary preferences of this xenacanth but it is probable that it was an active predator on other small fishes or invertebrates. The comparatively long, stout cusps of *X. tridentatus* suggest piercing and grasping of prey.

**Stratigraphic Distribution.**—Specimens of *Xenacanthus tridentatus* analyzed in this study are from Pottsville ("Lower Mercer", Boggs, Lower Mercer, Upper Mercer) and Allegheny (Vanport, Columbiana) rocks of Ohio. An additional specimen, derived from a sample provided by Donald Chesnut of the Kentucky Geological Survey, is from the Pennington Formation (Upper Chesterian) of Kentucky. Additional specimens in the collection are from the Wewoka Formation (Desmoinesian) of Oklahoma (provided by R. H. Mapes, Ohio University) and either the Heath Formation (Upper Chesterian) or Alaska Bench Formation (Lower Pennsylvanian) of Montana (provided by W. V. Goodhue, Jr., Oregon State University). The only other known specimen of *X. tridentatus* is the holotype, from the Lower Pennsylvanian (see above) of Oklahoma.

Specimens of xenacanthid teeth that may be referable to *Xenacanthus tridentatus* have been collected by Dr. C. R. Duffin from Visean limestones of Derbyshire, England. I
have not examined these specimens; however, SEM images of them provided by Dr. Duffin suggest that they are similar to the American material described herein. Such an occurrence is not surprising in view of the fact that the Carboniferous chondrichthyan faunas of Britain and North America bear many species in common, although that observation has not as yet received detailed published documentation.

In the Appalachian Basin it is possible that *Xenacanthus tridentatus* occurs as high as the Washingtonville shale, but the small number of samples from this unit did not produce any specimens. It can be said, with considerable certainty, that *X. tridentatus* does not occur in the Appalachian Basin stratigraphically above the Allegheny Group. The large number of samples from these higher horizons (Conemaugh Group) produced abundant chondrichthyan remains but not a single specimen of *X. tridentatus*. Tway and Zidek's (1982, 1983) samples from the Shawnee and Lansing Groups (Virgilian) of the midcontinent apparently did not produce any *X. tridentatus* specimens either. These data suggest that this xenacanth may define Upper Mississippian to Middle Pennsylvanian rocks.
The stratigraphic distribution of *Xenacanthus nebraskensis* is less well defined. In addition to Johnson's (1984) specimens from the Upper Pennsylvanian Towle Shale, Tway (1982) has reported *X. nebraskensis* (her subtype number 173) from the Heebner Shale of Kansas and Nebraska and from the Plattsmouth Limestone of Iowa, Kansas, Missouri, Nebraska, and Oklahoma. These units are Virgilian (Shawnee Group) in age. No specimens of *X. nebraskensis* have been reported from older rocks. The specimen illustrated by Koehler (1975, Pl. 3, Fig. 15), from the Moleen Formation (Lower Pennsylvanian) of Nevada, appears possibly to be a xenacanth tooth but it cannot be ascertained from the single, lingual view of the specimen if it is referable to *X. tridens*, *X. nebraskensis*, or perhaps even to *Zangerlodius williamsi*, a new ctenacanth described in this report.

No specimens of *Xenacanthus nebraskensis* were found in the numerous Upper Pennsylvanian samples processed during the course of this study. In addition to the many marine samples analyzed, some samples of nonmarine limestones from the Allegheny, Conemaugh, and Monongahela Groups (Pennsylvanian) and the Dunkard Group (Pennsylvanian/Permian) were processed and examined for microvertebrates (to be reported elsewhere). Although a
number of these samples produced xenacanth teeth, referable to **Orthacanthus compressus** and **Xenacanthus luedersensis**, no teeth of **X. nebraskensis** were recovered. This evidence suggests that **X. nebraskensis** is not present in the Appalachian Basin in either marine or nonmarine rocks.

The stratigraphic distributions of these two closely related species, **Xenacanthus tridentatus** and **X. nebraskensis**, suggest that they may both be useful in biostratigraphy. The former species appears to define Late Mississippian through early Middle Pennsylvanian rocks, whereas **X. nebraskensis** appears to be restricted to Upper Pennsylvanian rocks. The apparent absence of **X. nebraskensis** from the Appalachian Basin is not readily explained with present data; however, the Appalachian Pennsylvanian chondrichthyan fauna lacks many species represented in Midcontinent rocks of comparable age. Future detailed studies will perhaps clarify and define the stratigraphic and geographic distributions of these marine xenacanths.

**Evolutionary Relationships.** - The considerable morphological similarity between the teeth of **Xenacanthus tridentatus** and **X. nebraskensis** suggests that they are closely related species and suggest that they are in a
direct ancestor/decendant relationship. The position of the nutrient foramen within the lingual notch in *X. nebraskensis* teeth is interpreted to be apomorphous, in contrast to the more primitive position of this feature on the aboral surface of the tooth base in *X. tridentatus* teeth.

Ancestors and descendants of the *Xenacanthus tridentatus/X. nebraskensis* lineage cannot be determined with certainty at this time. The teeth of *X. luedersensis*, known from Pennsylvanian/Permian nonmarine deposits in Ohio and Texas, bear some morphological similarity to these two species; however, additional study will be required in order to determine relationships. Late Devonian and Early Carboniferous xenacanths are poorly known at this time and none can with certainty be presumed to be ancestral to the lineage of *X. tridentatus/X. nebraskensis*. These species are significant, however, in that they are apparently both marine. The widely espoused view that xenacanths are indicative of nonmarine conditions is obviously an oversimplification and applies principally to specialized Late Carboniferous/Permian species. It is highly probable that early xenacanths were marine and that fresh and brackish waters were invaded many times by various xenacanth species. *Xenacanthus tridentatus* and *X. nebraskensis* may be descendants of this early marine lineage.

Comments on Xenacanth Evolution.— A comprehensive review of the evolution of xenacanthid sharks is beyond the scope of the present report; however, recent description of an Early Carboniferous xenacanth by Dick (1981), a Late Devonian shark referred to the xenacanths by Young (1982), and cladistic hypotheses of Schaeffer (1981) and Maisey (1984) elicit some additional comment.

Schaeffer (1981), Young (1982), and Maisey (1984) have concluded, through cladistic analyses, that xenacanths were derived from ctenacanths. Devonian and Early Carboniferous skeletal remains of either group are poorly known and teeth are scarcely in a better state of knowledge. Skeletal remains of xenacanths are principally known from Upper Carboniferous and Permian rocks and most of these specimens exhibit highly derived morphologies. A
convincing case has been constructed for the conclusion that xenacanths are derived from ctenacanths (Maisey, 1984); however, the discussions cited above do not clearly establish criteria to differentiate xenacanths from ctenacanths.

Young (1982) described incomplete skeletal remains of a new chondrichthyan, Antarctilamna prisca, from Upper Devonian rocks (reported to be nonmarine) of Antarctica, which he interpreted to be a xenacanth on the basis of "diplododont" teeth. This shark possesses two ornamented dorsal fin spines that quite clearly fit the definition of the ctenacanth morphotype (Maisey, 1975, 1984).

The teeth assigned to Antarctilamna bear two enhanced, cristated lateral cusps and one or more small medial cusps. The tooth base is a simple, aborally concave structure that is elongated in the am-pl dimension and lacks any specialized articulating bosses (apical button, basal tubercle) typical of teeth previously referred to xenacanths.

The squamation of Antarctilamna is composed of composite scales of the synchromorial type, similar to those described for Orodus by Zangerl (1968) and for the xenacanth Diplodoselache woodi by Dick (1981). Similar scales are associated with an undescribed ctenacanth from the Upper Devonian Cleveland Shale, in the collections of
the Cleveland Museum of Natural History. The scale type reported for these chondrichthyans is similar to the isolated scales named *Williamssella striata* by Gunnell (1933).

*Antarctilamna* is therefore a chondrichthyan with squamation and dorsal spines typical of ctenacanths and teeth that are similar in some respects to those of xenacanths. Should *Antarctilamna* be interpreted as a primitive xenacanth or as a ctenacanth with specialized teeth resembling those of xenacanths? This question cannot be answered with present knowledge.

---

**Fig. 10. Hypothesis of relationships of various chondrichthyans according to Maisey (1984) and illustrating the relationship of xenacanths to ctenacanths. Modified slightly from Maisey (1984).**
The similarities in squamation between ctenacanths and xenacanths and, in Antarctilamna, teeth that appear to be intermediate between the two groups are two additional character states that point to a close relationship. Further detailed studies of scales and particularly teeth of the two groups may provide significant details of this evolutionary relationship. Teeth assigned to Phoebodus, particularly those from Middle and Upper Devonian rocks considered by Johnson (1979) to be assignable to xenacanths, may prove enlightening. Williams (1985) has demonstrated that Phoebodus heslerorum, the teeth of which are similar to but not identical with those from Devonian rocks, is a ctenacanth. Finally, the teeth from Upper Devonian rocks of Illinois, described by Eastman (1899) as "Diplodus" priscus and "D". striatus, appear to be very similar to teeth of Xenacanthus and may prove to be antecedent to X. tridentatus.
Order Euselachii Hay 1902
Superfamily Ctenacanthoidea Zangerl 1981
Family Phoebodontidae Williams 1985
Genus Phoebodus St. John and Worthen 1875

Type species.—Phoebodus sophiae St. John and Worthen 1875.

Phoebodus heslerorum Williams 1985
Pl. VI, Figs. 13, 14

Phoebodus heslerorum Williams, 1985, pp. 124-131, Pl. 16, figs. 1-10.
Cladodus occidentalis (in part), Ossian, 1974, pp. 111-114, Pl. 3, figs. 4-6.
"Cladodus" sp., Schultze, 1985, fig. 3, no. 5.

Holotype.—FMNH PF 8170, Mecca Quarry Shale, Parke County, Indiana.

Characterization.—Ctenacanth shark characterized by teeth with an outermost pair of lateral cusps as large as median cusp and a single pair of reduced innermost cusps. All cusps coarsely cristated labially, finely cristated to smooth lingually. Two knoblike basolabial articulating bosses separated by deep sulcus. Lingual torus bears paired apical articulating bosses.

Distribution.—Pennsylvanian of Ohio, Indiana, Kansas, Nebraska, and Oklahoma; Lower Permian of Kansas.
Referred specimens.- OSU 35438, 35439, 35440.

Description.- The following observations are based on the three specimens in the collection and supplemented by the observations of Williams (1985). These teeth are less than 5 mm in maximum dimension and have a large central cusp, a pair of outermost lateral cusps that are as large as the central cusp, and a pair of innermost lateral cusps that are reduced in size and situated slightly forward of the others. The outermost lateral cusps diverge laterally at an angle of up to 45 degrees. The cusps are nearly circular in cross section. Labially, the cusps bear widely spaced, coarse cristae that converge distally. Basally, weak cristae may be intercalated between the major cristae. Lingually, the cusps may bear very fine cristae or may be smooth. Lateral carinae are prominent and separate the two surfaces of the cusps. The cusps of all specimens in the collection are broken near the base (Fig. 11).

The tooth base is relatively straight across the labial margin and is rounded lingually with a well-developed lingual torus. Paired, knoblike basolabial articulating bosses are separated by a deep median sulcus. These bosses are approximately in line with the innermost pair of lateral cusps. Two prominent apical articulating bosses are on the oral surface of the lingual torus near
the lingual margin. These raised, rounded bosses may be fused in the midline or separated. Some specimens (OSU 35440) exhibit paired lingual foramina, one penetrating each apical articulating boss, whereas other specimens exhibit only a single foramen in the center of the lingual edge of the torus, between the apical articulating bosses. A deep lingual cleft may be present between the apical articulating bosses.

Aborally, the tooth base is concave and may exhibit a single, centrally located aboral foramen. A specimen (OSU 35440) with paired lingual foramina bears twin aboral foramina approximately in line with the lingual foramina. Numerous pitlike foramina are irregularly distributed on the aboral surface and on the lingual torus of the tooth base.

Fig. 11.—Morphology of a tooth of *Phoebodus heslerorum*, OSU 35439, location PA-1. A, labial; B, oral; C, aboral. Bar scale represents 1 mm. Abbreviations: aab, apical articulating boss; af, aboral foramen; bab, basolabial articulating boss; cc, central cusp; lc, lateral cusp; ms, median sulcus.
DISCUSSION

Taxonomy.- Williams (1985) has reviewed the taxonomic history of Phoebodus and related Bathycheilodus and Pristicladodus. This topic will be discussed only briefly here. St. John and Worthen (1875) based the genus Phoebodus on isolated teeth from Middle Devonian rocks near Waterloo, Iowa. Similarly, Bathycheilodus was based on isolated teeth from the same unit and locality. Pristicladodus was erected for isolated teeth from the "lower fish bed of the Kinderhookian", a unit that is now identified as the Maple Mill Shale of the Yellow Springs Group of Late Devonian age (Bergstrom and Hansen, 1980). Woodward (1889) placed Bathycheilodus and Pristicladodus in synonymy with Phoebodus. This synonymy has not received evaluation in modern studies.

A number of Devonian, Mississippian, and Triassic species of Phoebodus have been described (see Williams, 1985). Teeth assigned to this genus are in need of restudy and it is probable that several genera are represented in this long-ranging assemblage. Williams (1985) has correctly placed his specimens in Phoebodus as currently defined.

Three teeth in the collection are without doubt referable to Phoebodus heslerorum. It is possible that restudy of the various species of Phoebodus will indicate
that *P. heslerorum* deserves generic distinction from *Phoebodus*. Williams (1985) indicated that his specimens resemble *P. politus* Newberry, especially the specimen figured by Eastman (1906). This observation is correct with regard to the cusps; however, these species differ with regard to the articular bosses.

Teeth of *Phoebodus heslerorum* resemble those of cladodonts, especially *Symmorium reniforme*, except for the enlarged lateral cusps of *Phoebodus*. Ossian (1974) referred 467 teeth of *P. heslerorum* to the lower dentition of *Cladodus occidentalis* (=*Symmorium reniforme*) on the basis of their occurrence with, and similarities in morphology to, this simmoriid shark. Similarly, Schultze (1985) referred a specimen of *P. heslerorum* to "Cladodus" sp. Reference of teeth of *P. heslerorum* to cladodontids was a reasonable assumption, based on the similar morphologies, until the description of skeletal material of *P. heslerorum* by Williams (1985). These specimens possess two median fin spines, a condition that places them in the ctenacanthids and certainly excludes them from the anacanthus symmoriids. The scales of *P. heslerorum* appear to be of the synchronorial type and similar to those of other ctenacanthids and perhaps some xenacanths.
Dentition.—So few *Phoebodus heslerorum* teeth are available in the OSU collection that it is impossible at this time to determine variations in the dentition. Restudy of Ossian's (1974) collection of these teeth from the Peru fauna of Nebraska would be informative. It is probable that there was some heterodonty in this species but the teeth at hand show no indication of asymmetry or other variations except for minor differences in the spacing of the apical articular bosses.

The configuration of the articular bosses indicates that teeth of *Phoebodus heslerorum* were articulated in successional tooth rows in a manner very similar to that of *Symmorium reniforme*. Indeed, the articular bosses, particularly the basolabial ones, resemble those of *S. reniforme*. As in *S. reniforme* and some other chondrichthyans, this mode of articulation served to prevent dislocation of a tooth from the tooth file and protected the principal nutrient vessel that passed through the major foramina.

Teeth of *Phoebodus heslerorum* were designed for piercing and holding prey as in cladodontids and it is probable that this species was a top-level predator. These teeth are relatively small in relation to the size of the fish; a specimen with a Meckel's cartilage length of 110 mm has teeth of about 5 mm in maximum dimension (Zangerl, 1981).
Denticles.- Williams (1985) indicated that dermal denticles are abundant on his specimens from the Mecca Quarry Shale; however, preservation is such that these structures cannot be studied and assessed in detail. The illustrations of scales of *Phoebodus heslerorum* given by Williams (1985) are not sufficiently clear to determine the morphology in detail; however, these illustrations and Williams' description indicate that these scales are of a ctenacanthid morphotype such as has been described as *Williamsella* (which see) by Gunnell (1933). Williams (1985) was not able to observe any branchial denticles on his specimens but suggested that they should be present.

Paleoecology.- The occurrence of *Phoebodus heslerorum* in shallow-water carbonates and in the black shale Mecca fauna suggests that this shark was widespread throughout a wide variety of marine environments. Its presence in the Mecca fauna suggests that it preyed on other fishes or nektic invertebrates and did not rely on benthos as a food source. Such an observation is consistent with the morphology of the teeth.

Remains of *Phoebodus heslerorum* are uncommon in Pennsylvanian rocks except for the large postmortem accumulation described by Ossian (1974) from Nebraska. This species is not particularly commonly represented in
the Mecca fauna either. This comparative rarity of *P. heslerorum* teeth explains why the distinctive median fin spines had not been reported prior to the description of this species by Williams (1985). The rarity of the teeth, of which there must have been tens or hundreds in one individual, suggests that the frequency of occurrence of median fin spines (2 per individual) would be quite low.

**Stratigraphic and geographic distribution.**—*Phoebodus heslerorum* is represented in Allegheny and Conemaugh rocks of the Appalachian Basin; the Wewoka Formation (Desmoinesian) of Oklahoma; the Mecca Quarry Shale (Desmoinesian) of Indiana (Williams, 1985); Virgilian of Nebraska (Ossian, 1974); White Cloud Sandstone (Virgilian) of Kansas (Williams, 1985); and the Threemile Limestone (Chase Group, Gearyan, Lower Permian) of Kansas (Schultze, 1985).

This distribution suggests that *Phoebodus heslerorum* is both long ranging and widely distributed. The apparently low frequency of teeth and other remains and the confusion of these teeth with those of cladodontids are factors that have hampered reporting of this species.

Family Phoebodontidae?

Genus *Zangerlodus* n. g.

**Characterization.**—A ctenacanth shark characterized by microscopic teeth with three, rarely four, labiolingually compressed, stout, major cusps of nearly equal length that bear, labially, three triangular, imbricated cristae on each cusp. Tooth base reniform with two prominent knoblike basolabial articulating bosses and a large, central aboral foramen. Lingual torus prominent with a large lingual foramen and no specialized articulating bosses.

**Type Species.**—(Here designated) *Zangerlodus williamsi* sp. nov.

**Distribution.**—Pennsylvanian (Morrowan through Virgilian) of the Appalachian Basin and Virgilian of the Midcontinent Basin, U.S.A.

*Zangerlodus williamsi* n. sp.

Pl. II, Figs. 1-17

Subtype No. 169, Tway and Zidek, 1983, figs. 50a-e.
Subtype No. 083, Tway and Zidek, 1983, figs. 43a-d.

**Holotype.**—OSU 35368, Cambridge limestone (Conemaugh), location Nn-13.
Referred Specimens. OSU 35210, 35223, 35360, 35361a,b, 35368 (holotype), 35369 (hypotypes), 35372, 35373, 38628, 38641.

Etymology.- The genus is named in honor of Dr. Rainer Zangerl, Curator Emeritus, Field Museum of Natural History, for his many contributions to chondrichthyan paleontology. The species is named in honor of Dr. Michael E. Williams of the Cleveland Museum of Natural History.

Figure 12.- Morphology of teeth of Zangerlodus williamsi n.g., n. sp., based on the holotype, OSU 35368. A, labial; B, lingual; C, lateral; D, aboral; E, oral. Abbreviations: bab - basolabial articulating bosses; bf - basal foramen; cr - cristae; lf - lingual foramen; lt - lingual torus; s - sulcus. Bar scale represents 0.5 mm.
**Description.**—The holotype (OSU 35368; Pl. II, figs. 11–14; Fig. 12) has three stout, labiolingually compressed cusps of nearly equal length. Each cusp bears three principal, imbricated, orally convergent cristae that form sharp cutting edges. The cusps are joined together throughout the basal two-thirds of their lengths and are differentiated into separate cusps in the oral third. Basally, the tooth crown is separated from the tooth base, labially, by an indistinct horizontal crease. Comparatively large, rounded, bulbous articulating bosses are present on the basolabial portion of the crown. Each boss is connected to the tooth crown by a distinct, upward continuing ridge. The crown is concave mediolabially, between the articulating bosses, and forms a deep sulcus.

The tooth base is laterally (am-pl) elongate, measuring 0.65 mm in this dimension, and 0.40 mm in the labiolingual (1-1) dimension. The tooth base is relatively indistinct labially, forming a narrow border across the base of the tooth, but lingually it consists of a prominent, expanded lingual torus. The oral surface of the lingual torus is higher and expanded medi ally but is slightly depressed on each side of the medial expansion. A large foramen is present medially on the lingual portion of the torus. Aborally, the tooth base is relatively flat. A large foramen is present medially and slightly labiad. A depressed area labiad of the aboral foramen forms a
distinct sulcus between the two labial-projecting basal articulating bosses.

As might be expected in a multielement dentition, the large number of additional teeth in the collection exhibit a variety of morphological variations. The number of cusps is nearly always three, although rarely a fourth or even a fifth cusp may be present (Pl. II, figs. 7-9). The cusps are of nearly equal length; however, in some specimens the central cusp may be slightly longer than the lateral ones. Labially, each cusp bears at least three stout, triangular, imbricate cristae that decrease in size basally. The cristae form sharp cutting edges, especially the distal ones on relatively unworn teeth, and are aligned from cusp to cusp, particularly on lower-crowned teeth. Irregular and less distinct cristae may be present on the basolabial portion of the cusps. Lingually, the cusps are smooth and on only a few specimens do they bear a few small, weak cristae. In most specimens the medial cusp is nearly vertical and the lateral cusps may diverge laterally at a small angle, commonly about 20 degrees. In some specimens all cusps exhibit a pronounced inclination to either the right or left. Cusps range from short and robust to comparatively long and slender.

In aboral view, tooth bases have a reniform shape, with a relatively deep sulcus on the labial margin, and range from subcircular to laterally elongate. The aboral
surface of all specimens is weakly concave and has a large foramen slightly labial of center. Smaller foramina are common aborally, just lingual to the basolabial articulating bosses. These bosses are present on all specimens although their precise location and degree of prominence may vary slightly.

Lingually, the tooth base is relatively thick with high, rounded margins and a relatively abbreviated, although prominent lingual torus. A large foramen on the lingual side of the tooth base forms a shallow lingual notch. The lingual foramen forms a canal that connects with the aboral foramen, as is exhibited by some specimens in which the canal is completely free of sediment.

DISCUSSION

Teeth of *Zangerlodus williamsi* have not previously been described although Tway and Zidek (1983, figs. 50a–e) figured a specimen (their subtype no. 169) from the Stoner Limestone (Lansing Group), Cass County, Iowa. Only one other form resembling *Zangerlodus* has been described from Pennsylvanian rocks. The specimens assigned by Baird (1978) to the ctenacanth *Bandringa rayi* Zangerl 1969, from the Upper Kittanning coal (Allegheny Group) at Cannelton, Pennsylvania, have a morphology similar to that of *Zangerlodus williamsi*. 
I have examined Baird's specimen (PU 19814) and my interpretation of the morphology of these presumed teeth does not differ appreciably from his. Although a large number of the millimeter-sized teeth are preserved on the shale slab, none is well exposed and preparation is difficult because of their small size and delicate nature. Baird's (1978, fig. 9c) depiction of them appears to be accurate. These tricusped specimens have a relatively thin, aborally concave base that lacks, as best as can be determined, any articulating bosses or specialized foramina. Small foramina are present labially just above the base-crown juction.

The labial cristae of Baird's specimen of *Bandringa rayi* are similar to those on specimens of *Zangerlodus williamsi* but only a single, triangular crista is present on each cusp, in contrast to the three prominent ones on cusps of *Z. williamsi* teeth. Morphological differences between the specimens assigned to teeth of *B. rayi* by Baird (1978) and teeth of *Zangerlodus williamsi* are sufficient to consider them as generically distinct. In addition, *B. rayi* is a nonmarine chondrichthyan whereas *Z. williamsi* is undoubtedly marine.

A further cautionary note on Baird's (1978) specimen referred to *Bandringa rayi* is warranted. Structures Baird interpreted as teeth of this specimen are similar in
general morphology to dermal denticles from the head and trunk region of a specimen of *Hybodus delabechi* illustrated by Woodward (1889, Pl. VIII, figs. 2-5). This specimen, from the Jurassic at Lyme Regis, is certainly not conspecific with Baird's (1978); however, the apparent morphological similarity of the denticles of *H. delabechi* and the presumed teeth of *B. ravi* raises the possibility that the specimens described by Baird are actually dermal denticles from a hybodontid shark. The simple morphology of the base of Baird's specimens is more typical of dermal denticles than teeth. This question cannot be answered with available material, but the possibility should be kept in mind in future references to Baird's specimen of *B. ravi*. In either case, the specimens of *Z. williamsi* are most certainly teeth.

**Morphology.**—Nearly all the specimens available (162) exhibit three cusps of nearly equal length. On a few specimens there is a very small fourth cusp on one side of a major lateral cusp. Several specimens in the collection, however, are unusual in exhibiting three principal cusps of nearly equal length and two relatively short cusps on either side of the principal lateral cusps (Pl. II, figs. 7-9). These symmetrical teeth, with labiolingually
compressed tooth bases, are without doubt referable to
*Zangerlodus williamsi* and are interpreted to possibly be
symphyseal teeth. Their relative rarity in the collection
would support a derivation from tooth files of limited
frequency in the dentition. This tooth type was figured by
Tway and Zidek (1983, figs. 43a–d) as their subtype no.
083, illustrating, again, the disadvantage of their
utilitarian classification system as applied to obvious
dentition teeth of Late Paleozoic age.

Many teeth exhibit an asymmetry of the cusps; that is,
the cusps are inclined either left or right at a slight
angle. Most of these specimens are relatively low-crowned
teeth with laterally elongate tooth bases. This morphology
suggests that they are probably teeth derived from lateral
tooth files. Teeth with relatively symmetrical cusps, that
is, without any preferred right or left inclination,
possess nearly equilateral tooth bases and are interpreted
to have been derived from medial tooth files. These
morphological variations suggest gradient monognathic
heterodonty (Fig. 13).
Fig. 13.–Hypothetical tooth files on a ramus of Zangerlodus williamsi n.g., n.sp., showing morphological variation from symphyseal (I), posteriorly to (V). Tooth files illustrate major variations in a morphological gradation series. It is probable that each ramus bore considerably more tooth files. Teeth drawn proportionally but not to scale.

The mode of articulation of successive teeth in a tooth file is highly specialized and is similar, but not identical to that exhibited by many xenacanths and some symmoriids. In Zangerlodus williamsi the prominent basolabial articulating bosses rested on the lingual torus of the preceding tooth in the file, on either side of the somewhat raised central area. Unlike those of xenacanths and some symmoriids, however, Z. williamsi teeth lack apical buttons (apicolingual articulating bosses). Instead these teeth have only an unspecialized depressed area for articulation of the basolabial bosses of the succeeding
tooth. This mode of articulation served to maintain the position of individual teeth in the tooth file. It is probable that a generally similar mode of articulation has been developed independently in each of these groups of chondrichthyans.

An additional function of the articulating structures in *Zangerlodus williamsi* and in some xenacanthids and cladodontids, which to my knowledge has not been previously considered, is to prevent crimping of the principal nutrient vessel. This vessel entered the tooth through the prominent lingual foramen, exited through the basal foramen, continued labially through the median sulcus between the basolabial articulating bosses and entered the lingual foramen of the preceding tooth (Fig. 14). An apically oriented vessel branched off from the main nutrient vessel in order to furnish nutrients to the pulp cavity of each tooth. This arrangement protected the nutrient vessel in each tooth file from becoming injured during prey capture or other vigorous activities when teeth were subjected to significant angular stress (Fig. 14).
Fig. 14.-Teeth of Zangerlodus williamsi illustrating their mode of articulation and the path of the principal vascular or nutrient canal through the lingual and basal foramina. Abbreviations: bf - basal (aboral) foramen; lf - lingual foramen; vc - vascular canal.

**Taxonomic Relationships.**—Superficially, the teeth of *Zangerlodus williamsi* might be considered to be xenacanthid, on the basis of three cusps of nearly equal length, or they might be considered to be cladodontid on the basis of twin basolabial articulating bosses and general cusp morphology. Alternatively, *Z. williamsi* teeth might be allied with those of ctenacanthids on the basis of morphological similarity to the teeth of *Phoebodus heslerorum* Williams 1985, which he has demonstrated to be a ctenacanthid. If the specimen described by Baird (1978) is confirmed to be a ctenacanthid, *Bandra gua rayi*, then the structures interpreted by him to be teeth further support the assignment of *Z. williamsi* to the ctenacanthids.
Placement of the teeth of *Zangerlodus williamsi* in the Ctenacanthoidea appears to be the most parsimonious approach with present knowledge. The articulating bosses on the teeth of xenacanthids consist of a single apical button and a single basal tubercle—a relatively constant feature in xenacanthid teeth (Johnson, 1979). Among the cladodontids, the symmoriids are relatively well known from both teeth and other skeletal remains (Williams, 1985; Zangerl, 1981). Although teeth of symmoriids are generally similar to one another, the articulating bosses are considerably different in representatives of each genus (see symmoriids, herein). This suggests to me that the mode of articulation of teeth in tooth files is apomorphous and not necessarily indicative of close relationship. The teeth of *Zangerlodus williamsi* have greater similarity to those of *Phoebodus heslerorum* Williams 1985 than to any others with which I am familiar. They differ from *P. heslerorum* teeth principally by lacking intermediate cusps between the central and lateral cusps and lacking distinct apical articulating bosses.

An additional question that must be considered concerns other remains in the fauna that are representative of ctenacanthid sharks. Maisey (1975, 1981) has clearly defined a large group of median-fin spines that fit the morphology for ctenacanthid sharks. It is probable that not all of these spines were derived from
ctenacanthid sharks; however, if *Zangerlodus williamsi* is a ctenacanthid shark, by definition, it should have possessed such spines. No ctenacanthid median-fin spines were recovered from samples processed in this study; however, the large collection of macroscopic chondrichthyan remains available to me from Pennsylvanian rocks of Ohio contains a small number of such spines. Most of these specimens are comparatively large, measuring between 10 and 20 cm in length when complete. This size would suggest that these spines were derived from medium-to-large-sized sharks. Teeth of *Zangerlodus williamsi* and *Phoebodus heslerorum* are the only ones in either the micro or macroscopic collection from Ohio that appear to have any similarity to teeth of described ctenacanths. It is unlikely, although not impossible, that the spines are from a ctenacanth of which no teeth have yet been recovered. However, this possibility becomes particularly remote when Johnson's (1979) frequency data for hybodontid teeth and spines are considered. A ctenacanthid shark, with a multielement dentition, would have had tens and perhaps hundreds of teeth but only two median fin spines at any one time. The ctenacanthid spines from the Pennsylvanian of Ohio are of several distinct morphologies, which implies that several ctenacanthid-spine-bearing species are represented. Data are insufficient to indicate
if the teeth of *Zangerlodus williamsi* came from a shark that bore one of these spine morphotypes. If one of the spine morphotypes was derived from *Z. williamsi*, this would imply that a relatively large shark had comparatively small teeth.

Of additional consideration in regard to *Zangerlodus williamsi* are scales that may have belonged to this chondrichthyan. An undescribed ctenacanthid in the Cleveland Museum of Natural History collections (Upper Devonian Cleveland Shale) has numerous scales similar to those named *Williamsella striata* by Gunnell (1933, Pl. 33, fig. 48). Similar scales have also been described from an Upper Devonian presumed xenacanthid, *Antarctilamna prisca* (Young, 1982) and from a Lower Carboniferous xenacanthid (Dick, 1981). Such scales are not uncommon in the microfauna examined in this study (see *Williamsella striata* elsewhere in this report). There is the probability, should *Z. williamsi* be confirmed to be a ctenacanth, that these scales were derived from this shark. Although the above evidence suggests that they could have also been derived from a xenacanthid, *Xenacanthus tridentatus*, these scales occur stratigraphically far above this xenacanth and generally coincident with teeth of *Z. williamsi*. Should associated
remains of *Z. williamsi* ever be discovered, it is probable that a name applied to either a median-fin spine or a scale will be the senior synonym.

**Stratigraphic Distribution and Paleoecology.**—Teeth of *Zangerlodus williamsi* were recovered from samples of nine marine units 20 localities in Ohio and adjacent areas. These teeth are most abundant and widespread in Conemaugh marine rocks (17 localities) and every marine unit in this group of rocks, except the irregularly distributed Gaysport limestone, produced at least a few specimens. Samples from Pottsville rocks (Boggs, Lower Mercer, Upper Mercer) at four localities produced a total of four specimens. None was recorded from Allegheny rocks, although there is no reason to suspect that they do not occur in marine units of this group. It is probable, therefore, that *Z. williamsi* occurs throughout Pennsylvanian marine rocks of the Appalachian Basin. Based on frequency data, high abundance of teeth of *Z. williamsi* may be indicative of Conemaugh rocks.

Tway (1982) recorded *Zangerlodus williamsi* teeth (her subtypes nos. 083 and 169) from the Leavenworth Limestone, Heebner Shale, and Plattsmaouth Limestone (Shawnee Group, Virgilian) in Iowa, Kansas, Missouri, and Nebraska. Specimens were reported from 29 samples at 8 localities.
These distributions of *Z. williamsi* in the Midcontinent and Appalachian Basins suggest that this chondrichthyan was widespread in Pennsylvanian seas.

All of the specimens obtained in this study and those of Tway (1982) were derived from marine limestones indicative of relatively open marine conditions, with normal salinity. No specimens were derived from nonmarine limestones sampled in this study and none was collected from samples of rocks thought to represent brackish conditions.

Owing to the small size of the teeth, it is probable that *Zangrelodus. williamsi* was a diminutive fish. The acuminate cusps of these teeth are suited to piercing and grasping, an activity that was probably aided by the imbricated cristae on the cusps. Prey of *Z. williamsi* may have consisted of other diminutive chondrichthyans, paleoniscoids, aiscanthodians, or various invertebrates.

**Occurrence.**- Boggs, Hwa-1, (1): Lower Mercer, Hfg-5, (2): Upper Mercer, Ts-5, (1); Ty-7, (1): Brush Creek, Aw-47, (14): Cambridge, GAs-1, (1); Gca-5, (6); Gwe-1, (4); Nn-13, (42): Portersville, Acn-31, (8); At-45B, (9); Aw-47, (11): Noble, Go-1, (1); Nbu-1, (46); Nn-12, (4): Ames, Acn-31, (40); Cma-10, (16); Gwi-3, (28); HAr-1, (4); Nbu-4, (5); Nn-3, (4); Pb-4, (4); PA-, (6): Skelley, Nbu-3, (7).
Superfamily Hybodontoidea Zangerl 1981
Family Hybodontidae

**Lissodus** Brough 1935

Characterization—Hybodont sharks with small to moderately large, deep-crowned teeth. Labial peg small to well developed. Occlusal crest strong to moderate. Crown with a single low central cusp that is commonly flanked by very low lateral cusplets. Lateral margins of crown incline steeply to an incised crown/tooth base junction. Tooth base with simple, large vascular foramina in an anaulacoarhize organization. Tooth base directed lingually, but not developed into a conspicuous torus. Thick, single-crystallite enameloid layer covers crown and is thickest labially. Teeth overlap in successive tooth files. (Modified from Duffin, 1985).

**Lissodus zideki** (Johnson) 1981

Plate III, Figs. 20-26


**Holotype.**—SMP-SMU 64443
Referred Specimens.—OSU 35362, "Portersville", GAgr-1; OSU 38624, Ames, PA-4; OSU 38632, Ames, PA-3.

Distribution.—Conemaugh of the Appalachian Basin; Virgilian of Nebraska; Lower Permian of Texas.

Characterization.—A species of *Lissodus* characterized by a moderately heterodont dentition. Teeth small; crown symmetrical, but labial side may be thicker, especially in posterior teeth; crown moderately arcuate (lateral view) in lateral teeth, more so in anterior teeth, and less so, or even straight, in medial and posterior teeth; in occlusal view, crown slightly arcuate (concave lingually) in anterior and lateral teeth, but usually straight or nearly so in medial and posterior teeth; cusp single, generally well developed, except in posterior teeth; longitudinal and transverse occlusal crests well developed; crenulations absent, labial and lingual processes well developed; labial accessory processes usually present, but poorly developed; lingual accessory processes absent. Root (tooth base) sulcus shallow, closed in anteromedial and posterior teeth, but open in lateral teeth, with convergent oral and basal margins; specialized foramina present. (Johnson, 1981, p. 9).
Figure 15.—Morphological features of tooth of Lissodus zideski, from the Portersville?, location GAg-1, OSU 35362. A, labial; B, lingual; C, oral; D, lateral. Bar scale represents 0.5 mm. Abbreviations: am-pl, anteromedial-posterolateral; br, basal ridge; f, foramina; lap, labial articulating process; lt, lingual torus; oc, occlusal crest; s, sulcus; toc, transverse occlusal crest.

Description.—The tooth crown is highest in the center and slopes laterally, along a sharp ridge (occlusal crest) at an angle of about 20 degrees. There is only slight development of a lateral cusp on each side of the occlusal crest, which continues to the lateral margins of the tooth where it unites with a raised ridge that encircles the basal crown border (Fig. 15). A ridge or crest (transverse occlusal crest) also extends labially and lingually, at right angles to the occlusal crest, from the acuminate coronal cusp and unites with the basal crown ridge. These raised ridges or crests serve to divide the crown into
four quadrants, each of which is slightly concave. The basal crown ridge is comparatively weakly developed lingually, but more massively developed labially, and divided into bulbous segments, the largest of which is medially located, forming a labial articulating process (labial peg).

The tooth base is nearly as deep as the height of the crown, laterally elongate, and flattened basally approximately parallel to the base of the crown. The tooth base projects lingually, forming a broad lingual torus. The tooth base is constricted, forming a shallow sulcus, just beneath the base of the crown. A transverse row of specialized foramina is present along the basolabial portion of the tooth base. Lingually, comparatively large foramina are irregularly distributed across the lingual torus.

DISCUSSION

The reference of these specimens to Lissodus zideki is made without question. Dr. Gary Johnson has examined these specimens and has confirmed the identification. Hybodontid teeth were poorly known from Upper Paleozoic rocks before Johnson's (1979, 1981) description of abundant and diverse hybodontid faunas from Upper Pennsylvanian and Lower Permian rocks of north-central
Texas. This circumstance is not surprising in view of the fact that these teeth are of microscopic dimensions and have not received previous detailed study. It is probable that a variety of hybodontid teeth will be found in future investigations over a wide geographic area and perhaps in some abundance in rocks older than Pennsylvanian. Indeed, Duffin (1985) has recently described teeth of *Lissodus* from Lower Carboniferous (Visean) rocks of Britain.

Johnson (1981) indicated that *Lissodus zideki* is the most abundant, easily identified, and most widespread hybodontid tooth in the collections from north-central Texas. He indicated that heterodonty is only weakly developed in this species and that crown morphologies are relatively simple. Johnson (1981, figs. 47-74) illustrated the morphological variation of the teeth of *L. zideki*.

Johnson (1981) has also described the microscopic anatomy of *Lissodus zideki* teeth. He indicated that the tooth crown is composed primarily of orthodentine. Johnson's (1981, figs. 162-173) thin sections show thick orthodentine penetrated by dentinal tubules and a thin outer covering of a clear substance that I interpret to be enameloid. The microscopic anatomy of these teeth is similar to that exhibited by many Paleozoic elasmobranchs and represents a relatively unspecialized condition.
Johnson (1981) placed these teeth in *Polyacrodus* Jaekel 1889. In a recent revision of *Lissodus*, Duffin (1985) placed them in this latter genus. *Lissodus*, as now constituted, consists of 21 species ranging stratigraphically from Lower Carboniferous to Upper Cretaceous and environmentally from freshwater to marine. I have some doubt if Duffin's (1985) species should all be placed in *Lissodus*. As with other hybodontid genera, such as *Hybodus*, it is probable, in my opinion, that *Lissodus* is perhaps a taxonomic catch-all for similar teeth. Investigation of this problem is far beyond the scope of the present study; however, extensive revision of hybodontid teeth is greatly needed.

Johnson (1981) referred Upper Pennsylvanian hybodontid teeth described by Ossian (1974) to *Lissodus zideki*. Ossian did not recognize that these were hybodontid teeth and referred them to the genus *Orodus* and a new manuscript species, *O. hemiplicatus*. This species name has no taxonomic validity, however, because it was never formally published.

**Stratigraphic Distribution and Paleoecology.**—One of the specimens of *Lissodus zideki* (OSU 35362) reported here is from a silty, fine- to medium-grained, calcareous sandstone that Blake (1952) determined to be at the position of the Portersville shale (Conemaugh). The
geology of Gallia County has received little investigation other than Blake's (1950) reconnaissance study. It is very probable that this tooth was derived from Conemaugh rocks; however, the identification of the specific horizon as the Portersville is tenuous at best with present data. The remainder of the *L. zideki* teeth in the collection are from the Ames limestone at two localities in western Pennsylvania.

These specimens are the first reported occurrences of *Lissodus zideki* in the Appalachian Basin and only the second occurrence outside of Texas. Additional specimens referable to this species were reported by Ossian (1974) from the Towle Shale (Upper Pennsylvanian) of Nebraska. These occurrences suggest that *L. zideki* defines strata of Late Pennsylvanian to Early Permian age.

The habitat of *Lissodus zideki* is a matter for discussion and speculation. Johnson (1979, 1981) indicated that his collection of hybodont teeth were derived from rocks interpreted to represent a nearshore environment. His collections from these rocks consist of teeth and other elements that can be referred reliably to both marine and nonmarine chondrichthians. He speculated that many of these occurrences could be the result of nonmarine chondrichthyan remains being carried from stream mouths out into a nearshore marine environment where they were
mixed with marine chondrichthyan skeletal elements or, conversely, the deposits could have been generated from storm waves casting skeletal material of marine chondrichthyan shoreward into environments inhabited by nonmarine chondrichthyans. The Towle Shale of Nebraska contains a similar mixture of marine and nonmarine chondrichthyan skeletal elements (see Xenacanthus tridentatus for more detailed discussion of this locality).

The occurrence of the single Ohio specimen of Lissodus zideki does not offer a definitive solution to the problem of the habitat of this species but it does clarify the nature of the problem. The Ohio locality, GAg 1, in Gallia County, is near the depositional edge of Conemaugh marine units in this general region (see Fig. 00). The sample of this silty sandstone yielded, in addition to the specimen of L. zideki, a single tooth fragment of a marine cochliodont, Sandalodus, a single tooth of a marine symmoriid, Danaea saltsmani, teeth and scales of paleoniscoids, a single acanthodian scale, and several dermal denticles. This sparse fauna suggests a marine origin of the sandstone; however, no invertebrates, including conodonts, were noted.
There can be little doubt that the two Ames localities in Pennsylvania that yielded teeth of *Lissodus zideki* represent a marine environment. These localities yielded a variety of marine chondrichthyan remains and conodonts. It is uncertain, however, if these localities were nearshore or offshore. It is of interest to note that *L. zideki* teeth were absent in other marine units sampled during this study and none of these teeth was recovered from a limited number of nonmarine units. Tway and Zidek (1982, 1983) did not illustrate any teeth of this species. This evidence, along with that derived from the occurrences in Texas (Johnson, 1981) and Nebraska (Ossian, 1974), suggests that *L. zideki* occupied a restricted environment, perhaps a nearshore-marine one.

One additional note on the occurrence of this hybodont is that Johnson (1981) indicated that *Lissodus zideki* was the most abundant and widely distributed, both geographically and stratigraphically, of any of his hybodontid species. He also noted that it was very rare in Ossian's Towle Shale fauna from Nebraska.

The acuminate teeth of *Lissodus zideki*, with their knifelike coronal crests, suggest that this hybodont was an active predator capable of slicing prey. The small size of the teeth probably indicates a small shark that may have preyed upon diminutive paleoniscoids and perhaps soft-shelled invertebrates.
Occurrence.—Portersville?, GAgr-1, (1); Ames, PA-3, (4); PA-4, (1).
**Lissodus duffini** n. sp.

Pl. III, Figs. 1-5

*Lissodus* sp., Duffin, 1985, p. 117-118, fig. 10a-e.

Subtype 107, Tway and Zidek, 1983, fig. 77a-c.

Subtype 216, Tway and Zidek, 1983, fig. 78a-d.

*?Orodua hemiplictus*, Ossian, 1974, p 125-126, Pl. 5, figs. 1-4.

**Characterization.**—A species of *Lissodus* characterized by small, blunt, low-crowned, triangular teeth. Lingual margin of crown nearly straight; presumed labial margin bulging, forming the apex of a triangle, with a robust labial buttress or peg. Principal cusp acuminate, labially oriented, and located centrally and labiad of the crown center. Occlusal crest well defined and traversing the tooth from the lateral margins of the crown to the principal cusp. Tooth base unknown. (Modified from Duffin, 1985).

**Holotype.**—OSU 38630, Noble limestone, Nbu-1.

**Etymology.**—Named in honor of Dr. Christopher J. Duffin for his work on hybodonts and other fossil chondrichthyan remains.

**Distribution.**—Noble and Skelly limestones (Conemaugh) of the Appalachian basin; Leavenworth Limestone, Heebner Shale, Plattsmouth Limestone, and ?Towle Shale (all Virgilian) of the Midcontinent basin.
**Referred Specimens.**- OSU 35445a-d, Noble limestone, Nbu-1.

**Paratypes.**

**Description.**- Teeth of *Lissodus duffini* are range from 0.7 to 0.8 mm in anteromedial-posterolateral (am-pl) dimension. Available specimens are morphologically relatively homogeneous and exhibit little inclination towards heterodonty. The presumed lingual margins of the teeth are nearly straight and show only a slight inward flexure in the medial portion. The labial edge of the crown is produced into a robust labial peg or buttress in the median portion. The lateral margins of the crowns are rounded.

A single, acuminate, labially inclined cusp is located medially on the crown, slightly labiad of center. A sharp, slightly curving occlusal ridge extends from the central cusp to the lateral margins of the crown. Very tiny, bumplike cusps may be present on the occlusal ridge. The basal margin of the crown slopes sharply inward to the junction with the tooth base to form a prominent overhang. On either side of the labial buttress, on some specimens, are shallow, broad pits or indentations. The tooth base is not preserved on any of the specimens in the collection.
DISCUSSION

The tiny, superficially simple teeth of *Lissodus duffini* are among the rarest specimens in the OSU collection; only six were recovered. Tway and Zidek (1983) apparently were the first to illustrate them, although the teeth assigned informally to *Orodus hemiplicatus* in Ossian's (1974) dissertation may be referable to this species or possibly to *Lissodus zideki*. Recently, Duffin (1985), on the basis of Tway and Zidek's figures, assigned their subtype 107 to the hybodont *Lissodus* (Fig. 16). Although Duffin (1985) did not include Tway and Zidek's (1983, fig. 78a-d) specimen of subtype 216 in this genus, it is included herein. This specimen is incomplete and exhibits a higher central cusp, a less well-developed labial buttress, and a vertical ridge that appears to reinforce the principal cusp.

![Diagram of teeth](image)

Fig. 16.—Principal morphological features of teeth of *Lissodus duffini* n. sp. A, occlusolingu al; B, occlusolabial; C, basal; D, lingual; E, lateral. Abbreviations: lb, labial buttress; oc, occlusal ridge; pp, principal cusp; ps, pressure scar; tb, position of tooth base. Bar scale represents 1 mm. Drawing by Duffin (1985) from tooth illustrated by Tway and Zidek (1983, fig. 77a-e).
Lissodus, as recently revised by Duffin (1985) is extremely broad and includes a large number of species of Lower Carboniferous through Cretaceous hybodonts. Teeth of this diverse assemblage bear some morphological similarities; however, it is possible that at least some of them deserve generic distinction. Lissodus duffini is possibly in this category but, with such limited material on hand, it appears best to retain this species in this genus for the present.

Duffin (1985) also suggested that a shark from the Mazon Creek fauna of Illinois, Dabasacanthus inskasi Zangerl 1979, is referable to Lissodus on the basis of tooth morphology. Teeth of this chondrichthyan appear to be very similar to those of L. duffini based on Zangerl's (1979, 1981) sketches. Dr. Zangerl (personal communication, 1985) indicated to me that the teeth of L. duffini appear to be shorter in amplitude dimension than those of D. inskasi. He also indicated that the dentition of this latter shark was poorly preserved and that only one tooth was visible on the specimen. A detailed examination of Zangerl's specimen, as suggested by Duffin, will be required in order to establish the possible relationships of D. inskasi and L. duffini. It should be noted that if D. inskasi teeth are determined to represent a species of Lissodus then this specimen and L. africanus (L. Triassic,
South Africa) would be the only members of this genus for which articulated remains are known. Obviously, a comparison of skeletal features of these two sharks is in order; however, such an examination is beyond the scope of the present study.

An additional comment on Dabasacanthus inskasi is in order. Zangerl (1979) interpreted this shark to be a ctenacanth that represents an intermediate level between ctenacanths and hybodonts, principally on the basis of features of the mandibular arch, palatoquadrate, and Meckel's cartilage. He noted, however, that the teeth are unlike those of any other known ctenacanths, and the dorsal spines and dermal denticles are not strictly of the ctenacanth form either. Little is known at this time as to organizational levels of various Paleozoic chondrichthyan groups and Zangerl may indeed be correct in his placement of D. inskasi; however, the teeth, dorsal spines, and teeth of this shark are more like those interpreted herein to be hybodonts than rather than those of ctenacanths.

Functional Morphology.—The robust teeth of Lissodus duffini suggest durophagy with small, perhaps shelled, benthos as prey. Too few specimens are available for thin sections to be made, but it appears probable that the tooth crowns have thick orthodentine. The labial buttress
fits into the medial indentation on the lingual side of the preceding tooth and serves as a spacer to keep each tooth in its proper position in the tooth row.

Fig. 00.—Postulated arrangement of the teeth of Lissodus duffini n. sp. In this model, tooth rows interlock as suggested by indentations or pressure scars on the undersides of the lateral margins of the labial buttresses of teeth. The labial buttresses serve as spacers to keep teeth in proper position. Labiad is towards the top of the diagram.

Duffin (1985) has suggested that the broad indentations (pressure scars) on either side of the labial buttress of some teeth accommodated the lateral margins of teeth in adjacent tooth rows. According to this interpretation, which appears to be likely, teeth in adjacent rows interlocked to form a stable pavement from which individual teeth were anchored at three points and thus could not be easily dislodged (Fig. 17).
Stratigraphic Distribution and Paleoecology.— Appalachian Basin specimens of *Lissodus duffini* are known from the Noble and Skelley limestones at two localities. Undoubtedly, additional specimens eventually be recovered from other units. Present data suggests that these teeth may indicate Conemaugh strata.

Tway (1982) noted specimens of *Lissodus duffini* in nine samples from the Heebner Shale, Leavenworth Limestone, and Plattsmouth Limestone of Iowa, Kansas, Missouri, Nebraska, and Oklahoma. These specimens occurred in low frequency in all samples. These units are Virgilian in age and roughly correlative to Conemaugh strata in the Appalachian Basin. Ossian's (1974) specimens, herein questionably referred to *L. duffini*, are from the Towle Shale of Nebraska, a Virgilian unit. He recorded a total of 166 specimens in his samples. Undoubtedly, this material should be re-examined.

Occurrences of *Lissodus duffini* teeth are in beds interpreted to have been deposited under normal marine conditions. Based on the low frequency of these teeth in the samples, *L. duffini* is interpreted to have been a minor predator on small marine benthos.

Genus *Maiseyodus* n. g.

Characterization.- Hybodont shark characterized by teeth with three to at least 10 blunt, conical, coarsely cristated cusps, one of which is commonly higher. Tooth base simple, lacking articulating processes, a lingual torus, or specialized foramina. Internally, teeth consist of a thick layer of enameloid which is underlain by thick orthodentine.

Type Species.- *Maiseyodus johnsoni* n. sp.

Distribution.- Pennsylvanian (Morrowan through Virgilian) of the Appalachian Basin; Virgilian of the Midcontinent, U.S.A.

*Maiseyodus johnsoni* n. sp.

Plate III, Figs. 6-19.

*Protacrodus* cf. *P. vestustus*, Ossian, 1974, p. 120-121, Pl. 4, figs. 1,2,5,6.

*Hybodus nebraskensis*, Ossian, 1974, p. 122-123, Pl. 4, figs. 7,8.

Subtype No. 009, Tway and Zidek, 1983, Figs. 35a-e.

Subtype No. 069, Tway and Zidek, 1983, Figs. 41a-e.

Holotype.- OSU 35383, "Lower Mercer" limestone, location Vel-34.
Referred Specimens.—OSU 35192-35193, 35212, 35225, 35363a-c, 35383, 35402-35417.

Etymology.—The genus is named for Dr. John G. Maisey of the American Museum of Natural History for his work on hybodont sharks. The species is named for Dr. Gary D. Johnson of the South Dakota Geological Survey for his extensive work on teeth of hybodont sharks.

Description.—The holotype (OSU 35383, Fig. 18, Pl. III, figs. 9-12) is a nearly perfect medial tooth. Measurements of this specimen are: width (am-pl), 1.85 mm; total height (from tip of central cusp to aboral edge of tooth base), 0.75 mm; maximum thickness of the tooth base, 0.2 mm; height of principal cusp, 0.55 mm; height of first lateral cusp, 0.35 mm; labiolingual width of tooth base (1-1), 0.6 mm.

The crown consists of seven cusps set on the labial edge of the tooth base. All cusps are labiolingually compressed and bluntly acuminate. The central cusp is the largest and is inclined to the right at an angle of about 10 degrees. The cusps become progressively smaller laterally and appear to diverge at increasingly greater angles from a horizontal plane intersecting the lateral edges of the tooth base. This apparent divergence is caused, however, by the arcuate shape of the tooth base of the tooth base.
Fig. 18.—Morphology of a tooth of *Maiseyodus johnsoni*, based on the holotype, OSU 35383. A, labial; B, lingual; C, aboral; D, lateral; E, oral. Abbreviations: cc, central cusp; cr, cristae; f, foramina; lc, lateral cusps; lt, lingual torus; tb, tooth base. Bar scale represents 1 mm.

Each cusp is adorned with distinct and prominent cristae, which are three in number on the labial faces of the central, first, and second lateral cusps. These cristae converge apically and appear to be fewer in number on the lateralmost cusps. A weak cista appears to be nearly continuous along the lateral edges of the cusps and forms a sharp edge or "occlusal crest." Lingually, the cristae are less prominent, less regular, and appear to be fewer in number. The entire crown is covered by a thin, transparent layer of enameloid, which is thickened to form the cristae.
The tooth base is roughly rectangular outline and is slightly narrower at the lateral edges. It is gently arched and highest medially. The lingual torus is short and slightly thicker than the lateral portions of the tooth base. Labially, the tooth base has a slight basolabial shelf that projects labial of the cusps. Aborally, the tooth base is relatively smooth and slightly concave with a shallow mediolabial depression that contains a single foramen.

Labially, the tooth base has at least 14 small, circular, irregularly distributed foramina. At least 9 slightly larger foramina are present lingually. Most of these foramina, both labially and lingually, are distributed along a line parallel to the tooth base. Some of the lingual foramina appear to connect with the basal foramen.

Additional teeth in the OSU collection exhibit considerable variation in morphology, as might be expected in a multielement dentition. The holotype is interpreted to be a tooth from a medial, perhaps parasymphysial, position. Other teeth in the collection are assigned to symphysial, mediolateral, and lateral positions.

Symphysial teeth (Pl.III, figs.6-8; Fig. 19) are symmetrical, with a high, stout, vertical medial cusp and one or two pairs of considerably smaller lateral cusps. A
a third pair of very small lateral cusps may be present. Bases of these teeth are relatively robust and crescent shaped with the concavity of the crescent forming a mediolabial sulcus.

Table 4.—Summary of numerical data for teeth of *Maiseyodus johnsoni* from the Appalachian Basin. Abbreviations: CR. WD., crown width; TOT. HT., total tooth height; W/H, width/height ratio. Measurements are in millimeters.

<table>
<thead>
<tr>
<th>REPOSITORY</th>
<th>UNIT</th>
<th>LOCAL</th>
<th>CR. WD.</th>
<th>TOT. HT.</th>
<th>W/H</th>
</tr>
</thead>
<tbody>
<tr>
<td>OSU 35402</td>
<td>Lowellville</td>
<td>Tfr-1</td>
<td>1.25</td>
<td>0.3</td>
<td>4.17</td>
</tr>
<tr>
<td>OSU 35403</td>
<td>&quot;L. Mercer&quot;</td>
<td>Vc-9</td>
<td>1.90</td>
<td>0.45</td>
<td>4.22</td>
</tr>
<tr>
<td>OSU 35383</td>
<td>&quot;L. Mercer&quot;</td>
<td>Vc-34</td>
<td>1.85</td>
<td>0.75</td>
<td>2.47</td>
</tr>
<tr>
<td>OSU 35363a</td>
<td>&quot;L. Mercer&quot;</td>
<td>Vc-34</td>
<td>1.90</td>
<td>0.75</td>
<td>2.53</td>
</tr>
<tr>
<td>OSU 35363b</td>
<td>&quot;L. Mercer&quot;</td>
<td>Vc-34</td>
<td>1.35</td>
<td>0.40</td>
<td>3.38</td>
</tr>
<tr>
<td>OSU 35363c</td>
<td>&quot;L. Mercer&quot;</td>
<td>Vc-34</td>
<td>1.90</td>
<td>0.60</td>
<td>3.17</td>
</tr>
<tr>
<td>OSU 35363d</td>
<td>&quot;L. Mercer&quot;</td>
<td>Vc-34</td>
<td>1.45</td>
<td>0.25</td>
<td>5.80</td>
</tr>
<tr>
<td>OSU 35405a</td>
<td>L. Mercer</td>
<td>CS1-1</td>
<td>1.15</td>
<td>0.80</td>
<td>1.44</td>
</tr>
<tr>
<td>OSU 35405b</td>
<td>L. Mercer</td>
<td>CS1-1</td>
<td>1.90</td>
<td>0.30</td>
<td>6.33</td>
</tr>
<tr>
<td>OSU 35406</td>
<td>L. Mercer</td>
<td>Hfg-5</td>
<td>1.30</td>
<td>0.50</td>
<td>2.60</td>
</tr>
<tr>
<td>OSU 35407</td>
<td>Brush Creek</td>
<td>Ph-3</td>
<td>2.20</td>
<td>0.96</td>
<td>2.44</td>
</tr>
<tr>
<td>OSU 35408</td>
<td>Portersville</td>
<td>At-45B</td>
<td>2.20</td>
<td>0.60</td>
<td>3.67</td>
</tr>
<tr>
<td>OSU 35409</td>
<td>Portersville</td>
<td>Av-47</td>
<td>1.60</td>
<td>0.55</td>
<td>2.91</td>
</tr>
<tr>
<td>OSU 35410</td>
<td>Ames</td>
<td>Gv-1</td>
<td>1.35</td>
<td>0.55</td>
<td>2.45</td>
</tr>
<tr>
<td>OSU 35411</td>
<td>Ames</td>
<td>Gwi-3</td>
<td>2.20</td>
<td>0.50</td>
<td>4.40</td>
</tr>
<tr>
<td>OSU 35412</td>
<td>Ames</td>
<td>Har-1</td>
<td>2.10</td>
<td>1.75</td>
<td>1.20</td>
</tr>
<tr>
<td>OSU 35415a</td>
<td>Ames</td>
<td>PA-3</td>
<td>1.20</td>
<td>0.50</td>
<td>2.40</td>
</tr>
<tr>
<td>OSU 35415b</td>
<td>Ames</td>
<td>PA-3</td>
<td>1.20</td>
<td>0.20</td>
<td>6.00</td>
</tr>
<tr>
<td>OSU 35414a</td>
<td>Ames</td>
<td>PA-2</td>
<td>1.10</td>
<td>0.35</td>
<td>3.14</td>
</tr>
<tr>
<td>OSU 35414b</td>
<td>Ames</td>
<td>PA-2</td>
<td>0.95</td>
<td>0.55</td>
<td>1.73</td>
</tr>
<tr>
<td>OSU 35414c</td>
<td>Ames</td>
<td>PA-2</td>
<td>1.20</td>
<td>0.30</td>
<td>4.00</td>
</tr>
<tr>
<td>OSU 35413</td>
<td>Ames</td>
<td>PA-1</td>
<td>0.95</td>
<td>0.70</td>
<td>1.36</td>
</tr>
<tr>
<td>OSU 35417a</td>
<td>Ames</td>
<td>PA-5</td>
<td>1.10</td>
<td>0.60</td>
<td>1.83</td>
</tr>
<tr>
<td>OSU 35417b</td>
<td>Ames</td>
<td>PA-5</td>
<td>1.70</td>
<td>0.30</td>
<td>5.67</td>
</tr>
<tr>
<td>OSU 35416a</td>
<td>Ames</td>
<td>PA-4</td>
<td>1.45</td>
<td>0.95</td>
<td>1.53</td>
</tr>
<tr>
<td>OSU 35416b</td>
<td>Ames</td>
<td>PA-4</td>
<td>1.10</td>
<td>0.70</td>
<td>1.57</td>
</tr>
</tbody>
</table>
Teeth interpreted to be from mediolateral positions are relatively low crowned; however, a principal cusp, near the medial position, is higher than others on the tooth (Fig. 19). All of these cusps are strongly inclined, either left or right, and cristae may continue from one cusp to the next, especially in specimens in which the cusps appear to be fused at their bases. Commonly, fewer cusps are present anteromedially to the principal cusp than are present posterolaterally.

Teeth interpreted to be from lateral tooth positions are very low crowned and commonly do not have a cusp that could be considered as the principal cusp because of its dominance in size (Fig. 19). The number of cusps on lateral teeth may be 10 or possibly more. These teeth are very laterally elongate and cusps in some of them show inclination to either left or right. Tooth bases are extremely thin and have irregularly distributed foramina.

Many teeth in the OSU collection have more cristae on the cusps than are present on the holotype. These cristae form prominent ridges that converge apically and may bifurcate basally. Relatively short cusps may exhibit an equal number of cristae on both labial and lingual sides. These short cusps may also be nearly circular in cross section and not exhibit the labiolingual compression of medial cusps of high-crowned teeth of symphyseal and medial teeth.
The microscopic anatomy of teeth of *Maiseyodus johnsoni* has been determined on the basis of three thin sections of teeth from location Ale-19 ("Buffalo"=Cambridge) and one section of a tooth from location Nn-13 (Cambridge). None of the sections exhibits excellent preservation and only the one from Nn-13 is of a complete tooth in sagittal section through the principal cusp. The other sections are of principal cusps.

A thick layer of enameloid coats the cusps and crown of the tooth. This substance is clear in its outer portion and is penetrated along its inner margin by very fine, somewhat wavy, dentinal tubules. The enameloid is underlain by a thick layer of orthodentine that appears to occupy the entire internal portion of the cusp except for a narrow pulp cavity in its central, proximal portion. The orthodentine is a dense tissue that has numerous more or less parallel dentinal tubules. Vascular canals are not apparent within this tissue in the cusp portion of the tooth.

The tooth base appears to be composed of trabecular dentine that surrounds a centrally located pulp cavity. This portion of the tooth is the poorest preserved in the available sections; these observations are therefore tentative. The aboral portion of the tooth base is composed of a dense tissue that lacks apparent vascular
canals or cell spaces. This material may be acellular bone, as has been reported in this morphological position in other Paleozoic chondrichthyans.

**DISCUSSION**

**Taxonomy.** Teeth of *Maiseyodus johnsoni* were briefly described and figured by Ossian (1974) and figured by Tway and Zidek (1983). Ossian, in his dissertation (1974, Pl. 4, figs. 1, 2, 5, 6), figured two teeth that he referred to *Protacrodus* cf. *P. vetustus*, a species described by Jaekel (1925) and redescribed by Gross (1938). Ossian also figured a specimen (1974, Pl. 4, figs. 7, 8) that he described as a new species of *Hybodus, H. nebraskensis*. Ossian's name for this specimen is not valid because it was described only in a dissertation. I interpret the teeth that Ossian (1974) referred to *Protacrodus* cf. *P. vetustus* to be mediolateral and lateral teeth of *Maiseyodus johnsoni* and the tooth Ossian described as *Hybodus nebraskensis* to be a medial tooth, similar to the holotype of *M. johnsoni* described above.

Tway and Zidek (1983, figs. 35a-e) figured a lateral tooth of *Maiseyodus johnsoni* as their subtype number 009. These authors (1983, figs 41a-e) also figured a symphyseal tooth of this species as their subtype number 069. Each of
these well-preserved specimens exhibits morphological features common to specimens from the Appalachian Basin and serve once again to illustrate the problems associated with utilitarian systems of classification.

Teeth of *Maiseyodus johnsoni* are generally similar to those of *Protacrodus vetustus*, described by Jaekel (1925) and Gross (1938). This shark, from Middle and Upper Devonian rocks of Germany, has teeth with a dominant principal cusp that is flanked laterally by at least three smaller cusps on each side. All cusps are coarsely cristated. The tooth base is simple and is penetrated by numerous foramina.

A reconstruction of a jaw of *Protacrodus vetustus* by Gross (1938) indicated six tooth files per ramus. The teeth decrease in size posteriorly but do not, apparently, exhibit much variation in number of cusps or relative cusp height. Lateral teeth of *Maiseyodus johnsoni* resemble those of *Protacrodus vetustus* but differ in having a greater number of cusps and in having inclined cusps. This similarity prompted Ossian (1974) to refer lateral teeth of *Maiseyodus johnsoni* to *Protacrodus cf. P. vetustus*.

Ossian (1974) also referred fused masses of conical dermal denticles to *Protacrodus cf. P. vetustus*, however; these denticles are very unlike the dermal denticles of *P. vetustus* illustrated by Gross (1938). Ossian (1974) did
not illustrate scales of the latter type from his fauna. Such scales do occur in the Appalachian basin fauna and could be from *Maiseyodus johnsoni*, but evidence is insufficient at this time to make that connection.

The teeth of *Maiseyodus johnsoni* have similarity to teeth of some Mesozoic species of *Hybodus*, both in general tooth morphology and in variation of the dentition. These similarities persuaded Ossian (1974) to assign teeth interpreted herein as medial teeth of *M. johnsoni* to *Hybodus nebraskensis* (informal manuscript designation). The possibility exists that the teeth in Ossian's fauna represent a hybodont that is distinct from *M. johnsoni*, although this possibility is unlikely because of the similarity and morphological gradation of these teeth with the presumed lateral teeth of *M. johnsoni*. In addition, if Ossian's specimens represent a distinct species, then this species would have had a homodont dentition—an unlikely possibility in view of the variation in other described teeth of *Hybodus*.

A parsimonious assessment of the teeth herein assigned to *Maiseyodus johnsoni* would, perhaps, lead to the conclusion that they be assigned to *Hybodus*. It is probable, in my opinion, that a detailed analysis of teeth of *Hybodus* would indicate that some, if not many, of
presently included species should be placed in new genera. This revision may be particularly needed for *Hybodus* teeth from Paleozoic rocks.

There remains a possibility that teeth of *Maiseyodus johnsoni* could be referred eventually to a previously described form. A number of teeth have been reported in the literature that have some morphological similarity to *M. johnsoni* teeth. All of these teeth are insufficiently preserved or have been insufficiently illustrated to allow detailed comparison. In addition, there is the possibility that a previously described median fin spine or dermal denticle is a senior synonym of *Maiseyodus johnsoni*.

Orvig (1966) described a partial squamation and a few presumed teeth referred to *Holmsella*? sp. This genus was originally described from isolated acanthodian-like scales (Gunnell, 1931) that have been demonstrated by Orvig (1966) and Zangerl (1968) to be scales of an elasmobranch.

The scales of *Holmsella*? sp. are similar in general morphology to those of *Protacroodus vetustus*. Orvig described specimens interpreted to be teeth which show a faint similarity to *Maiseyodus johnsoni* teeth. The single-cusped teeth described by Orvig have cristae similar to those of *M. johnsoni*. Zangerl (1981) has suggested that the specimens interpreted by Orvig to be teeth are actually mucous membrane denticles. No specimens have
been recovered from the Appalachian Basin that are identical to the presumed teeth described by Orvig (1966). The possibility remains that better preserved teeth of Holmsella? sp. would indicate that they are conspecific with M. johnsoni.

There is also some general similarity of the teeth of Maiseyodus johnsoni to teeth of Tristychius arcuatus Dick 1978. The blunt, cristated cusps of T. arcuatus are similar to those of M. johnsoni; however, the teeth of the former species have only one pair of lateral cusps and a large lingual torus. The general similarity of teeth of these two species does suggest that the assignment of M. johnsoni to the hybodonts is correct.

Teeth of Maiseyodus johnsoni also have some similarity to teeth of Sphenacanthus serrulatus, although the two forms of teeth do not appear to be identical. Dick (1978, p. 103) indicated that the teeth described by Stock (1883) as Tristychius arcuatus, from the Lower Carboniferous of Britain, are actually teeth of Sphenacanthus serrulatus. The poor figures of these specimens (Stock, 1883, Pl. VII, figs. 9-12) indicate teeth with a crown width slightly less than a centimeter and a central cusp flanked laterally by three smaller cusps. Some of the teeth figured by Stock appear to be asymmetrical, with the central cusp flanked laterally by more cusps on one side
than the other. Stock (1883) indicated that the cusps are strongly cristated on these teeth. The teeth of *Sphenacanthus serrulatus* appear to have knoblike protrubances at the base of the cusps, a feature not present on teeth of *M. johnsoni*. These protrubances probably served as "spacers" in the tooth file. Undoubtedly, the teeth of *Sphenacanthus serrulatus* should be restudied and refurred.

Teeth of *Maiseyodus johnsoni* are also similar to teeth of *Mesodmodus* St. John and Worthen 1875 (Kinderhookian). Of the three species of this genus described by these authors, teeth of *Mesodmodus exsculptus* appear to have greatest similarity to teeth of *Maiseyodus johnsoni*. There can be no question that these genera are distinct, but the somewhat similar morphology of teeth of these two forms suggests that *Mesodmodus* may be a hybodont and that this traditionally Mesozoic group may have been established by the early in the Carboniferous and probably had its origins in the Middle or Late Devonian.

**Dentitional Organization and Function.**—The precise organization of the dentition of *Maiseyodus johnsoni* cannot be determined directly; however, the teeth of this species can be divided into at least five distinct morphological variants within a morphological gradation
series (Fig. 19). It is probable that each ramus of the jaws bore more tooth families than are depicted in this illustration, if it is appropriate to draw from the analogs provided by articulated dentitions of Mesozoic hybodonts, and by the fact that teeth in some adjacent tooth families are probably so similar to one another that they are difficult to separate. A definite problem in deciphering morphological breaks (tooth families) in this gradation series is the relatively small number of complete or nearly complete teeth in the OSU collection—most specimens are broken fragments bearing only a few cusps.

Figure 19. Morphological variation in the dentition of *Maiseyoidus johnsoni*. The diagram illustrates major morphotypes within a morphological gradation series on one ramus of the jaw. "S" represents a presumed symphyseal tooth and the Roman numerals represent additional tooth files.

The general similarity of the teeth of *Maiseyodus johnsoni* to teeth of some well known Mesozoic hybodonts is of value in reconstructing the dentition. Patterson's
(1966) study of teeth of *Hybodus brevicostatus*, from the British Wealden, indicated that this shark had a symphyseal tooth file and nine files in each ramus. The teeth are lower crowned and less symmetrical posterolaterally and the cusps point away from the symphysis. The largest teeth are in the fifth tooth file. Patterson (1966, p. 303-304) was able to distinguish between upper and lower teeth on the basis of greater concavity of the aboral surface of the tooth base in teeth from the lower jaws.

Maisey (1983) described a well-preserved specimen of *Hybodus basanus* in which the dentition is more or less in place. He noted 10 tooth files in the upper right ramus, 11-12 files in the upper left ramus and 10 files in each lower ramus. Teeth in adjacent tooth files are arranged in alternating fashion so that a tooth in any replacement series cannot be shed until the preceding tooth in an adjacent file is lost. Upper and lower teeth are offset so that when the mouth was closed the cusps interlocked, but did not occlude. Maisey also noted that there are no symphyseal teeth in the upper jaw, central cusps are inclined posterolaterally, and teeth are most symmetrical near the symphysis. He indicated that one or two teeth are functional in each file and 2 or 3 replacement teeth are visible behind the functional teeth.
From these descriptions, some inferences can be drawn in regard to the dentition of *Maisiyodus johnsoni*. Most teeth of this species in the OSU collection show either right or left inclination of the cusps, except for a few specimens which are symmetrical, relatively stout, and high crowned. These latter teeth also occur in low frequency in the collection, suggesting that these symmetrical teeth are from a symphyseal tooth file (Pl. III, figs. 6-8; Fig. 19, "S"). Other relatively high-crowned teeth in the collection have a greater number of lateral cusps and most exhibit a slight inclination of the principal cusp. The holotype is of this tooth form. Owing to the relatively slight inclination of the cusps, their relative symmetry, and because they are relatively high crowned, these teeth are interpreted to be from medial tooth positions; that is, parasymphyseal tooth files and perhaps a few adjacent tooth files (Fig. 19, "I").

Teeth placed in file "II" (Fig. 19) are relatively symmetrical and similar to those from file "I", except they are lower crowned. Teeth in file "III" are low crowned and have a strong inclination of the cusps. They also exhibit variation in the number of cusps on either side of the principal cusp, with fewer cusps in the direction of inclination. Tooth file "IV" must certainly
represent several tooth files in the dentition. These teeth are very low crowned and may exhibit 10 or more cusps. In many of these specimens a principal cusp is difficult to distinguish.

By comparison with Mesozoic hybodont dentitions, summarized above, and from the morphological variation of the dentition of *Maisevodus johnsoni*, it is probable that there were perhaps 9 or 10 tooth files in each ramus and a symphyseal file in at least one jaw. The presence of sharp-cusped piercing or grasping teeth in the medial portion of the dentition and lower-crowned "crushing" teeth in the posterolateral portions of the dentition suggests that *M. johnsoni* could potentially capture and process a variety of prey including perhaps small fishes and invertebrates that lacked thickly calcified shells.

It is probable that *Maisevodus johnsoni* was a diminutive fish. Most teeth in the OSU collection are less than 2 mm in maximum dimension (Table 4). Incomplete specimens, from the "Buffalo sandstone" (=Cambridge) at location Ale-19 (OSU 35192, 35193), suggest maximum tooth dimensions of about 1 cm. Comparison of these teeth with those of a hybodont, *Tristychius arcuatus* Dick, 1978, indicate that teeth in the 1 mm to 2 mm size range were borne by a shark of about a half meter in length.
No characteristic hybodont cephalic spines have been found in the microfossil samples nor are they present in the macrofossil collection. This fact is not surprising in view of the large number of teeth and only a few cephalic spines that Johnson (1979) noted in his collections of hybodont elements from Texas. He also noted a similar infrequency of dorsal fin spines. The relatively small number of *Maiseyodus johnsoni* teeth in the Appalachian Basin collection suggests that cephalic and dorsal fin spines would be rare. There is a possibility that *M. johnsoni* did not possess cephalic spines, but it is unlikely that it did not possess dorsal fin spines.

**Stratigraphic Distribution and Paleoecology.**—Teeth of *Maiseyodus johnsoni* range through the entire Pennsylvanian sequence of Ohio. These teeth were recovered from every marine unit except the Boggs, Vanport, Columbiana, Washingtonville, and Gaysport; however, relatively few samples were taken from these units. A total of 271 specimens were recorded from samples representing 44 localities. The highest frequency at any locality sampled for microfauna (which excludes the "Buffalo sandstone" at location Ale-19) was 30 specimens at location Gwi-3. Specimens are most abundant in Conemaugh marine units.
Tway (1982) recorded teeth of *Maiseyodus johnsoni* from one locality in the Leavenworth Limestone of Iowa, 9 localities in the Heebner Shale in Iowa, Kansas, Missouri, Nebraska, and Oklahoma, and from 10 localities in the Plattsmouth Limestone of Iowa, Kansas, Missouri, and Oklahoma. Specimens occurred at relatively low frequency at all of these Virgilian localities.

Ossian (1974) recorded more than 1,800 specimens of *Maiseyodus johnsoni* from the Towle Shale (Virgilian) of Nebraska. This large suite of specimens may be informative in statistical studies of the dentition.

All of the Appalachian Basin localities are interpreted to represent sediments deposited in open marine conditions, except for the "Buffalo sandstone" locality (Ale-19) which has a mixture of marine and nonmarine forms. Ossian's (1974) Nebraska localities are similar to the "Buffalo sandstone" in that there is a mixing of marine and nonmarine elements. Tway's samples apparently all represent normal marine environments.

**Occurrence.** - Lowellville, Tfr-1, (1): "Lower Mercer", Vc-8, (1); Vc-9, (1); Vel-6, (1); Vel-34, (11): Lower Mercer, CS1-1, (2); Hfg-5, (2); Sb-4, (2); Tl-1, (1); Tl-7, (1): Upper Mercer, Mp-3, (5); Ts-5, (2): Putnam Hill, Td-4, (1); Vel-15, (1): Brush Creek, Aa-64, (2); Ale-18, (1);
At-9, (1); Aw-47, (7); Pb-3, (4): Cambridge (= "Buffalo sandstone"), Ale-19, (71); GA-5, (4); Gca-5, (1); Nn-13, (12): Portersville, Acn-31, (2); At-45B, (4); Aw-47, (12): Noble, Nbu-1, (8); Nn-12, (4): Ames, Aa-64, (1); Aam-19, (3); Acn-31, (16); At-45B, (2); At-64, (1); CAC-2, (10); Cma-10, (13); Gwi-3 (30); HAr-1, (4); Nbu-4, (8); M0m-1, (7); Nn-3, (11); Pb-4, (9); PA-1, (10); PA-2, (1); PA-3, (8); PA-4, (17); PA-5, (3); PA-6, (3): Skelley, Aal-14, (2); Nbu-3, (4): Atoka, OK-2, (1).
Hybodont Tooth "A"

Pl. VI, Figs. 1-2

Subtype 177, Tway and Zidek, 1983, figs. 79a-b.

Characterization.- Teeth of a hybodont shark that are low-crowned, laterally elongate, with short crowns and a small, low, conical medial cusp. Lateral portions of crown with a central apical ridge and vertical ribs and sulci that meet along the apical ridge. Lingual torus moderately developed and with irregular foramina. Labial portion of base undercut with a shelf-like ridge and small, specialized foramina.

Referred Specimens.- OSU 35134, Lower Mercer, CS1-1; OSU 38361, Upper Mercer, Mp-1.

Distribution.- Pennsylvanian of the Appalachian Basin; Plattsmouth Limestone (Virgilian) of the Midcontinent.

Description.- Most specimens of this taxon in the collection are incomplete as is the specimen illustrated by Tway and Zidek (1983); therefore, some observations are tentative and subject to revision. The tooth crown is laterally elongate (in the ampl dimension) and the crown height is homogeneous throughout its length except for a slightly raised central cusp that is present on some specimens that appear to belong to this taxon. The central cusp is cone-shaped, low, and has a few apically converging ridges or cristae.
The lateral portions of the crown have vertical ridges with intervening sulci that extend from the crown/base junction to a longitudinal apical ridge. The apical crown ridge has a series of valleys and ridges that correspond to the vertical ridges and sulci of the labial and lingual portions of the tooth. Some of the ridges bifurcate near the apical ridge. One incomplete specimen, OSU 35134, exhibits at least 12 such vertical ridges. Lingual and labial surfaces of these teeth are very similar except the vertical ridges are slightly expanded near the bases on the labial side. Specimens from the Lower Mercer limestone at location CS1-1 and the specimen illustrated by Tway and Zidek (1983) exhibit a peculiar fretted pattern on the basolinguai portion of the crown. A few specimens tentatively placed with this taxon, that have the central cusp preserved, show a slight, bulbous labial and lingual expansion of the crown at the medial cusp.

The tooth base has a moderately expanded lingual torus which is roughened and irregular with relatively large, irregularly distributed foramina. Labially, the tooth base has a thin, shelf-like ridge beneath which the tooth is sharply undercut. Several small foramina are aligned along the base of this labial ridge.
DISCUSSION

These teeth do not appear to be similar to any previously named taxon and may deserve designation as a new genus and species of hybodontid shark. So few complete specimens are available in the collection that I defer such designation until better material is available. Dr. Gary Johnson has examined these specimens and has noted (personal communication, 1985) that they are not, in his opinion, referable to Polyacrodus (or Lissodus of Duffin, 1985), Hybodus, or Acrodus—teeth of which are common in fauna from Lower Permian rocks of north-central Texas.

The specimen illustrated by Tway and Zidek (1983, figs. 79a-b) is definitely referable to this taxon. Tway (1982) recorded these teeth in very low frequency from the Plattsmouth Limestone (Virgilian) at two localities in Kansas and one locality in Missouri.

A total of seven specimens of hybodont tooth "A" have been recorded in samples from five localities in four stratigraphic units in the Appalachian Basin. These units are referable to the Pottsville, Allegheny, and Conemaugh Groups.

Occurrence.—Lower Mercer, CS1-1, (3); Vanport, Mp-3, (1); Ames, Aa-63, (1); Gv-1, (1); Skelley, Nbu-3, (1).
ADDITIONAL HYBODONT TEETH
Pl. VI, Figs. 3-6

The OSU collection contains a few fragmentary teeth in that appear to be referable to hybodonts. Most of them are insufficiently preserved to permit more than a rudimentary description.

The Skelley limestone bone bed at location Nbu-3 yielded several incomplete specimens that Dr. Gary Johnson (personal communication, 1985) has suggested are possibly referable to *Hybodus*. These specimens have a high, labiolingually compressed, conical central cusp that is bordered laterally by at least three much smaller cusps. Each cusp bears several widely spaced cristae that converge apically. Labial and lingual surfaces of these tooth crowns do not differ markedly. The tooth base is not preserved on any of these specimens.

Although these fragmentary specimens resemble some teeth of *Hybodus* from Mesozoic rocks, they do not resemble teeth of these sharks in precise detail. *Hybodus* has numerous species, many of which are probably nominal, and is in great need of restudy. In my opinion it is not likely that Paleozoic hybodont teeth, such as those under discussion, are referable to the genus *Hybodus*. It should be noted also that teeth from the Skelley limestone are not similar to those described by Lund (1970) as *Hybodus*.
allegheniensis, from the nonmarine Duquesne limestone (Conemaugh) of Pennsylvania. Teeth of Lund's species bear small subsidiary cusps on the labial portion of the lateral cusps. As noted above, it is probable, in my opinion, that Lund's specimens should be referred to a genus other than *Hybodus*.

Two fused tooth whorls from the Ames limestone at location PA-3 also may be referable to hybodonts. The first specimen (OSU 38668) consists of the left half of three teeth with laterally elongate, smooth, rounded crown that lack ornamentation. These tooth crowns appear to be highest and broadest (in the 1-1 dimension) in the central portion of the tooth. These teeth are not in contact with one another in the whorl and bear no articulating processes or projections for maintenance of spacing in the tooth row. The tooth bases are indistinct and the teeth are fused to a curved, bony? base. Cross sections of broken teeth suggest that the crowns are composed of orthodentine with an enameloid cap.

A second set of fused teeth (OSU 38634; Pl. VI, figs. 5-6) from this locality consists of five teeth that become progressively larger and different in shape lingually. The teeth articulate by means of a prominent labial process. Labially, the smaller teeth are nearly conical in shape and become progressively wider (am-pl dimension) and
longer (1-1 dimension). All of the tooth crowns are fused to a bony base which projects through an arc that terminates considerably below the teeth. The presumed bony base is concave on the undersurface. The shiny, polished surface of these teeth suggests that enameloid caps orthodentine. Schultze (1985, fig. 4, no. 6) illustrated a similar fused tooth whorl; however, it cannot be stated with certainty that the specimen under discussion is identical to his specimen.

These two sets of fused teeth appear to be referable to hybodonts rather than to anterior teeth of cochliodonts or orodonts because they lack tubular dentine characteristic of the latter groups. It is possible that the second tooth whorl is from a symphyseal dentition and that the first described whorl represents a lateral tooth file. It is also possible that these tooth whorls are from different species. It is worth of considering that the second whorl (OSU 38634) may be referable to Lissodus duffini n. sp. because the posterior teeth in this whorl have the same general shape as do specimens of L. duffini. The few known specimens of L. duffini do not precisely resemble the teeth in the whorl from the Ames limestone, although these isolated teeth may be from lateral tooth positions whereas the specimens in the whorl may be from a
medial or symphyseal position. The first tooth whorl (OSU 38668) does not have teeth that resemble those of _L. duffini_. It is of interest to note that none of the specimens of _L. duffini_ in the collection preserve tooth bases. This may be because the crowns were fused to a bony base and did not have separate tooth bases.
Order Symmoriida Zangerl 1981

Comments on cladodontid teeth.—Teeth of cladodontid sharks are perhaps one of the most poorly understood and misinterpreted assemblages of chondrichthyan fossils. These teeth are constructed on a simple plan—a flattened, superficially simple tooth base from which arise, along the labial margin, a series of sharp-pointed, conical cusps, the central one of which is the largest. Cursory examination of collections of these teeth may lead to the conclusion that they are all so similar that they are undifferentiable or, alternatively, that they are all so different in minor details that no reliable species can be recognized. However, no worker has undertaken such a study of large collections of cladodontid teeth since the original descriptive studies such as those of St. John and Worthen (1875) and Davis (1883).

The common "solution" to this problem has been to place most of these teeth in Cladodus, a genus which Zangerl (1973) has demonstrated to have been applied to a large number of generically distinct shark teeth. Williams (1985) has, accordingly, relegated the name Cladodus to a nomen dubium (Chorn and Whetstone, 1978).

This seemingly unresolvable taxonomic maze was, in part, deciphered by study of associated skeletal material, including teeth, of cladodontid sharks from Pennsylvanian
fissile black shales of the Eastern Interior and Midcontinent Basins. The description of *Cobelodus aculeatus* by Zangerl and Case (1976) and *Denaea meccaensis*, *Stethacanthus altonensis*, and *Symmorium reniforme* by Williams (1985) indicated that each of these species possessed clearly differentiable teeth. It was not until the current study was undertaken, however, that it was demonstrated that isolated specimens of cladodontid teeth from Pennsylvanian rocks could be reliably identified and referred to the species listed above and to a new species of *Denaea*. In addition, all Pennsylvanian cladodont teeth examined in this study and in numerous other collections can be reliably referred, if sufficiently well preserved, to these species. This study demonstrates that the century-old enigma of isolated chondrichthyan teeth can be solved with adequate collections and detailed study.

**Family Symmoriidae Dean 1909**

**Genus Symmorium Cope 1893**

**Characterization**.—Medium to large cladodont shark with short rostrum, lacking dorsal crests on the braincase. Teeth typically cladodont with reniform tooth bases that bear paired basolabial articular bosses and corresponding apical articular bosses (Modified from Williams, 1985).
**Symmorium reniforme** Cope 1893

Plate IV, Figs 19-20

*Symmorium reniforme* Cope, 1893, p. 999-1001; 1894, p. 427, Pl. xviii, figs. 1-5; Zangerl, 1981, p. 70-71, fig. 77a,b. Williams, 1985, p. 103-116, Pl. 6, figs.3-4; Pl. 7, figs. 1-17.

*Cladodus acuminatus* Newberry, 1875, p. 45-46, Pl. LVIII, fig. 4.

*Cladodus carinatus* St. John and Worthen, 1875, p. 279, Pl. 4, figs. 6a-c, 7a-b.

*Cladodus gracilis* Newberry and Worthen, 1866, p. 30-31, Pl. 1, fig. 17.

*Cladodus lamnoides* (Newberry and Worthen), Trautschold, 1874, Pl. 1, figs. 3a-d.

*Cladodus mortifer*, Newberry and Worthen, 1866, p. 22, Pl. 1, fig. 5; St. John, 1870, p. 431-432; 1872, p. 239, Pl. III, fig. 6, Pl. VI, fig. 13; Newberry, 1897, p. 285, pl. 22, figs. 2, 2a.


*Cladodus occidentalis*, Leidy, 1859, p. 3; 1873, p. 311, Pl. 17, figs. 4-6; Eastman, 1903, p. 168, Pl. 2, figs. 3, 8, 9; Branson, 1916, p. 652-653, Pl. 2, figs. 23, 24; Zidek, 1973, p. 92, fig. 2a-c.

*Cladodus yunnanensis* P'an, 1964, p. 156-157, 167-168, Pl. 7, fig. 4a-b.
Cladodus sp., Easton, 1942, Pl. XII, fig. 11; Case, 1973, figs. 13-18; Bendix Almgreen, 1975, Pl. 2, figs. A-E; Zidek, 1975, p. 7, fig. 1b; Miller, 1981, p. 894-895, figs. 1a-d.

Ctenacanthus occidentalis, Obruchev, 1967, Pl. 3, figs. 10-12.

Styptobasis knightiana, Cope, 1891, p. 447, pl. 28, fig. 2; Cladodus knightiana (Cope), Eastman, 1903, p. 168-169, pl. 2, fig. 4.

?Scolopodus sigmoidalis, Harris and Hollingsworth, 1933, p. 194-195, Pl. 1, figs. 4a-b.

Characterization.—As for the genus, which is monotypic.

Distribution.—Upper Mississippian, Pennsylvanian, and Lower Permian of U.S.A.; Middle Carboniferous, U.S.S.R.; Lower Pennsylvanian, Greenland.

Referred specimens.—OSU 35431, 35432, 35433.

Description.—The following description of teeth of Symmorium reniforme is based on 29 specimens in the OSU microscopic collection and about 40 specimens in the macroscopic collection, the descriptive information provided by Williams (1985), and observations on many additional specimens in numerous other collections. Morphological features of these teeth are illustrated in Fig. 20.
Teeth of *Symmorium reniforme* commonly have four cusps; a large central cusp and two pairs of smaller lateral cusps. Williams (1985) indicated that additional paired lateral cusps may be present. The central cusp is broad at its base but tapers rapidly to a sharp-pointed tip that may be blunt in heavily worn specimens. This cusp exhibits a noticeable sigmoid flexure in lateral view and is almost always vertically oriented. Williams (1985) reported some specimens in which this cusp is directed lingually. In cross section, the central cusp is relatively flat on its labial side but is markedly convex on the lingual surface. Very fine, longitudinally oriented cristae cover the
lingual margin of the cusp and bifurcate proximally. Labially, cristae are less prominent and dissipate before reaching the base of the cusp. A prominent ridge or carina is present on each side of the central cusp and demarcates lingual and labial faces of the cusp. The lateral cusps are smaller than the central cusp and the outermost pair are larger than the innermost pair. These cusps are conical and circular in cross section. The innermost pair of cusps may point labially and the outermost pair may diverge laterally.

The tooth base is reniform in outline, flattened in the oral-aboral dimension, and has a prominent lingual torus. The cusps are set along the labial margin of the tooth base. The lingual torus is broad, convex, and bears two flattened, knoblike apical articulating bosses that are situated approximately in line with the interior pair of lateral denticles. Numerous small foramina penetrate the lingual torus and one or more larger foramina may be present centrally on the lingual edge of the torus. Aborally, the tooth base is concave and bears numerous foramina, including, on some specimens, one or more slightly larger foramina near the labial margin.

Two prominent knoblike articulating bosses are present on the aboral-labial margin of the tooth base approximately in line with the lateral edges of the
central cusp. Between these basolabial articulating bosses is a deep sulcus. Teeth in the collection range in size from approximately 3 mm to 35 mm in maximum dimension (from the tip of the central cusp to the aboral side of the tooth base).

DISCUSSION

Williams (1985) and Zangerl (1981) have thoroughly reviewed the taxonomic history and skeletal morphology of Symmorium reniforme; these topics are therefore treated only briefly here. Cope (1893, 1894) described this shark from a partial skeleton (FMNH UF 574) from the Mecca Quarry Shale (Desmoinesian) of Illinois. In his 1894 paper, Cope illustrated teeth and branchial denticles of S. reniforme but later workers were unable to relate his small and inadequate illustrations to isolated elements in other collections. Consequently, isolated teeth of S. reniforme consistently have been referred to Cladodus Agassiz, as have most other cladodont teeth. Branchial denticles of symmoriid sharks have been referred to a variety of organ species. By rules of priority, Cope's (1893) species should be suppressed as a junior synonym of Leidy's (1859) species of Cladodus, C. occidentalis, yielding the new combination, Symmorium occidentalis.
Until Leidy's holotype, if extant, can be restudied, however, Cope's original combination, *Symmorium reniforme*, is provisionally retained.

A large number of isolated cladodont teeth described from Pennsylvanian rocks are, with little question, referable to *Symmorium reniforme* (see synonomy). The morphology of these teeth is distinctive and should not be confused by workers who carefully examine their specimens. Indeed, there appears to be no further need to use "*Cladodus*" for Pennsylvanian specimens. The central cusp of *S. reniforme* teeth is distinctive and reliable identifications can be made from this element alone. A specimen probably referable to the central cusp of *S. reniforme* has been described from microscopic samples as *Scolopodus sigmoidalis* (a conodont genus) by Harris and Hollingsworth (1933, p. 194-195, Pl. 1, figs. 4a-b). Teeth of *S. reniforme* are comparatively common in collections of macroscopic teeth of Pennsylvanian age.

**Mucous Membrane Denticles.**—The skin of *Symmorium reniforme* was devoid of dermal denticles; however, the buccal cavity and branchial area bore numerous denticles that appear to be distinctive of symmoriid sharks. Williams (1985) indicated that these denticles range from comparatively simple, conical, recurved forms with a
bulbous base to those with six or more cusps fused in a coxcomb pattern to complex, double-rowed, fused cusps. Similar branchial denticles appear to be present in other symmoriid sharks (see Symmoriid Mucous Membrane Denticles, herein). At this stage of knowledge they appear to be typical of the group rather than a particular species.

Denticles of this type have been described under the name Stemmatias simplex (St. John and Worthen) 1875 for the single-row, coxcomblike variety and under the name Stemmatius bicristatus (St. John and Worthen) 1875 for the double-row variety (originally designated Stemmatodus, preoccupied; Williams, 1985). Similar branchial denticles, including the single-cusp variety, have been described as Idiacanthus Gunnell 1933, Gunnellodus Wilimovsky 1954 (substitute name for Idiacanthus, preoccupied), Scolopodus (in part) Harlton 1933, and Multidentodus Harlton 1933. Zangerl and Case placed these genera and their included species in synonomy with a symmoriid shark, Cobelodus aculeatus. As indicated above, these mucous membrane denticles appear to be morphotypes typical of the group rather than individual species (see section on denticles for additional details).

Tway and Zidek (1983) also illustrated a number of mucous membrane denticles of symmoriid sharks from Pennsylvanian rocks of the Midcontinent. With their
utilitarian scheme of classification these denticles were assigned the following subtype numbers: 017, 018, 032, 057, 074, 105, 124. Their subtype number 156 (figs. 26a-c) appears to be an isolated cusp of a Symmorium reniforme tooth.

**Functional morphology.** Teeth of **Symmorium reniforme** were organized in successional rows along the jaw rami and each tooth family was situated within a lingual dental furrow or groove (Mapes and Hansen, 1984). The spacing between tooth files was about equal to the width of the tooth base (am-pl) so that teeth in opposite jaws interlocked when the mouth was closed. There is no evidence of purposeful occlusion of the teeth.

The number of teeth in an individual tooth file is uncertain; however, a radiograph of a specimen of **Symmorium reniforme** from the Mecca Quarry Shale of Indiana (Field Museum of Natural History PF 7366), provided by Rainer Zangerl, shows five teeth in one file. It is probable that several teeth in a file were simultaneously in a functional position; an observation suggested by reconstruction of an articulated tooth file and by patterns of punctures on cephalopod shells interpreted to have been preyed upon by **S. reniforme** (Mapes and Hansen, 1984).
Teeth of *Symmorium reniforme* articulated by means of a pair of knoblike bosses on the basolabial portion of the tooth base that rested upon two corresponding platformlike knobs on the apicolingual surface (lingual torus) of the preceding tooth (Mapes and Hansen, 1984). This arrangement is functionally similar to that of certain other chondrichthyan described in this report and provided a mechanism by which point-specific stresses placed on the apex of the central cusp during prey capture would have been distributed throughout the tooth file. This arrangement prevented an individual tooth from being ripped from its anchoring connective tissue. In addition, such an organization protected vascular vessels that passed from tooth to tooth in a particular file.

Teeth of *Symmorium reniforme* are designed for piercing and stabbing and grasping and retention of prey. The central cusp was the main prey-penetrating portion of the tooth and presumably dealt the "lethal blow". The lateral cusps, situated at slight angles to the central cusp, assisted in grasping and retaining slippery, wriggling prey such as other fishes. Central cusps of *S. reniforme* teeth are very sharp pointed when unworn, but some specimens in the OSU collection are heavily worn by antemortem abrasion. This condition suggests that these teeth were retained in the mouth for considerable periods
of time—in contrast to the "revolver" dentition of modern sharks in which teeth are shed at a rapid rate (Newberry, 1889; Williams, 1979, 1985; Mapes and Hansen, 1984).

Paleoecology.—Symmoriurn reniforme must have been one of the dominant, top-level predators in Pennsylvanian seas. These sharks reached large sizes—Mapes and Hansen (1984) suggested that a specimen with a tooth of 21 mm in maximum dimension may have been 2.5 m in length. Zangerl (1981) indicated the presence of teeth, probably referable to this species, from Pennsylvanian black shales of the Eastern Interior Basin, that are as large as 40 mm in maximum dimension. Although there may not be a strictly linear relationship between increase in tooth size and proportional increase in body size, it is probable that these sharks may have reached lengths of 4 m or more.

The teeth and body proportions of these sharks indicate active predation (Williams, 1985; Zangerl, 1981), probably as an opportunistic predator. Certainly, other fishes would have constituted the principal portion of the diet of Symmoriurn reniforme and few fishes in Pennsylvanian seas would have been immune to attack. However, the opportunistic nature of this shark has been demonstrated by Hansen and Mapes (1983) and Mapes and Hansen (1984) with description of a nautiloid from the
Kendrick Shale of Kentucky that appears to have been bitten by *Symmorium reniforme* (Fig. 21). Additional cephalopods, including specimens from Pennsylvanian rocks of Ohio, that appear to have been bitten by *S. reniforme*, have been reported by Hansen and Mapes (in press).

Remains of *Symmorium reniforme* are widely distributed in rocks that represent a variety of marine environments. Teeth are common in marine limestones representing shallow water, normal marine conditions and partial skeletons as well as isolated teeth are abundant in the Eastern Interior and Midcontinent Basins in fissile black shales that have been interpreted as representing shallow-water deposition (Zangerl and Richardson, 1963) or deep-water environments (Heckel, 1977).

![Fig. 21. Reconstruction of Symmorium reniforme pursuing a nautiloid. Body proportions after Zangerl (1981). From Mapes and Hansen (1984).](image-url)
Stratigraphic and geographic distribution.- The samples examined in this study yielded 29 Symmorium reniforme teeth from 5 stratigraphic units at 13 localities. In addition, the OSU collection contains 42 teeth of this species in the macroscopic size range from the Sharon ironstone, Putnam Hill ("Zaleski"), Vanport, Columbiana, Washingtonville, Brush Creek, Cambridge, Portersville, Noble, Ames, and Skelley. This species appears to range through the entire Pennsylvanian marine sequence of the United States. S. reniforme may range as low as Chesterian rocks, if the specimen described by Miller (1981) as Cladodus sp. is referable to this species, and may range as high as the Lower Permian (Embar Formation, Wyoming) if the species described as Cladodus occidentalis by Branson (1916) is conspecific.

In addition to numerous occurrences throughout the United States, specimens probably referable to Symmorium reniforme have been reported from other continental areas in rocks of Pennsylvanian age. Trautschold (1874) described teeth of Cladodus lamnoides from Myachkovian rocks of the Moscow basin, U.S.S.R., that appear to be referable to S. reniforme. Obruchev (1967) figured a tooth, from the same rocks and area as Trautschold's specimens, of Ctenacanthus occidentalis. The specimen is undoubtedly referable to S. reniforme. Bendix Almgreen
(1975) described and figured a specimen of *Cladodus" sp. from the Upper Marine Group of Amdrup Land, Greenland, that appears to be a tooth of *S. reniforme*. P'an (1964) described and illustrated a cladodont tooth, referred to a new species, *Cladodus yunnanensis*, from Carboniferous rocks of China. This specimen, illustrated only in labial view, is similar to *S. reniforme* in regard to basolabial articular bosses, a labi ally flattened central cusp with lateral carinae, and similar lateral cusps. Based on available information, *C. yunnanensis* appears to be provisionally referable to *S. reniforme*. It is probable that teeth of *S. reniforme* will eventually prove to be nearly ubiquitous in marine rocks of Pennsylvanian age.

**Occurrence.**—"Lower Mercer", Vel-34, (1); Putnam Hill, CS0-2, (1); Spk-1, (1); Td-7, (1); Tg-6, (1); Vel-19, (1); Vanport, Lw-2, (1); Columbiana, HOb-1, (1); MUho-14, (2); Ss-4, (1); Washingtonville, CAr-2, (1); Tj-2, (1); Brush Creek, Aa-64, (2); At-9, (4); Aw-47, (1); Gca-6, (2); Pb-3, (1); Cambridge, PMo-10, (2); Portersville, Aw-9, (1); Pb-1, (1); Noble, Nbu-1, (2); Ames, Aa-63, (3); Aam-19, (6); Acn-31, (4); At-64, (2); Aw-58, (1); CAc-2, (2); Cma-10, (1); Gwi-3, (5); M0v-1, (2); MUm-1, (2); Wn-1, (5); WVA-1, (3); Skelley, Aal-14, (1).
Genus **Cobelodus** Zangerl 1973

Characterization.- Symmoriid sharks with large numbers of teeth of minute size. Teeth on palatoquadrate monocuspid, recurved, cristated, and needlelike with small, bulbous tooth bases and simple pulp cavities. Mandibular teeth cladodont with conical, cristated, asymmetrical central cusp and commonly a single pair of comparatively large, cristated lateral cusps that are widely spaced from the central cusp. Tooth base slightly triangular with a reduced lingual torus, saddle-shaped in labial or lingual views, and lacking articular bosses. (Modified from Zangerl and Case, 1976).

**Cobelodus aculeatus** (Cope) 1894  
Pl. IV, figs. 12-15

**Styptobasis aculeata** Cope, 1894, p. 434, Pl. 20, figs. 1-5.


Subtype No. 100, Tway and Zidek, 1983, Fig. 44a-d.  
Subtype No. 95, Tway and Zidek, 1983, Fig. 11.  
Subtype No. 96, Tway and Zidek, 1983, Fig. 12.  
Subtype No. 193, Tway and Zidek, 1983, Fig. 30a,b.

Characterization.- As for the genus, which is monotypic.
Distribution.—Pennsylvanian of the Appalachian, Eastern Interior, and Midcontinent Basins.

Referred specimens.—OSU 35205, 35218, 35359a-b, 35427, 38601, 38666.

Description.—Monocuspid teeth associated with the palatoquadrate have a single, laterally compressed, conical cusp that is wide at the base and tapers distally to a long, sharp point. This cusp is recurved lingually and possesses numerous cristae that traverse the length of the cusp and commonly bifurcate basally. The tooth base is a simple, bulbous, oval to triangular, roughened structure that may be set at an angle of up 60 degrees to the principal orientation of the cusp. This structure lacks any articular bosses or principal foramina. Internally, these teeth appear to be simple, hollow cones of orthodentine and lack development of trabecular dentine.

The cladodont teeth are associated with the Meckel's cartilages and have long, sharp-pointed central cusps that recurve lingually and are asymmetrically inclined to either the right or left. The central cusp is circular to slightly oval in cross section and bears fine, broadly spaced cristae that traverse the length of the cusp. The lateral cusps almost always consist of a single pair, although rarely a specimen may exhibit a small lateral cusp intercalated between the central cusp and one of the
main lateral cusps. The lateral cusps are widely spaced from the central cusp and are situated near the lateral edges of the tooth base. These cusps also bear widely spaced cristae.

The tooth bases are saddle-shaped, in labial or lingual views, with the arch or highest point of the saddle being in the central part, commonly off center in the direction of asymmetry of the principal cusp. The tooth bases are slightly triangular in oral view with a short lingual torus. Some specimens exhibit a rectangular outline and lack a lingual torus. No prominent articular bosses are visible on these teeth. The basolabial portion of the tooth base is thin and appears to be scooped-out. The lateral margins of the tooth base are thickened and have an aborally oriented projection. A small lingual foramen is commonly present as is an aboral foramen in the lingual half of the aboral surface. Morphological characteristics of the teeth are presented in Fig. 22.

Fig. 22.- Morphology of teeth of *Cobelodus aculeatus*. Cladodont teeth in: A, labial; B, lingual; C, oral. Needlelike teeth in: D, lateral; E, labial. Bar scale represents 0.5 mm. Abbreviations: cc, central cusp; cr, cristae; lc, lateral cusp; lf, lingual foramen; tb, tooth base.
DISCUSSION

Zangerl and Case (1976) described and illustrated teeth and other skeletal structures of *Cobelodus aculeatus* from black shales of the Eastern Interior and Midcontinent Basins. As noted by these authors, Cope (1894) originally assigned this species to *Styptobasis*, the type species is *S. knightiana*. The holotype of *S. aculeata* is a worn cusp of a cladodont shark; however, it is so poorly preserved that its morphology cannot be determined. Zangerl and Case (1976) indicated that the holotype of *Styptobasis aculeata* was, however, clearly distinct from specimens of *Styptobasis knightiana*. Zangerl (1973) therefore proposed *Cobelodus* for Cope's species, *C. aculeatus*.

Zangerl and Case (1976) indicated that no tooth wells or grooves are visible on the jaws of *Cobelodus aculeatus*. In addition, they noted that the abundant single-cusped teeth appear to always be associated with the palatoquadrates whereas the less abundant cladodont teeth are always associated with the Meckel's cartilages. None of the specimens studied by Zangerl and Case (1976) had teeth exactly in place on the jaws and they carefully and appropriately used caution in advancing this interpretation. It is likely, however, that they correctly interpreted the general distribution of teeth in this shark. *Cobelodus aculeatus* is the only Paleozoic
chondrichthyan, of which I am aware, that exhibits such extreme dignathic heterodonty. It should be noted, lest this extreme exception be misconstrued as the rule, that the pattern of cristae on both tooth forms is very similar and careful analysis eventually may have connected them to a single species had not more or less complete skeletal material become available.

Tway and Zidek (1983) illustrated a cladodont tooth (their Subtype No. 100) of *Cobelodus aculeatus* from Virgilian rocks of the Midcontinent basin. In addition, their Subtype Nos. 95, 96, and 193 appear to be needlelike teeth from the upper dentition of *Cobelodus aculeatus*.

**Mucous membrane denticles.**- As noted in the discussion of *Symmorium reniforme*, the branchial or mucous membrane denticles placed in synonymy with *Cobelodus aculeatus* by Zangerl and Case (1976) appear to be typical of symmoriids as a group rather than individual species within this group. Zangerl and Case (1976) indicated that the anterior branchial arches of *C. aculeatus* bear single-cusped denticles similar to and perhaps indistinguishable from the monocuspid teeth associated with the palatoquadrates. They suggested that, in general, the single-cusped branchial denticles tend to be shorter and stouter than the needlelike dentition teeth. The posterior branchial arches, according to these authors, bear composite
denticles consisting of two to at least six fused, conical, recurved denticles aligned in a row and sharing a common base ("Stemmatias simplex").

Functional morphology.—The cladodont teeth of Cobelodus aculeatus lack well-developed articular bosses; however, it is evident that these teeth did articulate in successional tooth rows. The basolabial portion of the tooth base is very thin and exhibits a scooped-out area in its central portion. The lateral extremities of the tooth base accentuate this condition, giving a saddle-shaped appearance, by being thickened and projected aborally.

The effect of this arrangement is that the short lingual torus of the preceding tooth in the tooth file nested in this scooped-out area beneath the successional tooth behind it. The descending lateral extremities of the tooth served to "embrace" the lingual torus of the preceding tooth, thereby preventing dislodgment of teeth in the file during prey capture. This arrangement aligned the aboral foramen with the lingual foramen of the preceding tooth, thereby protecting the principal nutrient vessel. This mode of articulation is simply a variation on a theme and is portrayed by other symmoriids and, indeed, a variety of other Paleozoic sharks.
The asymmetry of the cladodont teeth, in which the principal cusp is inclined either right or left, probably indicates teeth from either right or left lower rami. Presumably, the inclination of the central cusp was directed posteriorly. As yet, no symmetrical teeth of Cobelodus aculeatus have been found. Such teeth would probably represent symphyseal or medial tooth families, if such families were present in this species. The size of the collection available for this study is so small, however, that it is not surprising that such teeth have not been found.

The monocuspid, needlelike teeth are not as easily interpreted as are the cladodont teeth. These simple teeth lack any articulating structures and it is unknown if they were even organized into tooth files. It is likely, however, that these teeth occupied a "tooth field", similar to a dense pattern of dermal denticles present on the skin of many chondrichthyans.

The unusual dignathic heterodonty of the dentition of Cobelodus aculeatus, in which cladodont teeth occupied the lower jaws and simple, monocuspid, needlelike teeth occupied the upper jaws, can be interpreted as a specialized "division of labor". The multicusped, posteriorly inclined cladodont teeth would have impaled and retained prey, whereas the needlelike teeth would have
penetrated deeply and lethally into the prey immobilized on the cladodont teeth. Presumably, the delicate, needlelike teeth would have been prone to breakage during prey capture and their much greater abundance would have counteracted this predilection. Presumably, these monocuspid teeth were shed frequently. Both the abundance of these teeth in the jaws and the tendency, perhaps, for rapid shedding would also explain the significantly greater abundance of monocuspid teeth in microsample residues in comparison to the cladodontid teeth.

Zangerl and Case (1976) made an additional observation that bears repeating. They noted that the teeth of Cobelodus aculeatus are very small in relation to the overall size of this shark (adult specimens are in the range of 150 to 200 cm whereas the teeth are commonly in the range of 1 to 2 mm). A cladodont tooth of C. aculeatus, measured in the labiolingual dimension, represents only 1.1 percent of the length of the mandible. In Symmorium reniforme this same comparison is 7.5 percent. It is apparent, therefore, that small teeth were not always derived from small sharks; however, again, this exception should not necessarily be accepted as the rule.

Paleoecology.—Cobelodus aculeatus is one of the most common sharks in the black shales of the Eastern Interior Basin and in the Midcontinent Basin complex of the U. S.
A. (Zangerl, 1981). Cladodont teeth of this species, the most definitive element in microsample residues, are not common in the shallow-water carbonates of the Appalachian Basin. The monocuspid, needlelike teeth are more common, which, as noted above, may be a reflection of their greater abundance in the mouth and a more rapid rate of replacement. That C. aculeatus was probably not a dominant and abundant constituent of the carbonate environments is further reinforced by data gathered by Tway (1982) who recorded these cladodont teeth (her subtype number 100) in low frequency from only three localities in the Plattsmouth Limestone of the Midcontinent Basin. It appears reasonable to conclude, at this juncture, that C. aculeatus was numerically more abundant in the black shale environments and may have been only a transient shark in the carbonate-producing environments.

As noted previously, the teeth of Cobelodus aculeatus suggest an active predator that probably captured small fishes and perhaps weakly shelled invertebrates. The body form (Zangerl and Case, 1976; Zangerl, 1981) also suggests a fast-swimming, highly maneuverable predator (Fig. 23).
Fig. 23.—Reconstruction of *Cobelodus aculeatus*. Body proportions and fins based on Zangerl and Case (1976). Facial features are speculative.

**Stratigraphic and geographic distribution.**—Zangerl and Case (1976) recorded specimens of *Cobelodus aculeatus* from Desmoinesian rocks of the Eastern Interior Basin and from Desmoinesian, Missourian, and Virgilian rocks of the Midcontinent Basin. Tway's (1982) specimens of cladodont teeth of this species were derived from the Plattsmouth Limestone (Virgilian) of Iowa and Kansas. She recorded needlelike teeth of this species from numerous localities in Virgilian rocks in the Midcontinent Basin. An additional specimen in the collection, from the Wewoka Formation (Desmoinesian) of Oklahoma, has been provided by R. H. Mapes.
Most of the Appalachian specimens were derived from Conemaugh rocks (Brush Creek, Cambridge, and Portersville). Incomplete and poorly preserved specimens from the Upper Mercer (Pottsville) and Vanport (Allegheny) are tentatively referred to this species. No specimens clearly attributable to Cobelodus aculeatus have as yet been reported from Morrowan rocks.

Genus *Denaea* Pruvost 1932

Characterization.—Small cladodont shark with numerous small (0.5 to 1 mm) teeth with 3 to 7 cusps. Tooth bases lack well-developed articular bosses. Branchial denticles highly variable, with palmate, blunt-cusped forms common. Pectoral fin bearing a single, fused piece, the metapterygium, and a very long, thin metapterygial axis. Dorsal surfaces of haemel arches in the caudal peduncle fused and expanded into a thin wedge. (Modified from Williams, 1985).

Type species.—*Denaea fournieri* Pruvost 1922. Lower Carboniferous Marbre Noir of Belgium.

*Denaea saltsmani* n. sp.

Plate IV, figs. 1-5

Subtype No. 021, Tway and Zidek, 1983, Fig. 38a-e.

Characterization.—Very small teeth (less than 1 mm) with long, slender cusps as in *Denaea meccaensis* and a triangular tooth base with a prominent lingual foramen on the lingual edge of the tooth base.

Holotype.—OSU 38638, Brush Creek, location KY-2.

Referred Specimens.—OSU 35425, 35426, 38639.
Distribution.—Pennsylvanian of the Appalachian Basin; Virgilian of the Midcontinent Basin.

Etymology.—Named in honor of Alan L. Saltsman, who contributed several important samples of microscopic chondrichthyan remains from the Ames limestone of Pennsylvania.

Description.—The following description is based on 46 specimens, many of which are poorly preserved, from the Appalachian Basin collection. In addition, 328 exquisitely preserved specimens (OSU 35423, 35424), from Desmoinesian rocks of Oklahoma and inequivocally referred to *Denaea meccaensis*, were available for comparison through the courtesy of R. H. Mapes of Ohio University.

The teeth assigned to *Denaea saltsmani* are small (less than 1 mm in maximum dimension) and are of a typical cladodont morphology with the cusps positioned along the labial edge and at a right angle to the tooth base. The central cusp is long, slender, circular in cross section, and curves markedly linguad with only slight sigmoid flexure. Fine, delicate, relatively widely spaced cristae extend the length of the cusp from the base to the tip. The cristae are equally spaced both labially and lingually and lateral carinae are absent (See Fig. 24 for morphology).
Teeth of this species possess from one to three pairs of lateral cusps. The holotype (OSU 38638) has a relatively large pair of first lateral cusps and a comparatively small (although broken) pair of outer cusps. In other specimens with two pairs of lateral cusps the outermost pair is the largest (OSU 38640). The middle pair of cusps are the largest in specimens with three pairs of lateral cusps. These cusps are long, slender, sharp-pointed, and recurve lingually. The outermost pairs of cusps exhibit a slight lateral flare. These cusps possess very fine, delicate cristae.

The tooth base is relatively thin in the oral-aboral dimension and, when viewed either orally or aborally, is triangular — the base of the triangle forms the straight labial margin and the distal part of the lingual torus forms the apex of the triangle. Specimens in the collection exhibit little deviation from this general shape. The average 1-1/am-pl ratio for 18 specimens from the Ames limestone at location PA-4 is 0.55, with the range of this ratio being 0.38 to 0.67 (Table 5). Three specimens from the Brush Creek limestone at location KY-2 (the holotype and two paratypes) have an average 1-1/am-pl ratio of 0.49.
The lingual edge of the central part of the lingual torus is produced into a rounded, raised, bulbous, lingually extended area, in the center of which, on the lingual margin, is a prominent, circular lingual foramen. This foramen may form an open channel or groove which is common aborally, but rarely present orally.

The oral surface of the lingual torus has a roughened, irregular appearance owing to the presence of numerous, irregularly distributed, shallow pits. These pits resemble foramina but do not appear to be connected internally to the tooth base. They are interpreted as anchoring pits for connective tissue. The aboral surface of the tooth base is relatively flat and smooth. The lateral edges of the tooth base on some specimens are slightly downturned. A large foramen is present in the center, or slightly linguad of center, on the aboral surface. This foramen may be in the form of a shallow groove that connects with the lingual foramen. Two or more smaller foramina may be present near the labiolateral margins of the aboral surface. On the labial margin of the aboral surface, beneath the central cusp, is an elongate (am-pl), slightly raised, weak, articular boss.
DISCUSSION

These teeth are the most perplexing of the cladodont teeth in the OSU collection and they cannot easily be assigned to a previously described species. They bear similarities to the teeth of *Denaea meccaensis* and clearly less similarity to teeth of *Stethacanthus altonensis*.

The cusps of the teeth assigned to *Denaea saltsmani* are identical to those of *Denaea meccaensis* in size, number, and morphology. The overall size of the teeth of these two species is similar and the tooth bases are similar in possessing a straight labial margin and in having weak articular bosses. The tooth bases of *Denaea saltsmani* differ from those of *D. meccaensis* in having a
triangular rather than a roughly hexagonal shape, in the
development of a lingually produced, bulbous lingual
torus, and in the location of the major foramina. In
Denaea saltsmani the lingual foramen is located on the
lingual edge of the tooth whereas in D. meccaensis this
foramen is on the oral surface of the tooth base. The
aboral foramen is located near the labial edge of the
tooth base whereas in D. saltsmani this foramen is in the
lingual half of the tooth base. In addition, the 1-1/ampl
ratio for Denaea saltsmani teeth is 0.55 whereas for D.
meccaensis teeth this ratio is 0.63 (see Tables 5 and 6).
The weakly developed articular boss present on D.
saltsmani teeth is even more weakly developed in D.
meccaensis teeth. The former teeth also lack well-
developed lateral depressions on the aboral surface.

Teeth of Denaea saltsmani differ from those of
Stethacanthus altonensis in a number of respects.
Stethacanthus altonensis teeth are narrower in the
labiolingual (l-l) dimension (l-l/ampl=0.47 versus 0.55
for Denaea sp.) and have well-developed articular bosses
on the tooth base. The central cusps of S. altonensis
teeth have very closely spaced and more numerous cristae
which are separated labiolingually by lateral carinae—the
latter features are lacking in teeth of Denaea saltsmani
and *D. meccaensis*. In addition, lateral cusps of *S. altonensis* teeth do not appear to be as long as are those of *Denaea saltsmanii*.

There is little doubt that the teeth here assigned to *Denaea saltsmanii* deserve separation from *D. meccaensis* and *Stethacanthus altonensis*. It may be argued, as one facet of a multiple working hypothesis, that teeth of *Denaea saltsmanii* represent teeth of juvenile specimens of *Stethacanthus altonensis*. This possibility cannot be completely ruled out; however, the fauna from the Ames limestone at locality Gv-1 contains teeth of both *S. altonensis* and *Denaea saltsmanii*, including teeth which appear to be assignable to *S. altonensis* that are in the size range of those of *Denaea saltsmanii*. Although teeth in this fauna have undergone considerable postmortem abrasion, the teeth of both species in a similar size range appear to be differentiable.

It is also plausible, at this stage of knowledge, that teeth of *Denaea saltsmanii* deserve separate generic recognition. The available specimens generally are not well preserved and the most parsimonious approach is to place them in *Denaea*, the genus to which they are most closely related. It is probable that these specimens are a new species, whether or not they are retained in *Denaea*. A tooth, of *Denaea saltsmanii* was illustrated by Tway and Zidek (1983) as their subtype number 021.
Observations on the dentition of *Denaea meccaensis*.-
Williams (1985) presented a detailed account of the skeletal morphology and dentition of *Denaea meccaensis* based on a study of specimens from Pennsylvanian black shales of the Eastern Interior Basin. An assemblage of 328 extremely well-preserved teeth of *D. meccaensis*, from limestone nodules in the upper part of the Wewoka Formation (Desmoinesian) near Bixby, Oklahoma, have been provided by R. H. Mapes of Ohio University. These specimens add new information on the morphology and variation of the dentition of this species.

The most common form of *Denaea meccaensis* teeth (Morphotype I, Fig. 25) includes those described by Williams (1985). A comparison of *D. meccaensis* teeth with those of *D. saltsmani* was given at the beginning of the Discussion section and need not be repeated here. Perhaps the most intriguing aspect of the Oklahoma assemblage of *Denaea meccaensis* teeth is that three morphological variations were noted. The most common variety (Morphotype I, Fig. 25) was described above and noted by Williams (1985). A second variety (Morphotype II, Fig. 25) has a tooth base with a rectangular outline that lacks the angles that give rise to the "hexagonal" shape of the more common form. These teeth also do not have well-developed foramina as do the common forms of teeth (Morphotype I).
The cusps are similar to those of the common form except that there is only one pair of lateral cusps.

The third morphotype (III, Fig. 25) of *Denaea meccaensis* teeth is comparatively stout and has three pairs of lateral cusps. The most striking aspect of these teeth is the comparatively narrow (1-l dimension) tooth base. The l-l/am-pl ratio for three specimens averages 0.39—less than for the narrow teeth of *Stethacanthus altonensis* (l-l/am-pl=0.47). These teeth are similar to other *D. meccaensis* teeth in other aspects of morphology except that the lingual foramen is very close to the lingual margin because of the narrowness of the lingual torus.
It is probable that these two unusual tooth forms represent specialized tooth families in the dentition of *Denaea meccaensis*. It is possible that the three-cusped specimens with a rectangular tooth base (Morphotype II) are from a symphyseal position and that the forms with a narrow tooth base (Morphotype III) represent parasymphyseal families. This suggestion is speculative;
however, specialized tooth families, where known in Paleozoic sharks, tend to be concentrated in medial or extreme lateral positions. Commonly, those from extreme lateral positions exhibit strong asymmetry.

Functional morphology.—The weak basolabial articulating boss of a tooth of *Denaea saltsmani* appears to have rested on the bulbous portion of the lingual torus of the preceding tooth as a crude and unspecialized means of articulation of the teeth. This position placed the aboral foramen in line with the lingual foramen—thus producing a mechanism for protection of the principal nutrient vessel.

Williams (1985) suggested that the teeth of *Denaea meccaensis* lacked articulating structures and were held in place in a tooth file by connective tissue that was anchored in the lateral grooves on the aboral surface of the tooth base. A very weak basolabial articulation boss is present on the teeth of *D. meccaensis* from Oklahoma. A corresponding boss on the lingual torus (apical articulating boss) is not apparent on these teeth. However, the position of the aboral foramen near the labial edge of the tooth base and the position of the lingual foramen in the middle of the lingual torus suggests that teeth of *D. meccaensis* articulated in a manner functionally similar to that of other cladodonts.
Additional anchoring of the teeth by connective tissue, as suggested by Williams (1985), would have supplemented the stability provided by the weak articular bosses.

The thin, delicate cusps of both *Denaea saltsmani* and *D. meccaensis* teeth and the apparent lack of significant wear on these cusps suggests that teeth in both species were not retained for long periods of time as was the case for cladodonts such as *Symmorium reniforme*. The fact that nearly every specimen of both species exhibits broken cusps suggests rapid replacement due to antemortem breakage rather than postmortem destruction. Rainer Zangerl has indicated (personal communication, 1985) that radiographs of shale slabs from Bethel Quarry (Excello Shale, see Zangerl and Case, 1973) reveal thousands of *D. meccaensis* teeth dispersed through each slab. Such an abundance suggests that these teeth must have been shed frequently and, perhaps, accumulated in such density by a slow rate of sedimentation. Williams (1985) indicated also that radiographs from these black shales in the Eastern Interior Basin exhibit articulated tooth files of *D. meccaensis* apparently held together by connective tissue. Such files were undoubtedly detached from carcasses rather than shed as part of the tooth replacement process.
The tiny, delicate teeth of both *Denaea saltsmani* and *D. meccaensis* possess cusps designed for piercing and retaining prey. They do not appear to have had sufficient robustness to have dispatched and held anything but small and relatively weak prey that lacked significant dermal armor. It is probable that both of these species occupied niches distinct from those of other cladodontids in the fauna. *Denaea meccaensis* was a small (40 to 50 cm) cladodontid with a body form suggesting rapid locomotion (Fig. 26).

**Paleoecology.** *Denaea saltsmani* has been recovered from rocks representing shallow, normal marine environments in the Appalachian and Midcontinent Basins. *Denaea meccaensis* may have been environmentally restricted in its distribution. This species has previously been reported only from black shales of the Eastern Interior Basin (Williams, 1985). The additional specimens mentioned in this report, from the Wewoka Formation of Oklahoma, came from limestone nodules enclosed in a black, platy shale (R. H. Mapes, personal communication, 1985). The environment of deposition of this unit is uncertain at this time; however, it appears to have been different than "typical" shallow-water carbonates and may represent an environment similar to that in which the black shales of the Eastern Interior Basin were deposited. Nevertheless,
it is apparent at this early stage of sampling microscopic chondrichthyan faunas that there was some mechanism which restricted the distribution of this shark.

Fig. 26.- Reconstruction of *Denaea meccaensis*. From Zangerl (1985).

At this time, it appears that this restrictive mechanism was environmentally related. Only one tooth in the collection from the Appalachian Basin is tentatively referred to *Denaea meccaensis*. This specimen, from a carbonate nodule within the Washingtonville shale at location CAr-2, is similar to morphotype III of *D. meccaensis*. Little work has been done on the environment of deposition of the Washingtonville although this unit is a black shale; however, a benthic fauna is present and it is unlike the black shales studied by Zangerl and Richardson (1963).
Stratigraphic and geographic distribution.—Teeth of *Denaea saltsmani* appear to range through most of the marine sequence in the Appalachian Basin—these teeth have been recovered in small quantities from Pottsville, Allegheny, and Conemaugh rocks. The only other reported occurrence of teeth of this species was by Tway (1982) from 16 localities in Virgilian rocks of Iowa, Kansas, Missouri, Nebraska, and Oklahoma. It is probable that microsamples from other areas will yield additional specimens.

Teeth of *Denaea meccaensis* has been reported previously only from Missourian rocks of the Eastern Interior Basin (Zangerl, 1981; Williams, 1985). Zangerl (1981) noted that this species has not been recorded from the black shales of the Midcontinent Basin. The occurrence of the Oklahoma specimens in the Wewoka Formation (Desmoinesian) represents the first record of this species outside of the Eastern Interior Basin and extends the stratigraphic range also. Interestingly, Tway and Zidek (1983) did not record any teeth referable to *D. meccaensis* from their Midcontinent samples. This may be because of geographic restriction, stratigraphic restriction (their samples were from younger Pennsylvanian rocks), or possibly they did not recognize the morphological distinctions of *D. saltsmani* and *D. meccaensis* teeth.
Occurrence.— Lower Mercer, Tl-7, (1); Upper Mercer, Mp-3, (2); Ts-5, (1); Putnam Hill, CSo-2, (1); Vanport,Td-4, (1); Washingtonville, Car-2, (1); Brush Creek, Pb-3, (1); KY-2, (3); Cambridge, Nn-13, (5); Portersville, Aw-9, (1); Noble, Nbu-1, (7); Ames, CAc-2, (1); Cma-10, (1); Gv-1, (7); PA-4, 29: Skelley, Aal-14, (1); Nbu-3, (1).

Table 5.— Numerical characteristics of Denaea saltsmanii from the Appalachian Basin. Abbreviations: am-pl, anteromedial-posterolateral; 1-1, labiolingual. Ratio of 1-1/am-pl averages 0.55.

<table>
<thead>
<tr>
<th>REPOSITORY</th>
<th>UNIT</th>
<th>LOC.</th>
<th>L-L</th>
<th>AM-PL</th>
<th>RATIO</th>
</tr>
</thead>
<tbody>
<tr>
<td>OSU 38638</td>
<td>Brush Creek</td>
<td>KY-2</td>
<td>0.40</td>
<td>0.95</td>
<td>0.42</td>
</tr>
<tr>
<td>OSU 38639</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.40</td>
<td>0.65</td>
<td>0.58</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.45</td>
<td>0.96</td>
<td>0.47</td>
</tr>
<tr>
<td>OSU 35425</td>
<td>Ames</td>
<td>PA-</td>
<td>0.30</td>
<td>0.80</td>
<td>0.69</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.50</td>
<td>0.90</td>
<td>0.56</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.50</td>
<td>1.00</td>
<td>0.50</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.40</td>
<td>0.70</td>
<td>0.57</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.50</td>
<td>0.85</td>
<td>0.59</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.45</td>
<td>0.85</td>
<td>0.53</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.35</td>
<td>0.65</td>
<td>0.54</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.40</td>
<td>0.80</td>
<td>0.50</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.40</td>
<td>0.70</td>
<td>0.57</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.55</td>
<td>1.05</td>
<td>0.52</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.70</td>
<td>1.20</td>
<td>0.58</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.50</td>
<td>1.00</td>
<td>0.50</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.50</td>
<td>0.80</td>
<td>0.63</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.50</td>
<td>0.75</td>
<td>0.67</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.50</td>
<td>1.05</td>
<td>0.48</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.40</td>
<td>0.80</td>
<td>0.50</td>
</tr>
<tr>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.60</td>
<td>0.90</td>
<td>0.6</td>
</tr>
</tbody>
</table>
Table 6.- Numerical characteristics of *Denaea meccaensis* from Oklahoma. Abbreviations: am-pl, anteromedial-posterolateral; l-l, labiolingual. Ratio of l-l/am-pl averages 0.63.

<table>
<thead>
<tr>
<th>REPOSITORY UNIT</th>
<th>LOC</th>
<th>L-L</th>
<th>AM-PL</th>
<th>RATIO</th>
</tr>
</thead>
<tbody>
<tr>
<td>OSU 35423 Wewoka</td>
<td>OK-</td>
<td>0.55</td>
<td>0.80</td>
<td>0.69</td>
</tr>
<tr>
<td>&quot;</td>
<td>0.45</td>
<td>0.70</td>
<td>0.64</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>0.50</td>
<td>0.90</td>
<td>0.56</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>0.50</td>
<td>0.70</td>
<td>0.71</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>0.40</td>
<td>0.90</td>
<td>0.44</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>0.40</td>
<td>0.60</td>
<td>0.67</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>0.40</td>
<td>0.60</td>
<td>0.67</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>0.50</td>
<td>0.70</td>
<td>0.71</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>0.45</td>
<td>0.60</td>
<td>0.75</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>0.50</td>
<td>0.70</td>
<td>0.71</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>0.50</td>
<td>0.50</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>0.40</td>
<td>0.75</td>
<td>0.53</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>0.45</td>
<td>0.65</td>
<td>0.69</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>0.45</td>
<td>0.60</td>
<td>0.75</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>0.40</td>
<td>0.65</td>
<td>0.61</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>0.50</td>
<td>0.70</td>
<td>0.71</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>0.35</td>
<td>0.80</td>
<td>0.43</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>0.30</td>
<td>0.80</td>
<td>0.38</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>0.30</td>
<td>0.85</td>
<td>0.35</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>0.40</td>
<td>0.70</td>
<td>0.57</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>0.40</td>
<td>0.70</td>
<td>0.57</td>
<td></td>
</tr>
</tbody>
</table>
Characterization. - Medium-sized cladodont shark bearing a broad, subtriangular to falcate dorsal spine with a prominent anterior shoulder and variable posterior articular surface. Spine consisting of trabecular dentine only, lacking an external coating of orthodentine, vitrodentine, or ornamentation. Brushlike structure articulating with posterior border of spine and bearing variable, modified dermal denticles. Unique dermal denticles present on dorsal surface of head. Teeth cladodont with long, slender, finely cristated central cusp bearing lateral carinae. Two to four pairs of lateral cusps present. Teeth bear prominent rectangular basolabial articulating boss and corresponding triangular apical articulating boss on short lingual torus. (Modified from Williams (1985).

Type species. - *Physonemus altonensis* St. John and Worthen 1875.

*Stethacanthus altonensis* (St. John and Worthen) 1875
Pl. IV, Figs. 16-18

*Cladodus alternatus* St. John and Worthen, 1875, p. 265, Pl. 2, figs. 14-18.

*Cladodus exilis* St. John and Worthen, 1875, p. 258, Pl. 1, figs. 1-6.
Cladodus fuller St. John and Worthen, 1875, p. 276, Pl. 4, figs. 9, 9a.


Cladodus pandatus St. John and Worthen, 1875, p. 278, Pl. 4, figs. 8, 8a.

Cladodus pattersoni Newberry, 1875, p. 47, Pl. 58, figs. 6, 6a.


?Cladodus aculeatus Eastman, 1917, p. 255-256, Pl. 10, fig. 4; Pl. 18, fig. 1.


Lamodus hamulus St. John and Worthen 1875, p. 283, Pl. 5, fig. 26. (Lamodus hamatus on plate description).

Physonemus altonensis St. John and Worthen, 1875, p. 454-455, Pl. 19, figs. 1-3.


Stethacanthus compressus Newberry, 1897, p. 292, Pl. 23, figs. 3-4.

Stethacanthus exilis Hussakof, 1913, p. 249, Pl. 47, fig. 3.

Stethacanthus praeceptor Hussakof, 1918, p. 169, Pl. 54, figs. 1-2.
Stethacanthus productus Newberry, 1897, p. 291, Pl. 23, figs. 1-2.

Stethacanthus tumidus Newberry, 1889, p. 198, Pl. 25, figs. 1-2.

Characterization.—As for the genus, which is monotypic.

Distribution.—Upper Devonian through Upper Pennsylvanian of U.S.A.; Namurian of Scotland.

Referred specimens.—OSU 35143, 35213, 35315, 35428, 35429, 35430.

Description.—Stethacanthus altonenis is known only by rare teeth from Pennsylvanian rocks of Ohio. Description herein is based primarily on available specimens in the OSU collection but is also supplemented by the observations of Williams (1985). For detailed description of skeletal and spine morphology, consult Williams (1985) and Lund (1974).

The teeth are typically cladodont with the cusps set in a row along the labial margin of the tooth base. The central cusp is considerably larger than the lateral cusps and is elongate, slender, lingually recurved, circular to slightly oval in cross section, and has a gentle sigmoid flexure. The cristae of the central cusp are comparatively
fine, closely spaced, and are finer labially than lingually. The cristae do not bifurcate and continue to the base of the cusp with little decrease in intensity. A faint but noticeable lateral carinae is present on each side of the cusp and serves to demarcate labial and lingual fields of cristae. The lingual cristae on the lateral sides of the cusp curve labially and terminate against the lateral carina.

The lateral cusps are small and weak in comparison to the central cusp and are vertically oriented. Commonly, two pairs of lateral cusps are present. Three pairs of lateral cusps are not uncommon and some specimens exhibit four pairs. The second pair of lateral cusps is always the largest and the innermost cusps are considerably smaller. Some specimens exhibit very small, nearly vestigial cusps intercalated between the main pairs of lateral cusps. The lateral cusps are circular in cross section and weakly cristated.

The tooth bases range from laterally elongate (am-pl dimension) forms to more equilateral ones (Table 7). The labial margin is nearly straight, whereas the lingual margin is rounded and tapers laterally to a pointed, downturned margin. When viewed labially, the tooth base on many specimens has a broad, low, M-shaped profile (Fig. 27).
The most distinctive feature of these teeth is the articular bosses. The basolabial articulating boss is rectangular in outline and about as wide as, and located just beneath, the central cusp. It is compressed labiolingually, flattened aborally, and has sharp, right-angle corners. The labial margin may be concave. The apical articulating boss is rectangular in outline but is commonly divided into two rounded, squared prominences. This boss is divided by a prominent lingual foramen. The apical boss is preceded, labially, by a rectangle-shaped pit (Fig. 27).

The lingual torus is relatively short in most specimens and has a prominent lingual foramen. A shallow, vertically oriented sulcus is associated with this foramen. The aboral surface of the tooth is slightly concave and has one moderately prominent foramen located labiob of center. Several smaller foramina are present on either side of the main aboral foramen and are aligned in a row parallel to the labial edge of the tooth base. Typical morphological features of these teeth are depicted in Fig. 27.
Fig. 27.—Morphological features of a tooth of *Stethacanthus altonensis*. Bar scale represents 1 mm. Abbreviations: aab, apical articulating boss; bab, basolabial articulating boss; cc, central cusp; cr, crista; f, foramen; lc, lateral cusp; tb, tooth base.

DISCUSSION

*Stethacanthus altonensis* was originally defined by St. John and Worthern (1875) from peculiar, triangular median fin spines. They originally assigned these spines to *Physonemus* McCoy 1857. Newberry (1889) recognized the distinctiveness of these spines and placed them in *Stethacanthus*. The complicated taxonomic history of the various spines assigned to this genus has been reviewed by Williams (1985) and Lund (1974) and need not be discussed in detail here. These spines are listed in the synonomy above.

It was not until the 1970's that relatively complete remains of sharks referable to *Stethacanthus* became known. Lund (1974) described specimens of *S. altonensis* from the
Chesterian Bear Gulch Limestone of Montana and Williams (1985) described remains of this species from Pennsylvanian black shales of the Midcontinent and the Lower Mississippian Sunbury Shale of Ohio.

Table 7. Dimensions of the tooth base of *Stethacanthus altonensis* teeth from the Appalachian Basin. Average ratio for l-1/am-pl=0.47.

<table>
<thead>
<tr>
<th>REPOSITORY</th>
<th>UNIT</th>
<th>LOC</th>
<th>L-L</th>
<th>AM-PL</th>
<th>RATIO</th>
</tr>
</thead>
<tbody>
<tr>
<td>OSU 35143</td>
<td>Portersville</td>
<td>Aa1-11</td>
<td>1.8</td>
<td>4.1</td>
<td>0.44</td>
</tr>
<tr>
<td>OSU 35429</td>
<td>Wash'ville</td>
<td>Ti-2</td>
<td>2.2</td>
<td>3.5</td>
<td>0.63</td>
</tr>
<tr>
<td>OSU 35428</td>
<td>Kendrick</td>
<td>KY-</td>
<td>2.0</td>
<td>4.6</td>
<td>0.44</td>
</tr>
<tr>
<td>OSU 35213</td>
<td>Portersville</td>
<td>Pb-1</td>
<td>1.8</td>
<td>3.5</td>
<td>0.51</td>
</tr>
<tr>
<td>OSU 35430</td>
<td>Ames</td>
<td>Gv-1</td>
<td>1.9</td>
<td>3.9</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td>&quot;&quot;</td>
<td>&quot;&quot;</td>
<td>1.3</td>
<td>2.7</td>
<td>0.48</td>
</tr>
<tr>
<td>&quot;&quot;</td>
<td>&quot;&quot;</td>
<td>&quot;&quot;</td>
<td>0.8</td>
<td>2.0</td>
<td>0.40</td>
</tr>
<tr>
<td>&quot;&quot;</td>
<td>&quot;&quot;</td>
<td>&quot;&quot;</td>
<td>0.8</td>
<td>2.2</td>
<td>0.36</td>
</tr>
<tr>
<td>&quot;&quot;</td>
<td>&quot;&quot;</td>
<td>&quot;&quot;</td>
<td>0.9</td>
<td>2.3</td>
<td>0.39</td>
</tr>
<tr>
<td>&quot;&quot;</td>
<td>&quot;&quot;</td>
<td>&quot;&quot;</td>
<td>0.9</td>
<td>1.9</td>
<td>0.47</td>
</tr>
<tr>
<td>&quot;&quot;</td>
<td>&quot;&quot;</td>
<td>&quot;&quot;</td>
<td>1.5</td>
<td>3.1</td>
<td>0.48</td>
</tr>
<tr>
<td>&quot;&quot;</td>
<td>&quot;&quot;</td>
<td>&quot;&quot;</td>
<td>1.7</td>
<td>3.0</td>
<td>0.57</td>
</tr>
</tbody>
</table>

The specimens described by Lund (1974) and Williams (1985) revealed that *Stethacanthus altonensis* possessed teeth previously described as *Cladodus exilis* St. John and Worthen 1875 (not *Cladodus turritus* Newberry and Worthen 1866 as indicated by Lund, 1974). In addition, these studies revealed that the unusual spine of *S. altonensis* supported a peculiar brushlike appendage that was studded with denticles originally described from isolated, unicuspid elements as *Cladodus pattersoni* (Newberry,
1875). In addition, the dorsal surface of the head of this shark was found to be studded with denticles of the *Cladodus pattersoni* morphology and those of the form named *Lamodus hamulus* by St. John and Worthen in 1875 (Williams, 1985). Williams also noted a morphological gradation between these two denticle forms.

The skin of *Stethacanthus altonensis*, as in other symmoriid sharks, is essentially naked except for these bizarre denticle fields on the head and the "brush" complex of the spine. The function of these unusual features has engendered speculation. Lund (1974) suggested that the brush aided in swimming. Williams (1985) offered the idea that it was used in sexual display during mating. Zangerl (1984) interpreted the unusual brush/head denticles to have functioned in creating a threat posture; when viewed dorsally, the two denticle fields appear to mimic the open, tooth-studded mouth of a much larger fish.

No denticles of either the *Cladodus pattersoni* nor the *Lamodus hamulus* morphotypes have been recovered from the microsamples in the OSU collection. This is not unexpected, considering the relative paucity of *Stethacanthus altonensis* teeth in the collection. It is also possible, as suggested by Williams (1985), that not all of the sharks currently placed in *S. altonensis* possessed such denticle development. Additionally,
Williams suggests that better preserved remains of this long-ranging shark may indicate a much greater taxonomic diversity. The recent description of *Orestiacanthus fergusi* and *Falcatus falcatus* by Lund (1984, 1985), from the Bear Gulch fauna, indicates some of this probable diversity in stethacanthids.

**Mucous membrane denticles.**—Williams (1985) indicated that radiographs of Mecca Quarry Shale specimens show densely packed mucous membrane denticles in the throat region of *Stethacanthus altonensis*. Some specimens reveal abundant single-cusped forms. Less common are the single-row variety, "Stemmatias simplex", and the double-row form, "Stemmatias bicristatus". As indicated in the discussion of *Symmorium reniforme*, at this stage of knowledge these denticle morphotypes appear to be typical of the group rather than individual species.

**Teeth.**—*Stethacanthus altonensis* teeth are distinctive and can easily be differentiate from other Pennsylvanian cladodonts except. Although the arrangement and morphology of the cusps is not exactly like that of any of these other cladodonts, the most distinguishing feature of *S. altonensis* teeth is the articular bosses. These rectangular structures are unlike the articular bosses of other Pennsylvanian cladodont teeth.
Cladodus alternatus, C. exilis, and C. springeri, described by St. John and Worthen (1875) from Kinderhookian rocks, and C. fuller i and C. pandatus, also described by these authors, in the same publication, from Pennsylvanian rocks, are referable to Stethacanthus altonensis. Eastman's (1917) specimen of Cladodus aculeatus, which Zidek (1973) referred to Cladodus sp. and indicated was from the Johns Valley Formation rather than the Caney Shale, may also be referable to S. altonensis. This specimen is embedded in matrix; the articulating bosses are therefore not visible. However, the slender central cusp and pattern of cristae on this cusp suggests a tooth of S. altonensis.

The enigmatic holotype of Cladodus neilsoni (Traquair 1888, 1897), from the Lower Carboniferous of Scotland, has recently been confirmed to be Stethacanthus altonensis, on the basis of a new and spectacular specimen collected and figured by Wood (1982). Although Traquair's holotype of C. neilsoni apparently lacks the spine/brush complex, the teeth illustrated by Traquair (1897) are clearly those of Stethacanthus, a fact that became clear to me prior to the report of Wood (1982) of the new specimen from Namurian rocks of Scotland.

Williams (1985) and Lund (1974) suggested, on the basis of spine morphology, that it is probable that there are several species of Stethacanthus. A lack of samples
from Devonian and Mississippian rocks render it impossible at this time to determine if separate species of this genus are differentiable on the basis of isolated teeth. Such an analysis would require large samples of teeth, either isolated specimens, or preferably teeth associated with other skeletal elements, from throughout the stratigraphic range of this genus. The Pennsylvanian specimens in the OSU collection from the Appalachian basin appear to be assignable to a single species and, following a parsimonious approach, are placed in _S. altonensis_. Specimens of the stethacanthids _Orestiakanthus fergusi_ (Lund, 1984) and _Falcatus falcatus_ (Lund, 1985) apparently do not have well-preserved teeth and little can be said of them at this time.

The variations in shape of the tooth base of _Stethacanthus altonensis_ teeth in the OSU collection, ranging from laterally elongate to nearly equidimensional specimens, suggests tooth positions from various parts of the jaws. The teeth were organized into labiolingually successional tooth files as is indicated by the presence of tooth wells on the Meckel's cartilage and palatoquadrate (Williams, 1985), and by the mode of articulation of the teeth. Although the variance in shapes of the tooth bases is small in this species (Table 7), it
is probable that the more equidimensional teeth were from medial positions whereas laterally elongate specimens were from posterior tooth files.

The mode of articulation of *Stethacanthus altonensis* teeth is a variation on the theme displayed by most cladodonts, xenacanths, some probable ctenacanths, and even neoselachians. The articular bosses of *S. altonensis* teeth are clearly distinct from those of any other described cladodont tooth, although they bear some similarity to the very weak articular bosses of *Denaea*. The rectangular basolabial boss appears not to have rested directly on the divided apical articulating boss but to have resided in a groove in front of this boss. The concave labial edge of the basolabial articulating boss would have embraced the basolingual portion of the central cusp. The apical articulating boss served, if this interpretation is correct, to prevent the successional tooth, located linguad, from moving in a labiolingual direction in the tooth file. This mode of articulation also protected the nutrient vessel that passed through the large foramen in the center of the apical articulating boss.

**Paleoecology.**—Skeletal remains and teeth of *Stethacanthus altonensis* are found in rocks representing a wide variety of marine environments. Teeth from the Appalachian Basin
were derived from shallow water, normal marine, carbonate accumulating environments. Specimens from the Bear Gulch Limestone of Montana have been interpreted to have been deposited in a marine lagoon (Lund, 1974). Specimens from the Cleveland Shale, Sunbury Shale, and Midcontinent black shales apparently lived in an environment in which habitable water overlayed anoxic conditions in a stratified water column. Zangerl (1984) suggested that, on the basis of general body form, diminuitive fins, and the drag that would be exerted by the brush complex during rapid locomotion, *S. altonensis* may have been a sluggish bottom dweller (Fig. 28). This interpretation is reasonable, except in the black shale environments, where there were no bottom dwellers.

Fig. 28.- Skeletal reconstruction of a female specimen of *Stethacanthus altonensis*. From Zangerl (1984).
Relatively complete specimens of *Stethacanthus altonensis* from the Bear Gulch Limestone of Montana and Namurian rocks of Scotland indicate sharks of a meter or less. Teeth of this shark are less than a centimeter in maximum dimension; the largest in the OSU collection is only 4 mm in maximum dimension (am-pl). The long, slender central cusp suggests piercing and retention of prey, similar to the function of teeth of other cladodonts. *Stethacanthus altonensis* probably preyed on small fishes and perhaps weakly protected invertebrates.

**Stratigraphic and geographic distribution.** - Teeth of *Stethacanthus altonensis* range through nearly the entire Pennsylvanian sequence and have been recorded from the following units: Boggs, Lower Mercer, Upper Mercer, Washingtonville, Cambridge, Portersville, and Ames. An additional specimen in the collection is from the Kendrick Shale of Kentucky. As indicated previously, *S. altonensis* has been recorded in the United States from Upper Devonian through Pennsylvanian rocks of the Midcontinent, Eastern Interior, and Appalachian Basins. Lund's (1974) specimens were derived from the Chesterian Bear Gulch Limestone of Montana. The specimens collected by Wood (1982) are from the horizon of the Top Hosie Limestone, lowermost Namurian, of Scotland. Traquair's (1888, 1897) specimen of *Cladodus neilsoni*, herein assigned to *S. altonensis*, was
collected from rocks in East Kilbride similar in age to those of Wood's (1982) Bearsden locality. It is probable that *Stethacanthus* will be found to be a widely distributed chondrichthyan now that isolated teeth and other skeletal elements have been adequately defined.

Order Petalodontida Zangerl 1981

Teeth of petalodonts are the most common specimens in the macroscopic collection, particularly those of Petalodus ohioensis. In addition to this species, teeth of Cholodus (Fissodus) inaequalis, Janassa sp., Peripristis semicircularis, and Polyrhizodus sp. have been recorded in moderate to rare (Polyrhizodus) abundance. In the microfauna, however, petalodont teeth are rarely preserved as complete or nearly complete specimens and microsample residues commonly yield only fragments of these teeth. For a review of this order and its included genera, consult Zangerl (1981) and Hansen (1985).

Petalodont tooth fragments found in acid residues in the microscopic size fraction are not, in most cases, identifiable as to species or even to genus; however, they can be readily identified as teeth of petalodonts. These fragments are characterized by a dense external tissue layer that has variously been identified as orthodentine (Zangerl, 1981; Hansen, 1985) or enameloid (Lund, 1983). Resolution and discussion of these identifications is beyond the scope of the present report. This tissue, whatever its identification, is commonly whitish in color, very dense, and it has a smooth outer surface and a pustulose inner surface. Underlying this dense outer layer, and poorly preserved in most specimens subjected to acid preparation, is a strutwork of porous trabecular dentine.
Fig. 29.—Dentition of *Petalodus ohioensis*. A, Possible arrangement of teeth of this species as determined from studies of a large sample of isolated teeth from Pennsylvanian rocks of Ohio and other areas of the U.S.A.; B, isolated tooth in labial aspect; C, in lateral aspect; D, lingual aspect. Abbreviations: cr, crown; tb, tooth base. Teeth at approximately natural size.

Most identifiable fragments of petalodont teeth in the microsamples are referable to either *Petalodus ohioensis* or *Peripristis semicircularis*. Fragments of teeth of *P. ohioensis* commonly represent a small portion of the crown. The tooth bases, owing to their porous structure, are preserved only as unidentifiable fragments. A tooth of *Petalodus ohioensis* and a possible arrangement of the dentition in this species is depicted in Fig. 29. Teeth of *Peripristis semicircularis* are comparatively small. Only a
single tooth was present in each jaw (Hansen, 1978; 1985). These tooth crowns are characterized by triangular serrations along the coronal margins. Portions of this serrated coronal margin are readily identified and have been encountered in several microsamples in this study.

The lack of more or less complete petalodont teeth in the microscopic fraction of acid residues indicates that teeth in this group were not mineralized, even in newborn or juvenile specimens, until they were larger than teeth commonly associated with the microfauna. This observation suggests that juvenile petalodonts did not have teeth smaller than several millimeters to a centimeter in crown width.

The labiolingually compressed teeth of petalodonts suggest shearing, nipping, and some crushing of prey. A specimen of *Janassa bituminosa*, from Upper Permian rocks of Germany, has been reported by Malzahn (1972) to contain brachiopods, crabs, and foraminifers in the gut. Hansen and Mapes (in press) have reported a Pennsylvanian straight nautiloid that appears to have been bitten by *Petalodus ohioensis*. At present, no other direct evidence of petalodont dietary preferences is available. However, petalodonts are common constituents of Carboniferous shallow-water marine carbonates but appear to be nearly absent from the black shale faunas (Mecca fauna) of the
Eastern Interior and Midcontinent Basins (one isolated tooth of *Petalodus ohioensis* is known from these shales). This evidence suggests that petalodonts must have obtained their food principally from among the benthos—a faunal element that was absent in the black shale environments. The abundance of petalodont teeth in the carbonates suggests that this group constituted a major source of predation on benthic invertebrates during the Carboniferous.

**Occurrence.**—*Petalodus ohioensis*—Boggs, MUF-3, (1): Upper Mercer, Ts-5, (1); Putnam Hill, Ty-3, (1); Ames, Aam-19, (1); At-45B, (1); At-64, (1); MUu-5, (1); Pmo-3, (1).

*Peripristis semicircularis*—Boggs, Hwa-1, (1); MUF-4, (1): Lower Mercer, Sb-4, (1); Ty-7, (1); Brush Creek, Aw-47, (1); GAp-3, (1); Cambridge, Gwe-1, (1); Portersville, At-45B, (1); Ames, Aa-63, (1); Aam-19, (2); Acn-31, (2); At-45B, (1); Aw-58, (1); Cma-10, (1); HAr-1, (1); MOn-1, (1); Pb-4, (1): Skelley, MUbr-6, (1).


Uncertain petalodont—Lower Mercer, MUMu-3, (1); PA-10, (1): Vanport, Lw-2, (1): Cambridge, GAg-3, (1); Gca-5, (1).
Order incertae sedis

Genus Venustodus St. John and Worthen 1875

Characterization.—Teeth of a chondrichthyan in which the crown is platformlike with a prominent, lingually imbricated basal ridge. Cusps stout, conical; median cusp most prominent. Crown nearly horizontal or strongly arched giving a V-shaped profile. Surface of crown covered with thick enameloid. Internally, tooth composed of tubular dentine. Tooth base short, restricted, and platformlike.

Type species.—Venustodus robustus St. John and Worthen 1875. Burlington Limestone, Iowa.

Venustodus argutus St. John and Worthen 1875

Pl. VI, figs. 7-9.

Venustodus argutus, St. John and Worthen, 1875, pp. 352-353, Pl. IX, figs. 5a-h, 6a-e.

Characterization.—Teeth small (about 1 cm or less) with prominent and regular imbricated ridges on lingual margin of crown.

Distribution.—Mississippian (Chesterian) of Illinois and Indiana; Pennsylvanian of Ohio; Desmoinesian of Oklahoma.
Referred specimens.—OSU 35138, 35435, 35436, 35437, 38622; CM 27240.

Description.—The small number of specimens in the OSU collection from Pennsylvanian rocks are fragmentary except for one specimen in the macroscopic collection from the Ames limestone at location JEwa-1 (OSU 35435). Most of the description is based on this specimen (Fig. 30) and is supplemented by a large number of specimens, which are apparently conspecific, from the Haney Limestone (Chesterian) at Mulzer Bros. quarry at Derby, Perry County, Indiana.

The crown of OSU 35435 has a width (am-pl) of 0.9 mm and is gently arched in an asymmetrical, V-shaped profile when viewed labially or lingually. The lateral extremities of the tooth are projected linguad from the median cone of the crown when viewed aborally. The crown is asymmetrical with the left lateral extremity being shorter than the right extremity. The crown is platformlike and measures approximately 0.3 mm in the labiolingual dimension. A prominent basal ridge, with two imbrications, traverses the entire margin of the crown. A prominent median cone demarcates the central portion of the tooth. This cone is broken in OSU 35435 and has an oval cross section, being compressed slightly in the am-pl dimension. Basally, the
median cone bears a prominent knoblike projection on its labial side. A low ridge, which bears short conical cusps, extends laterally on each side from the median cusp. On the left side are 12 small cusps and on the right and longer side of the crown there are at least 14 cusps.

The tooth base is not well exposed in OSU 35435 nor in any other fragmentary specimens in the OSU collection from Pennsylvanian rocks. However, the Chesterian specimens from the Haney Limestone of Indiana have tooth bases that are simple, rectangular, shallow structures that mimic the general outline of the tooth crown but are smaller than the crown, giving rise to a prominent overhang of the crown, especially labially. Specialized foramina appear to be absent with only irregularly dispersed foramina visible on the available specimens. Morphological features of Venustodus argutus are depicted in Fig. 30.

Fig. 30.- Morphological features of a tooth of Venustodus argutus based on OSU 35435 from the Ames limestone at location JEwa-1. A, oral; B, lateral; C, lingual. Abbreviations: br, basal ridges; cc, central cusp; lb, labial boss; lc, lateral cusps; tb, tooth base. Bar scale represents 1 mm.
In thin section, teeth of *Venustodus* from Mississippian rocks (Haney Limestone, Chesterian) exhibit well-developed tubular dentine. The outer surface of the crown is covered by a thin, shiny layer which is interpreted to be enameloid. In many specimens the enameloid has been removed partly or completely by both attrition and chemical solution by weak stomach acids (Zangerl, 1981). This tissue grades, centripetally, into a dense substance that is penetrated by dentinal tubules. This tissue (interpreted to be orthodentine) is organized into fingerlike centripetal projections that extend into the trabecular-dentine-filled pulp cavity of the tooth. One specimen in the collection, OSU 35138, has the outer enameloid layer and most of the orthodentine removed and the surface of the tooth crown is covered by small papillae. This surface represents the interface between the trabecular dentine and the orthodentine. Another specimen in the collection, OSU 35435, exhibits the reverse circumstance—the underlying tissues have been removed, leaving a crown covering of orthodentine and enameloid which shows, on its inner surface, a pitted appearance where the denteons penetrated this material. The microscopic anatomy of *Venustodus argutus* is illustrated in Fig. 31.
DISCUSSION

Taxonomy.— Although teeth of *Venustodus* are not uncommon in Mississippian rocks, this genus is one of the most poorly known of Carboniferous chondrichthyans. Leidy (1857) described a tooth from the St. Louis Limestone of Illinois as *Chomatodus venustus* (*C. venusus* on plate description) which St. John and Worthen (1975) referred to *Venustodus*. These authors also referred the specimen of *Chomatodus* (*Helodus*) *denticulatus* described by McCoy (1855, p. 618, Pl. 3K, figs. 9a,b) from the Lower Carboniferous (Asbian) of Armagh, Ireland to this genus.

---

**Fig. 31.**— Microscopic anatomy of a tooth of *Venustodus argutus* from the Haney Limestone (Chesterian) of Perry County, Indiana. Sagittal section through the median cusp. Bar scale represents 1 mm. Note the well-developed tubular dentine. Abbreviations: en, enameloid; dn, denteon; dt, dentinal tubules; lr, lingual ridge; od, orthodentine; odp, orthodentine pillar; pc, remnants of pulp cavity; tb, tooth base; td, trabecular dentine. Labial is to the left.
St. John and Worthen (1875) described five species of *Venustodus*, two from the Burlington Limestone and one each from the Keokuk, St. Louis, and Chester. There has been no modern study of *Venustodus*; consequently, the taxonomic validity of these species is uncertain. The specimens from Pennsylvanian rocks of Ohio are placed here in *Venustodus argutus*, St. John and Worthen's (1875) Chesterian species. With present material and knowledge, the Pennsylvanian teeth cannot be reliably distinguished from the Chesterian ones; therefore, the most expeditious taxonomic procedure is the one followed here. Should additional and better preserved specimens from the Pennsylvanian become available, it is possible that these teeth will prove to be a new species. Such a study, however, should encompass detailed examination of all available Mississippian specimens in order to determine characterizations of previously described species.

The higher taxonomic position of *Venustodus* is equally uncertain. The microscopic anatomy of these teeth is similar to that of petalodonts, orodonts, cochliodonts, and eugeneodonts; however, tubular dentine is widely and correctly regarded as an apomorphous character, developed as an adaptation for durophagy. *Venustodus* also bears in common with petalodonts the presence of imbricated basal ridges on the tooth crown. These teeth differ
significantly from petalodonts in the lack of strong labiolingual compression of the tooth crown and considerable differences in the tooth base (see Hansen, 1985; and Zangerl, 1981, for a characterization of petalodont teeth). *Venustodus,* therefore, cannot be reliably placed in any described chondrichthyan order based on present knowledge. It is now apparent that Late Paleozoic chondrichthyans were considerably more diverse than previously supposed. It is possible, therefore, that *Venustodus* deserves assignment to a new order; however, such assignment should be deferred until these teeth can be studied in detail.

**Dentition.**—Teeth of *Venustodus* exhibit a moderate amount of heterodonty, indicating a multielement dentition. Some specimens exhibit a strongly arched profile when viewed labiolingually, and are probably derived from medial tooth positions. Some of these specimens exhibit considerable asymmetry, as in OSU 35435, suggesting that these teeth are from medial positions but not necessarily from a symphyseal one. Additional teeth from the Haney Limestone of Indiana show this arched profile and some specimens also exhibit no arching and are symmetrical. These latter specimens also have a relatively low median cusp, indicating, perhaps, that they were in lateral tooth positions.
It is apparent that teeth of *Venustodus* were organized into successional tooth files. No articulating structures are visible on the specimens at hand; however, the prominent knob labiad to the median cusp probably served as a spacer to maintain proper position of each tooth in the file. Zangerl (1981) has described functionally similar features in teeth of eugeneodontids.

**Paleoecology.** Teeth of *Venustodus* are common in shallow-water carbonates in both Mississippian and Pennsylvanian rocks. Teeth of this genus have not been reported from Midcontinent black shales. It is apparent that teeth of *Venustodus* were designed for durophagy and it is probable that this chondrichthyan fed on shelled benthic organisms. The stout conelike cusps, especially the median one, would have been suited for this function. Commonly, the median cusp exhibits considerable wear, the enameloid covering having been breached by attrition, thus exposing the distal ends of the vascular canals (denteons) between the fingerlike, centripetally-directed orthodentine papillae. The presence of tubular dentine is indicative of durophagy as this morphological feature permits a strong, wear-resistant tooth that maximizes the efficiency of phosphate usage by the organism.
Stratigraphic and geographic distribution. Teeth of *Venustodus argutus* have been collected at seven localities representing six stratigraphic units in the Appalachian Basin. An additional specimen, collected by R. H. Mapes, is from a microsample from the Wewoka Formation (Desmoinesian) near Ada, Oklahoma. It is probable that *Venustodus* is widely distributed in Pennsylvanian shallow-water carbonates but these teeth do not appear to be abundant in any of these rocks. This genus apparently reached its zenith during the Mississippian but persisted in diminished abundance throughout the Pennsylvanian.

"Cohort" Neoselachii
Superorder and Order **Incertae Sedis**
Family Anachronistidae Duffin and Ward 1983

Genus **Cooleyella** Gunnell 1933

**Anachronistes** Duffin and Ward 1983, p. 95.

**Characterization.**—Teeth of a neoselachian shark in which the crown possesses a lingually inclined central cusp, well developed lateral blades, and a basal flange. Tooth base with a prominent basolabial articulating boss beneath the basal flange and a deep pit lingual to this knoblike boss. Lingual torus prominent. Hemiaulacorrhizoid vascularization with a single median canal penetrating lingual torus. (Modified from Duffin and Ward, 1983).

**Type Species.**—**Cooleyella peculiaris** Gunnell 1933.

**Cooleyella peculiaris** Gunnell 1933

Plate V, figs. 1-18

**Cooleyella peculiaris**, Gunnell, 1933, p. 290, Pl. 31, figs. 65-66.

Subtype number 058, Tway and Zidek, 1982, Figs. 3a-e.

**Characterization.**—As for the genus, which is monotypic.

**Lectotype.**—University of Missouri 502-1 (new designation), Winterset Limestone (Missourian), Kansas City, Missouri.
Distribution.—Pennsylvanian and ?Lower Permian rocks of the U.S.A.

Referred Specimens.—See Table 8.

Description.—Gunnell's (1933) specimen of Cooleyella peculiaris, herewith designated the lectotype (University of Missouri 502-1, see Discussion, below), is redescribed. This specimen (Fig. 32) has a crown width (anteromedial-posterolateral) of 0.45 mm and a labiolingual (1-1) crown dimension of 0.30 mm. The crown is extremely worn, is highest in the mediolingual portion, and tapers laterally into winglike projections (lateral blades). A faint ridge parallels the crown margin on the labial and lateral portions of the tooth. The tooth base is narrow and considerably restricted at its junction with the lingual half of the crown. It projects aborally into a lingually directed, comparatively wide, fanlike lingual torus. Lingually, a large median foramen marks the opening of a large canal that passes through the tooth base to a similar foramen on the labial side of the tooth base. A large pit is present on the aboral surface of the crown immediately lingual to a prominent, knoblike, basolabial articulating boss.
All specimens in the collection from the Appalachian Basin are in the size range of about 0.40 mm to 1.0 mm (Table 8) in the anteromedial-posterolateral (am-pl) dimension. These specimens, in an unworn condition, can be separated into three principal morphotypes. Within each morphotypic division there is considerable ontogenetic variation and gradational variation caused by both masticatory abrasion and chemical etching. Morphological terminology follow Duffin and Ward (1983) with some modification (Fig. 33).
Fig. 33.—Morphological features of a tooth of *Cooleyella*. A, latero; B, aboral. Abbreviations: bf, basal flange; cc, central cusp; oc, occlusal crest; lc, lateral cusplet; cs, crown shoulder; lbl, lateral blade; lb, labial buttress (=basolabial articulating boss); cp, central pit; br, aboral surface of tooth base; lfb, lingual face of tooth base; lrf, labial face of tooth base; mc, median vascular canal; mif, mediointernal foramen; mef, medioexternal foramen. From Duffin and Ward (1983) with some modifications of terminology.

The most abundant and variable morphotype (Morphotype I) in the collection includes the lectotype of *Cooleyella peculiaris*. These teeth are narrower in the labiolingual than in the anteromedial-posterolateral dimension and are marked by a prominent, median, projecting area on the labial portion of the crown (basal flange of Duffin and Ward, 1983). The lateral portions of the crowns are narrowed, forming lateral blades. A high, triangle-shaped, sharp-pointed, lingually projecting central cusp is present in unworn to moderately abraded specimens. The cusp may exhibit varying degrees of lateral inclination, either right or left. Commonly, the entire crown of teeth
of this morphotype may exhibit asymmetry, with the lateral blade being deeper on one side than the other, giving a twisted appearance to the tooth crown. Very small lateral cusps may be developed on the lateral blades along a faint occlusal crest that traverses the crown. A faint basal ridge, which is most prominent in unworn teeth, parallels the labial edge of the crown.

Teeth of this morphotype exhibit varying degrees of wear in which the principal and lateral cusps are progressively reduced so that the crown surface is nearly smooth with a medially-arched profile. The specimens figured by Duffin and Ward (1983), of Coolevella fordi and Cooleyella sp., appear to all be referable to this morphotype.

The tooth base is considerably constricted at its junction with the crown, but flares aborally forming a broad, rounded lingual torus. The aboral surface of the crown has, labially, a deep pit that penetrates into the internal part of the crown. On one specimen in the collection (OSU 35393) this pit is free of sediment, revealing what appears to be a foramen for passage of the main vascular canal into the pulp cavity. Another specimen in the collection (OSU 35395) is preserved in such a manner that the dentinal tissues external to the pulp cavity are transparent when moistened with alcohol. The
pulp cavity, which is whitish and opaque, is small and has the general shape of the external profile of the tooth crown (Fig. 35).

The lingual torus of teeth of this morphotype has a large foramen on the lingual margin. The foramen is the external opening to a canal that penetrates the lingual torus and opens, via another foramen, on the basolabial portion of the tooth base just beneath the central pit described above. In a few specimens this canal is partially or wholly open on the aboral surface.

Just beneath the labial-projecting medial portion of the crown (basal flange) is a rounded, knoblike structure, that is part of the tooth base, and functions as a basolabial articulating boss (labial buttress of Duffin and Ward, 1983). This boss may be nearly circular, to triangular, to rectangular in shape. One specimen in the collection (OSU 35385) has two of these bosses, each much reduced in size, located adjacent to one another.

The second morphotype of Cooleyella peculiaris (Morphotype II) consists of teeth that are very deep labiolingually and comparatively narrow in the anteromedial-posterolateral dimension (Fig. 34). These teeth have am-pl/l-1 ratios close to 1.0 (Table 8). The crown is narrower on the labial margin than on the lingual margin and is at a very acute angle with the tooth base,
giving a sharp slope to the relatively flat crown face. The crown/tooth base junction is very constricted owing to a relatively narrow neck on the tooth base. Lingually, the crown margin is produced into three sharp, labiolingually compressed cusps. The medial cusp is the largest and exhibits little lateral inclination. The lateral cusps, which are large compared to lateral cusps in other morphotypes, may flare outward at a sharp angle.

Fig. 34.- Relatively unworn tooth of Morphotype II, suggested to be a symphysial tooth of Cooleveilla peculiaris. A, oral; B, aboral; C, lateral; D, lingual; E, labial. Bar scale represents 0.5 mm. OSU 35389, Putnam Hill lime stone, location Ty-3.

The tooth base of these teeth is similar to that of the first morphotype except that in Morphotype II the tooth base is narrower, relatively longer, and somewhat laterally compressed. Teeth of this morphotype are relatively uncommon in the sample and exhibit very little asymmetry, suggesting that they may be symphyseal teeth.
In specimens heavily worn by masticatory attrition, the cusps are completely removed and the lingual edge of the crown is worn to a chisel-shaped, beveled edge. Other heavily worn teeth in the collection with flattened, platelike crowns may also be abraded specimens of this morphotype or possibly they represent a separate morphotype referable to extreme lateral teeth.

The OSU collection also contains teeth that differ in some fundamental respects from other teeth of Cooleyella peculiaris; however, the crowns in unworn specimens are neoselachian in character and similar in many respects to those of C. peculiaris. In these teeth, Morphotype III, the crowns are extremely compressed labiolingually (1-1) resulting in a comparatively high am-pl/l-1 ratio (Table 8). In unworn specimens, the principal cusp is high, sharp, and triangular. Outwardly flaring lateral cusps are large in comparison to similar features in other teeth of C. peculiaris. All of the cusps may exhibit an asymmetrical orientation. A sharp, but faint, occlusal crest traverses the cusps. A pronounced shelf is present around the crown border.

The tooth base is perhaps the most unusual feature of these teeth. This structure is comparatively massive and deep with a broad lingual torus. The aboral surface of the tooth base slopes lingually at a sharp angle and is
scooped out on its labial portion, forming a crude articulating structure. A knoblike basolabial articulating boss, as is typical of other morphotypes of *Cooleyella peculiaris*, is not present. Vascularization of these teeth is provided by a labial and a lingual row of foramina, in contrast to the single labial and lingual foramina in other teeth of *C. peculiaris*.

In heavily worn specimens of this morphotype, the principal and lateral cusps may be so abraded that the crown appears rounded on its oral surface (Pl. V, figs. 3-6). These abraded teeth are orodontlike and could easily be mistaken for teeth of this group. This morphotype is relatively uncommon in the collection, suggesting, if indeed they are referable to *Cooleyella peculiaris*, that they occupied a specialized tooth position, perhaps parasymphysial tooth files.

**Microscopic Anatomy.**—A sagittal section through the labiolingual midplane of a relatively unworn tooth of *Cooleyella peculiaris* (OSU 35395), location Nbu-1, reveals a thin, optically clear outer layer of enameloid covering the crown. Other sections in the collection indicate a similar tissue. At its base, the enameloid is penetrated by the very tiny distal ends of dentinal tubules. In polarized light, the enameloid has a consistent birefringence that contrasts sharply with underlying tissue.
The entire crown, beneath the enameloid, is composed of dense orthodentine which shows a concentric, banded pattern. Anastomosing dentinal tubules, which are larger proximally and become finer distally, penetrate the orthodentine. A relatively small pulp cavity is present in the central portion of the crown and its shape mimics the general outline of the crown, thus confirming the evidence presented above for a tooth with transparent outer tissues. The pulp cavity appears to continue aborally through a narrow canal; however, the preservation in the section is such that its distal connections cannot be traced.

The tooth base is not as well preserved as the crown in the available sections but it appears to be composed of a relatively dense tissue. It does not appear to be typical trabecular dentine but could be a compact variety of this type of dentine or, more likely, orthodentine.
DISCUSSION

Taxonomy.—Coolevella was established by Gunnell (1933, p. 290) to include several species which he presumed to be chondrichthyan dermal denticles. This assessment was correct for *C. cuspidata*, *C. quadrolobata*, *C. quinqueloba*, *C. simplex*, and *C. spatulata* (herein placed in a new genus, Sturgeonella); however, the type species (genotype of Gunnell, 1933) is *Coolevella peculiaris*, an undoubted tooth that is now known to be from a neoselachian shark. All of Gunnell's species of *Coolevella*, except for *C. peculiaris*, appear to part of a morphological transition series of dermal denticles and are dealt with elsewhere in this report.

Examination of Gunnell's type specimens in the University of Missouri collections indicates that he designated two specimens, UM 502-1 and 502-2, as cotypes of *Coolevella peculiaris*. Both specimens, from the Winterset Limestone (Missourian) at Kansas City, Missouri, are referable to this species. Neither specimen is well preserved but UM 502-1 is the best preserved of the two and is the specimen figured by Gunnell (1933; Pl. 31, figs. 65-66). This specimen, UM 502-1, is herein designated as the lectotype of *Coolevella peculiaris*. 
Duffin and Ward (1983) described neoselachian teeth from Visean rocks of Britain as a new genus and species, *Anachronistes fordi*, and a tooth from Leonarian rocks of Nevada as *Anachronistes* sp. Unfortunately, Duffin and Ward were not aware of Gunnell's (1933) brief description and limited figures of *Coolevella peculiaris*. Dr. Duffin was kind enough to send me a preprint of the manuscript on *Anachronistes*, but by the time that I made the connection between Duffin and Ward's new genus and Gunnell's earlier described genus, it was too late for them to alter the manuscript.

There is no doubt, as Dr. Duffin concurs, that *Anachronistes* is congeneric with *Coolevella* and therefore the former genus must be suppressed. Dr. Duffin has now examined specimens of *C. peculiaris* from the Appalachian Basin collection and considers them, tentatively, to be distinct specifically from *C. fordi*. I am in tentative agreement with his conclusion, although at this time I cannot tabulate the morphological distinctions between *C. peculiaris* and *C. fordi*. The teeth of *C. peculiaris* in the Appalachian Basin sample do appear to have a greater degree of variation in tooth morphology than was described by Duffin and Ward (1983) for *C. fordi*; however, this inference may simply be the result of a smaller sample of British specimens.
The single specimen from Leonardian rocks of Nevada, described by Duffin and Ward (1983) as Anachronistes sp., is also referable to Cooleyella but I am uncertain at this time if it represents a species distinct from Cooleyella peculiaris or C. fordi.

**Microscopic Anatomy.**—Duffin and Ward (1983) apparently did not prepare thin sections of their specimens of Cooleyella fordi; however, they did analyze a tooth using scanning electron microscopy. These authors stated that this specimen did not have an outer enameloid layer and that the crown appeared to be composed of "compact osteodentine."

The thin sections of Cooleyella peculiaris from the Appalachian Basin appear to contradict the observations of Duffin and Ward (1983) because some of these sections clearly reveal an outer layer of enameloid. In addition, the internal portion of the crown is composed of orthodentine rather than osteodentine (= trabecular dentine). These authors gave no description of the tissue that they termed "compact osteodentine" but the Appalachian specimens contain no vascular canals nor, under polarized light, are any trabecules or other structures characteristic of osteodentine visible. Indeed, this tissue, with parallel dentinal tubules and
concentrically banded layers, clearly fits the definition of orthodentine and is similar to other "orthodont" chondrichthyans.

The discrepancy concerning the presence of enameloid in the Appalachian specimens and the apparent absence of this tissue in the British specimens requires further explanation and clarification. Several specimens in the collection (OSU 35387) show an enameloid covering that has been partially broken off. These specimens reveal that the enameloid is an extremely thin layer, a fact confirmed by thin sections.

Duffin and Ward (1983) stated that the lack of enameloid in their specimens of *Cooleyella fordi* was not due to postmortem wear nor excessive etching during acid preparation of the specimen for scanning electron microscopy. They did not consider, however, the possibility of antemortem etching of the tooth crowns during regurgitation of gastric residues. During this process, undigestable remains of prey such as scales, bones, and shells, are regurgitated along with strong hydrochloric stomach acid. Zangerl (1981) suggested that this process is responsible for uniform removal of outer dentine tissues in many chondrichthyan teeth and illustrated a tooth file of *Orodus* *tuberculatus* that clearly demonstrates this point. It is also very probable
that at least some isolated teeth of *Coolevella* obtained in washed residues have themselves been part of a gastric residue regurgitated by a larger chondrichthyan that preyed upon this apparently diminutive shark.

Most specimens of *Coolevella peculiaris* in the OSU collection do not have a brilliant, shiny outer crown surface, although many of these specimens have a relatively sharp definition to minute morphological features of the crown. A small number of specimens in the sample have this shiny surface, which is readily distinguishable from teeth in which the underlying orthodentine imparts a less shiny luster. These teeth have a remarkably sharp definition to coronal features and undoubtedly represent newly erupted teeth from which the enameloid has not been removed by either comminution of food or stomach-acid etching.

The specimens of *Coolevella fordi* illustrated by Duffin and Ward (1983, Pl. 13, Pl. 14) appear to be teeth that have been subjected to both stomach-acid etching and masticatory abrasion. It is therefore not surprising that these teeth do not exhibit any trace of this very thin enameloid layer. These observations point out the need for caution in regarding the absence of an outer tissue in a chondrichthyan tooth as a genetic factor. It is very probable that many isolated Paleozoic chondrichthyan
teeth, especially small teeth, have spent at least some time in the stomach of a predator before being cast onto the sea bottom in either a gastric residue or a fecal mass. Most teeth are further abraded by comminution of food, stomach acids during regurgitation, and mechanical abrasion by currents after they are deposited on the sea floor. Considering these factors and the fact that most Paleozoic chondrichthyans retained teeth in a tooth file for a considerable period of time, it is the exception rather than the rule when an isolated shark tooth exhibits a thin enameloid layer.

**Morphology and Functional Anatomy.** Teeth of *Cooleyella peculiaris* from the Appalachian Basin exhibit a considerably greater degree of heterodonty than the teeth of *C. fordi* from Britain. However, the Appalachian sample is more than four times larger than the British sample and many of the teeth appear to be better preserved than are the British ones.

The reconstruction of the dentition of *Cooleyella fordi* by Duffin and Ward (1983, Text-Fig. 6) requires some modification for *C. peculiaris* based on the morphological variations exhibited by the Appalachian Basin sample. It is probable that a larger sample of *C. fordi* teeth would exhibit some, if not all, of the variations shown by the
Appalachian Basin teeth. Duffin and Ward's reconstructions of the dentition are based solely on teeth of Morphotype I portrayed in varying degrees of wear. It is probable that teeth of this morphotype, certainly because of their abundance, occupied the majority of tooth positions along the jaws of Coolevella. The varying degrees of asymmetry of these teeth suggest also that they represent several tooth files that probably were in medial to lateral positions.

![Diagram of tooth morphology]

Fig. 36.—Hypothetical variation of tooth morphology along a jaw ramus of Coolevella peculiaris. Roman numerals indicate Morphotypes I, II, and III. Teeth of Morphotype I probably occupied most tooth positions along the ramus; those of Morphotype II are interpreted to be symphyseal and those of III are suggested to be parasymphyseal.

The most perplexing teeth in the sample are those of Morphotypes II and III. Those of Morphotype II, owing to their symmetry, low frequency in the collection, and labiolingual elongation, may have occupied a symphyseal position. Although the cusps of these teeth are relatively
small, the steep inclination of the crown surface would place the short cusps at a relatively high position in the tooth row. The nearly equilateral, platelike teeth in the collection appear in part to be greatly worn specimens of this morphotype, principally because many of them appear to have a relatively steep angle to the crown face, as in unworn specimens of morphotype II. Others in the collection appear to have relatively unangled crown faces but are nearly equilateral and platelike. They are also heavily worn. These teeth may represent lateralmost tooth positions or simply be worn end products of Morphotype I.

\[ \text{Fig. 37.} - \text{Histogram illustrating frequency of various tooth morphologies of Coolevella peculiaris based on the ratio of anteromedial-posterolateral (am-pl) dimension verses labiolingual (l-l) dimension. Roman numerals indicate the approximate distribution of Morphotypes I, II, III.} \]
Teeth of Morphotype III may possibly be referred in future studies to another species, as the tooth base differs significantly from other morphotypes of Cooleyella teeth and, indeed, this tooth base appears not to be a typical neoselachian one. However, the crowns of unworn specimens of this morphotype are so similar to the general configuration of Cooleyella that I will, provisionally, consider them as teeth of that genus. These teeth exhibit some asymmetry and are of relatively low frequency in the OSU collection. They may have occupied a parasymphyseal position.

The above evidence suggests that the dentition of Cooleyella peculiaris was more complex than that described for C. fordi by Duffin and Ward (1983). As indicated above, larger samples of C. fordi teeth may indicate a dental complexity in this species that is similar to that of C. peculiaris, which exhibits strong gradient monognathic heterodonty.

The modes of vascularization and articulation of teeth in a tooth file of Cooleyella peculiaris also deserve comment. The basolabial articulating boss on the aboral-labial portion of each tooth articulated with the apical surface of the lingual torus of the preceding tooth in the tooth file, serving both as a mechanism for proper spacing of teeth in the file and, particularly, to prevent injury...
to the principal nutrient vessel during prey capture when teeth are commonly subjected to strong vector forces. A similar but phylogenetically unrelated mechanism has been described elsewhere in this report for *Xenacanthus tridentatus* and *Zangerlodus williamsi*.

The prominent median canal that penetrates the lingual torus of the tooth base was obviously the principal conduit for the main vascular vessel in the tooth file. This vessel, as indicated by evidence presented above, entered the pulp cavity through the central pit on the aboral side of the labial portion of the crown. It is probable that a vessel branched apically from the main vessel into this central pit (Fig. 38).

![Diagram](image)

**Fig. 38.-** Mode of articulation and vascularization of three successional teeth in a tooth file of *Coolevella peculiaris*. The vascular canal (VC) passes through the canal penetrating each tooth base and, hypothetically, has a branch that penetrates each tooth through the central pit.
This pattern of vascularization was referred by Duffin and Ward (1983) to Casier's (1947) "hemiaulacorhize" condition. They correctly noted that the evolutionary scheme envisioned by Casier (1947) -- anaulacorhize-hemiaulacoarhize-holoaulocorhize-polyaulacoarhize -- is no longer accepted. The presence of a similar "hemiaulacoarhize" mode of vascularization in xenacanths, ctenacanths, and neoselachians would appear to support the observation that this pattern of vascularization is apomorphous and has appeared many times in chondrichthyan groups that are not closely related. If indeed the teeth of Morphotype III are referable to Coolevella peculiaris, it would further support this conclusion. These teeth have "anualcoarhize" vascularization in contrast to the "hemiaulacoarhize" vascularization of other morphotypes of C. peculiaris. These data appear to confirm Rief's (1973) view that the manner of tooth-base vascularization is not a useful taxonomic tool in determining neoselachian affinities.

Classification and Higher Taxonomic Relationships.—Duffin and Ward (1983) have adequately summarized the neoselachian assignment of teeth of Coolevella and have compared them with teeth of other neoselachians. The teeth from the Appalachian Basin add no new information in this regard. Fig. 39 (from Duffin and Ward, 1983) compares teeth of Coolevella with those of extant neoselachians.
Stratigraphic Distribution and Paleoecology.—The Appalachian Basin collection of *Cooleyella peculiaris* teeth consists of 153 specimens from 41 localities representing 12 stratigraphic units. The species ranges through the entire marine Pennsylvanian section and specimens were obtained from every stratigraphic unit or its equivalent, except for the Vanport and Washingtonville (Allegheny Group). Specimens occurred at relatively low frequency at each locality.

* Tway (1982) recorded specimens of *Cooleyella peculiaris* (her subtype number 058) from 47 samples at 14 localities in the Leavenworth Limestone of Iowa, Kansas, Nebraska, and Oklahoma; the Heebner Shale in Iowa, Kansas,
Missouri, Nebraska, and Oklahoma; and the Plattsmouth Limestone in Iowa, Kansas, Missouri, Nebraska, and Oklahoma. Most of the samples from these Shawnee Group (Virgilian) units produced specimens in low frequency; however, one sample from the Heebner Shale in Nebraska (HE-14-3) produced 37 specimens of *Cooleyella peculiaris* per kilogram of rock, more than double the highest frequency in the Appalachian Basin.

Gunnell's specimens of *Cooleyella peculiaris* were derived from the Winterset Limestone at Kansas City, Missouri. Duffin and Ward (1983) reported a specimen of *Cooleyella*, possibly referable to *C. peculiaris*, from the Lower Permian (Leonardian) Arcturus Formation of White Pine County, Nevada. Their additional specimens, referred to *C. fordi*, were derived from Asbian to Brigantian rocks of Derbyshire and Wales, United Kingdom.

These data indicate that *Cooleyella* is widespread, both stratigraphically and geographically. No specimens have been reported from Upper Mississippian rocks of the U.S.A.; however, it is likely that they will be found to occur in these rocks also. As suggested by Duffin and Ward (1983), the occurrences of *Cooleyella* indicate that neoselachian sharks had their origins considerably earlier
than previously thought. It is probable that their ancestry may eventually be traced to the early Mississippian or late Devonian.

All of the specimens of *Cooleyella* from the Appalachian Basin appear to have been derived from "platform carbonates" representing shallow, normal marine conditions. Duffin and Ward (1983) interpreted the rocks yielding their specimens to have been deposited in similar environments.

The teeth of *Cooleyella peculiaris* appear to be adapted to piercing, slicing, and crushing, depending upon the morphotype and its degree of abrasion. This morphological variation suggests that these presumably small fishes could have captured and processed a variety of prey, ranging from other small fishes to perhaps shelled invertebrates. The thick orthodentine of the tooth crowns would have permitted crushing of shells or exoskeletal coverings of various invertebrates; although the lack of specialized tissues for durophagy ("tubular dentine" of "bradyodonts") suggests that crushing of thick, calcified shells was not a primary food-gathering activity. The heavy wear on many teeth does suggest that they were retained for a considerable period of time. Duffin and Ward (1983) have surmised that *Cooleyella* was a bottom feeder.
Occurrence. - "Lower Mercer", Vel-7, (2); Boggs, Sb-4, (3); Lower Mercer, CS1-1, (3); MUm-3, (1); MUsp-4, (2); Tl-1, (1); Tl-7, (1); PA-10, (1); Upper Mercer, Mbe-1, (1); Mp-3, (5); Ts-5, (3); Putnam Hill, CSo-2, (1); Td-4, (1); Ty-3, (1); Columbiana, MUho-14, (3); Brush Creek, Aw-47, (4); Gca-6, (1); Pb-3, (1); Cambridge, GAs-1, (4); Gca-5, (1); Nn-13, (8); Portersville, Acn-31, (6); At-45B, (15); Aw-47, (2); Noble, Nbu-1, (16); Ames, Aa-64, (3); Aam-19, (4); Acn-31, (2); At-45B, (1); Aw-58, (1); CAc-2, (5); Gv-1, (5); Gwi-3, (5); HAr-1, (6); M0m-1, (2); Nbu-4, (3); Nn-3, (5); Wn-1, (1); PA-2, (3); PA-3, (2); PA-4, (13); Skelley, Nbu-3, (5).
Table 8.—Numerical data for teeth of *Cooleyella peculiaris* from the Appalachian Basin. Abbreviations: am-pl, anteromedial-posterolateral; l-l, labiolingual; loc., location; morph., morphotype. Measurements are in millimeters. Repository numbers are all OSU.

<table>
<thead>
<tr>
<th>REPOS.</th>
<th>UNIT</th>
<th>LOC.</th>
<th>AM-PL</th>
<th>L-L</th>
<th>RATIO</th>
<th>MORPH.</th>
</tr>
</thead>
<tbody>
<tr>
<td>35384a</td>
<td>&quot;L. Mercer&quot;</td>
<td>Vel-7</td>
<td>0.70</td>
<td>0.35</td>
<td>2.0</td>
<td>I</td>
</tr>
<tr>
<td>35384b</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.40</td>
<td>0.25</td>
<td>1.6</td>
<td>I</td>
</tr>
<tr>
<td>35385</td>
<td>L. Mercer</td>
<td>CS1-1</td>
<td>1.00</td>
<td>0.40</td>
<td>2.5</td>
<td>I</td>
</tr>
<tr>
<td>35386</td>
<td>&quot;</td>
<td>MUMu-3</td>
<td>0.80</td>
<td>0.40</td>
<td>2.0</td>
<td>I</td>
</tr>
<tr>
<td>35387</td>
<td>U. Mercer</td>
<td>Mbe-1</td>
<td>0.45</td>
<td>0.50</td>
<td>0.9</td>
<td>I</td>
</tr>
<tr>
<td>35388a</td>
<td>&quot;</td>
<td>Mp-3</td>
<td>0.70</td>
<td>0.30</td>
<td>2.3</td>
<td>I</td>
</tr>
<tr>
<td>35388b</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.45</td>
<td>0.30</td>
<td>1.5</td>
<td>I</td>
</tr>
<tr>
<td>35389</td>
<td>Putnam Hill</td>
<td>Ty-3</td>
<td>0.70</td>
<td>0.70</td>
<td>1.0</td>
<td>II</td>
</tr>
<tr>
<td>35390a</td>
<td>Columbiana</td>
<td>MUho-14</td>
<td>0.60</td>
<td>0.50</td>
<td>1.2</td>
<td>I?</td>
</tr>
<tr>
<td>35390b</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.60</td>
<td>0.45</td>
<td>1.3</td>
<td>I</td>
</tr>
<tr>
<td>35391</td>
<td>Brush Creek</td>
<td>Gca-6</td>
<td>0.45</td>
<td>0.25</td>
<td>1.8</td>
<td>I</td>
</tr>
<tr>
<td>35392a</td>
<td>Cambridge</td>
<td>GAs-1</td>
<td>0.85</td>
<td>0.40</td>
<td>2.1</td>
<td>I</td>
</tr>
<tr>
<td>35392b</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.60</td>
<td>0.35</td>
<td>1.7</td>
<td>I</td>
</tr>
<tr>
<td>35392c</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.70</td>
<td>0.30</td>
<td>2.3</td>
<td>I</td>
</tr>
<tr>
<td>35393a</td>
<td>Portersville</td>
<td>At-45B</td>
<td>0.65</td>
<td>0.40</td>
<td>1.6</td>
<td>I</td>
</tr>
<tr>
<td>35393b</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.50</td>
<td>0.35</td>
<td>1.4</td>
<td>II</td>
</tr>
<tr>
<td>35393c</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.80</td>
<td>0.35</td>
<td>2.3</td>
<td>I</td>
</tr>
<tr>
<td>35393d</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.75</td>
<td>0.40</td>
<td>1.9</td>
<td>I</td>
</tr>
<tr>
<td>35393e</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.80</td>
<td>0.35</td>
<td>2.3</td>
<td>I</td>
</tr>
<tr>
<td>35393f</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.45</td>
<td>0.25</td>
<td>1.8</td>
<td>I</td>
</tr>
<tr>
<td>35393g</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.75</td>
<td>0.30</td>
<td>2.5</td>
<td>I</td>
</tr>
<tr>
<td>35393h</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.80</td>
<td>0.55</td>
<td>1.5</td>
<td>I</td>
</tr>
<tr>
<td>35393i</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.60</td>
<td>0.25</td>
<td>2.4</td>
<td>I</td>
</tr>
<tr>
<td>35393j</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.65</td>
<td>0.30</td>
<td>2.2</td>
<td>I</td>
</tr>
<tr>
<td>35393k</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.70</td>
<td>0.25</td>
<td>2.8</td>
<td>I</td>
</tr>
<tr>
<td>35393l</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.60</td>
<td>0.35</td>
<td>1.7</td>
<td>I</td>
</tr>
<tr>
<td>35394a</td>
<td>&quot;</td>
<td>Aw-47</td>
<td>0.80</td>
<td>0.50</td>
<td>1.6</td>
<td>I</td>
</tr>
<tr>
<td>35394b</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.70</td>
<td>0.60</td>
<td>1.2</td>
<td>II</td>
</tr>
<tr>
<td>35394c</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.60</td>
<td>0.30</td>
<td>2.0</td>
<td>I</td>
</tr>
<tr>
<td>35394d</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.50</td>
<td>0.20</td>
<td>2.5</td>
<td>I</td>
</tr>
<tr>
<td>35394e</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.55</td>
<td>0.40</td>
<td>1.4</td>
<td>I</td>
</tr>
<tr>
<td>35394f</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.75</td>
<td>0.40</td>
<td>1.9</td>
<td>I</td>
</tr>
<tr>
<td>35394g</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.80</td>
<td>0.30</td>
<td>2.7</td>
<td>III</td>
</tr>
<tr>
<td>35394h</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.80</td>
<td>0.30</td>
<td>2.7</td>
<td>III</td>
</tr>
<tr>
<td>35394i</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.65</td>
<td>0.50</td>
<td>1.3</td>
<td>II</td>
</tr>
<tr>
<td>35394j</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.55</td>
<td>0.50</td>
<td>1.1</td>
<td>II</td>
</tr>
</tbody>
</table>
Table 8.— (continued).

<table>
<thead>
<tr>
<th>REPOS.</th>
<th>UNIT</th>
<th>LOC.</th>
<th>AM-PL</th>
<th>L-L</th>
<th>RATIO</th>
<th>MORPH.</th>
</tr>
</thead>
<tbody>
<tr>
<td>35395a</td>
<td>Noble</td>
<td>Nbu-1</td>
<td>0.70</td>
<td>0.45</td>
<td>1.6</td>
<td>I</td>
</tr>
<tr>
<td>35395b</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.50</td>
<td>0.30</td>
<td>1.7</td>
<td>I</td>
</tr>
<tr>
<td>35395c</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.55</td>
<td>0.25</td>
<td>2.2</td>
<td>I</td>
</tr>
<tr>
<td>35395d</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.70</td>
<td>0.40</td>
<td>1.8</td>
<td>I</td>
</tr>
<tr>
<td>35395e</td>
<td>&quot;</td>
<td>&quot;</td>
<td>1.05</td>
<td>0.50</td>
<td>2.1</td>
<td>I</td>
</tr>
<tr>
<td>35395f</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.50</td>
<td>0.25</td>
<td>2.0</td>
<td>I</td>
</tr>
<tr>
<td>35395g</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.75</td>
<td>0.40</td>
<td>1.9</td>
<td>I</td>
</tr>
<tr>
<td>35395h</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.50</td>
<td>0.30</td>
<td>1.7</td>
<td>I</td>
</tr>
<tr>
<td>35396</td>
<td>Ames</td>
<td>As-64</td>
<td>0.70</td>
<td>0.30</td>
<td>2.3</td>
<td>I</td>
</tr>
<tr>
<td>35397</td>
<td>&quot;</td>
<td>Gv-1</td>
<td>0.85</td>
<td>0.25</td>
<td>3.4</td>
<td>III</td>
</tr>
<tr>
<td>35398a</td>
<td>&quot;</td>
<td>HAr-1</td>
<td>0.65</td>
<td>0.20</td>
<td>3.3</td>
<td>III</td>
</tr>
<tr>
<td>35398b</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.80</td>
<td>0.30</td>
<td>2.7</td>
<td>III</td>
</tr>
<tr>
<td>35398c</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.60</td>
<td>0.25</td>
<td>2.4</td>
<td>I</td>
</tr>
<tr>
<td>35398d</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.75</td>
<td>0.45</td>
<td>1.7</td>
<td>I</td>
</tr>
<tr>
<td>35399a</td>
<td>&quot;</td>
<td>PA-2</td>
<td>0.70</td>
<td>0.40</td>
<td>1.8</td>
<td>I</td>
</tr>
<tr>
<td>35399b</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.75</td>
<td>0.45</td>
<td>1.7</td>
<td>I</td>
</tr>
<tr>
<td>35400a</td>
<td>&quot;</td>
<td>PA-3</td>
<td>0.50</td>
<td>0.20</td>
<td>2.5</td>
<td>III</td>
</tr>
<tr>
<td>35400b</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.70</td>
<td>0.30</td>
<td>2.3</td>
<td>I</td>
</tr>
<tr>
<td>35401a</td>
<td>&quot;</td>
<td>PA-4</td>
<td>0.80</td>
<td>0.60</td>
<td>1.3</td>
<td>II?</td>
</tr>
<tr>
<td>35401b</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.55</td>
<td>0.40</td>
<td>1.4</td>
<td>II</td>
</tr>
<tr>
<td>35401c</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.75</td>
<td>0.45</td>
<td>1.7</td>
<td>I</td>
</tr>
<tr>
<td>35401d</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.70</td>
<td>0.35</td>
<td>2.0</td>
<td>I</td>
</tr>
<tr>
<td>35401e</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.35</td>
<td>0.30</td>
<td>1.2</td>
<td>II</td>
</tr>
<tr>
<td>35401f</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.80</td>
<td>0.40</td>
<td>2.0</td>
<td>I</td>
</tr>
<tr>
<td>35401g</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.60</td>
<td>0.40</td>
<td>1.5</td>
<td>I</td>
</tr>
<tr>
<td>35401h</td>
<td>&quot;</td>
<td>&quot;</td>
<td>0.70</td>
<td>0.40</td>
<td>1.8</td>
<td>I</td>
</tr>
</tbody>
</table>
Subclass Subterbranchialia Zangerl 1981
Superorder Holocephali Bonaparte 1832-41
Order Bradyodontida Woodward 1921
Family Cochliodontidae Owen 1867

Teeth of cochliodonts are a major component of the macroscopic collection; however, remains of these organs commonly encountered in microfossil residues are, almost without exception, fragments which are unidentifiable as to genus. In a few cases, a sufficient portion of a tooth is preserved to make an identification. Many of the small fragments of presumed cochliodont teeth in the microfossil residues may belong instead to orodontids or eugeneodontids.

Teeth of cochliodonts and these latter groups consist of thick "tubular" dentine, a tissue characterized by closely spaced vertical pillars of dentine when viewed in cross section. Oral surfaces of tooth fragments from these chondrichthyan groups have a punctate surface—the pits being formed by the exposed distal ends of denteons. Although such tissues are easily recognized, a large portion of an individual tooth is necessary in order to make reliable identification. Detailed treatment of cochliodontids, orodontids, and eugeneodontids in the macroscopic fauna of the Appalachian Basin will constitute a portion of a future report.
It is probable that most of the fragments of cochliodont teeth in the microfossil residues are from *Deltodus angularis*, the most common cochliodont in the macrofauna. This cochliodont is characterized by triangle-shaped, platelike teeth in the lower jaws. Although St. John and Worthen (1883) long ago suggested that the upper tooth plates of this fish were those known as *Sandalodus carbonarius*, this association has only recently been confirmed by the collection of a disarticulated dentition by Gregory MacComas from the Brush Creek shale in Columbiana County, Ohio. The specimen has generously been donated to the Orton Museum collection and will be the subject of a future report.

**Occurrence.** — *Deltodus angularis*: "Lower Mercer", SCve-3, (1); Brush Creek, Aw-47, (2). Indeterminate cochliodonts: Upper Mercer, Mbe-1, (1); Ty-7, (1); Putnam Hill, Ty-3, (1); Vel-19, (1); Washingtonville, CAr-2, (1); Brush Creek, At-9, (1); Portersville, Acn-31, (1); At-45b, (1); Ames, Nn-3, (1).
Family Psammodontidae de Koninck 1878

Genus Lagarodus Jaekel 1898

Lagarodus angustus (Romanowsky) 1864

Plate VI, figs. 15-16

Psammodus angustus Romanowsky 1864, p. 159, Pl. 3, fig. 6;
Trautschold, 1874, p. 13-14, Pl. 1, figs. 5a-c, Pl. 2, figs. 4a-b, 5, 6; de Koninck, 1878, p. 45, Pl. 5, figs. 6a-c; Woodward, 1889, p. 106.

Lagarodus angustus Jaekel, 1898, p. 50; Ivanova, 1958, Pl. 9, figs. 3a-b; Obruchev, 1967, p. 370, Pl. 1, figs. 1a-c.

Lagarodus sp., Bendix Almgreen, 1975, p. 13-14, Pl. 1, figs. G-I, K.

Psammodus specularis. Trautschold, 1874, pp. 12-13, Pl. 1, figs. 4a-c, Pl. 2, figs. 3a-b.

Characterization.—A psammodont chondrichthyan with platelike teeth that are rectangular in outline and have one end of the tooth arched into a high, gibbous prominence. Additional teeth, presumably from the opposite dentition, are rhomboidal in shape.

Distribution.—Tournaisian of Belgium; Lower and Middle Carboniferous of the Russian platform, ?England; Upper Carboniferous of Amdrup Land, Greenland; Middle Pennsylvanian Colorado; Middle and Upper? Pennsylvanian of Ohio.

Referred specimens.—OSU 35066, 35352, 35441, 35442; UCD A-F.
Description.—The following description of Lagarodus angustus teeth is based on three specimens from the Appalachian Basin and 16 specimens from the Minturn Formation of Colorado. Six of the latter specimens are of the rhomboidal morphotype.

In oral view the more common morphotype (Fig. 40) is rectangular in outline with the lowest lateral side of the crown at a slight angle to the nearly parallel labial and lingual margins. The oral surface is pitted owing to exposure of the distal ends of vertically-oriented denteons. Many of the available specimens exhibit abrasion on the oral surface. When viewed labially or lingually, the coronal surface rises slightly on the presumed posterolateral side, then dips slightly, then rises abruptly, forming a high, gibbous prominence. The crown then slopes sharply in an aboral direction forming a nearly vertical edge on the presumed anteromedial side of the tooth. When viewed laterally, on the side of the tooth with the gibbous prominence, the labial and lingual portions of the crown converge basally, forming a sharp-pointed spur, the point of which is oriented in the presumed labial dimension (Fig. 40). This area of the tooth is commonly rugose in appearance. The presumed lingual surface of the crown is smooth, sharply undercut,
exhibits thick enameloid, and slopes sharply labiad in an aboral direction. The presumed labial side of the tooth crown has a rugose appearance.

Fig. 40.—Morphology of a tooth of *Lagarodus angustus*, OSU 35066, from the Vanport limestone, location Jmi-2. Bar scale represents 1 mm. A, presumed labial; B, presumed lingual; C, oral; D, presumed anteromedial. Abbreviations: as, aboral surface; f, foramina; sa, saddle; sp, spur; tb, tooth base; um, undercut margin.

The thickness of the tooth base is nearly equal to the thickness of crown and bears comparatively large, rounded nutrient foramina aligned in a single row. Smaller foramina are vertically elongate and irregularly distributed. The flattened aboral surface of the tooth base is composed of a dense, smooth tissue and has no foramina. The *am-pl/l-l* ratio for this morphotype averages 2.30.
The rhomboidal teeth (Fig. 41) are narrow and platelike and have a gently arching oral surface. They are thickest in the central part and thin towards the edges. These edges are oriented at a slight angle to the parallel (in long dimension) sides of the tooth, giving a rhomboidal shape. The rhomboid is slightly twisted so that the highest part of the surface of the tooth crown is along a line from the presumed linguolateral corner to the presumed labiomedial corner. The presumed lingual side of the crown is smooth and truncated and is sloped to form an undercut, similar to that on the gibbous morphotype. The labial edge of the crown has a rugose surface, as in the presumed labial edge of the gibbous morphotype. A regular row of circular foramina are present along both the labial and lingual edges of the tooth base. The aboral side of the tooth base is composed of a smooth, dense tissue identical to that of the gibbous morphotype. This surface exhibits the slight twist similar to that of the crown and has a small ridge, parallel to the lateral edge of the crown, on the presumed anteromedial side. The am-pl/l-1 ratio for rhomboidal teeth averages 2.38 (Table 9).
Fig. 41. Morphology of a tooth of the rhomboidal morphotype of *Lagarodus angustus*. UC-D specimen. Bar scale represents 1 mm. A, presumed labial; B, presumed lingual; C, oral; D, aboral. Abbreviations: as, aboral surface; cr, crown; f, foramina; tb, tooth base.

**DISCUSSION**

Psammodonts are characterized by and known only from flattened, rectangular-shaped teeth which are most common in rocks of Mississippian age. Although large numbers of these teeth have been described and illustrated in the great descriptive reports of the 19th century (see, Davis, 1883; St. John and Worthen, 1883) the group is one of the most poorly understood assemblages of chondrichthyans. Psammodonts have not received modern study. The psammodonts, along with the cochliodonts, copodonts, and petalodonts were united by Woodward (1921) into the Order Bradyodonti, a grouping that is now considered artificial by most workers. *Lagarodus angustus*, the focus of this report, is the youngest (and therefore the last) psammodont species.
The specimens from the Appalachian Basin of Ohio and the Minturn Formation of Colorado (provided by Martin Lockley of the University of Colorado-Denver) differ in no important respects from teeth of *Lagarodus angustus* (Romanowsky) 1864, known from the Lower and Middle Carboniferous of the Russian Platform. Specimens of *L. angustus* illustrated by Trautschold (1874), Ivanova (1958), and Obruchev (1967) are indeed identical to those described here. In addition, the Appalachian Basin specimens appear to be identical to de Koninck's (1878) specimen of *Psammodus angustus* from Tournaisian rocks of Belgium. A cast of this specimen (P. 1287) has kindly been provided by the Musee Royal D'Histoire Naturelle de Belgique. The specimens from the Appalachian Basin and Colorado are the first of this species to be reported from North America.

The rhomboidal teeth, herein assigned to *Lagarodus angustus*, appear to be identical to *Psammodus specularis* Trautschold 1874, known from the Middle Carboniferous of the Russian platform. These teeth, as discussed below, appear to represent the dentition that opposed the more familiar morphotype of *L. angustus*.

**Dentition.** The orientation and arrangement of psammodont dentitions has been a vexing problem since these teeth were first studied in the last century. Reconstructions of
Psammodont dentitions were attempted by de Koninck (1878) for *Psammodus porosus*, by Davis (1883) for *Psammodus rugosus*, and by St. John and Worthen (1883) for several species of *Psammodus*.

All of these authors postulated a dental pavement that covered the entire floor and roof of the mouth. Davis (1883) and de Koninck (1878) indicated a double row of rectangle-shaped teeth that were bordered laterally by narrow teeth similar to the rhomboidal ones of the "*Psammodus specularis*" morphotype described herein. St. John and Worthen (1883) followed this general plan in their interpretations; however, they did not include the rhomboidal teeth in their reconstructions and they indicated, in some species, the presence of a symphyseal series. Moy Thomas and Miles (1971) suggested that teeth of one ramus were wider than those in the ramus of the same jaw and that the asymmetry was reversed in the opposing jaws.

These authors all presented plausible reconstructions of psammodont dentitions. The variations in these reconstructions may only represent specific variations.

The teeth of *Lagarodus angustus*, of which 18 specimens from Pennsylvanian rocks are available for study, appear to bear considerable similarity to other species of psammodonts; however, there also appears to be significant
differences in the arrangement of the dentition of *L. angustgus*. Such differences cannot be properly assessed until additional study of other psammodont species is carried out.

The more familiar morphotype of *Lagarodus angustus* teeth, those with a gibbous prominence at one side, appear to have been arranged in labiolingually successional rows. In all known chondrichthyans, successional teeth are larger than their predecessors. The lateral margins of these teeth, on the side opposite the gibbous prominence, are at a slight angle to a line parallel to the direction of labiolingual succession. When arranged in successional rows, in which the tooth size decreases labially, this lateral angle conforms to what would be expected in the anterior tapering of the jaw, toward the symphysis.

This arrangement would place the angled margin of the tooth on the posterolateral side of the jaw, that is, towards the outside of the mouth, and place the side of the tooth with the gibbous prominence in the anterior orientation, that is, towards the inside of the mouth (Fig. 42). This orientation suggests that the side of the tooth with the smooth, undercut margin is lingual and the side of the tooth with the rugose surface is labial. The spur-like projection would therefore be oriented labial. This orientation appears to be the most logical
interpretation for *Lagarodus angustus*; however, it is opposite the interpretation of orientation made by Davis (1883), for example, for *Psammodus porosus*. In his reconstruction, the spur is oriented linguad.

![Diagram](image)

**Fig. 42.** Postulated arrangement of the dentition of *Lagarodus angustus*. A, presumed lower dentition with gibbous teeth. B, presumed upper dentition with rhomboidal teeth. The jaw symphysis is at the top of the figures.

The presumed anteromedial side of the tooth, that is, the high side with the spur, has no lateral articular facets and this side of the tooth, on its lower extremities, shows no signs of wear. This evidence suggests that there was no symphyseal series of teeth and that this side of the tooth did not articulate with the tooth in the other side of the jaw. These teeth are therefore interpreted to have been aligned along each ramus of the jaw with the central part of the mouth being non tooth-bearing (Fig. 42).
It is clearly apparent, as suggested by Woodward (1889), that the rhomboidal teeth, the *Psammodus specularis* morphotype, are from the same dentition as teeth of the typical *Lagarodus angustus* morphotype. The many morphological similarities between these two morphotypes and their mutual occurrence in a fauna in which psammodonts are rare, supports this interpretation.

The rhomboidal teeth appear to have been organized in labiolingually successional rows also. These teeth exhibit a smooth, undercut surface on one side, similar to that on the presumed lingual side of the gibbous teeth, and a rugose edge on the opposite side, similar to that on the presumed labial side of the gibbous teeth. The short sides of these teeth, the presumed lateral edges, exhibit no evidence of articular surfaces.

If these teeth are interpreted to be from a lateral row, located posterolaterally to the gibbous teeth, as in the models for *Psammodus porosus* by de Koninck (1878) and *Psammodus rugosus* by Davis (1883), then the smooth, undercut side of the tooth would have articulated with the lateral margins of two or more gibbous teeth. Several factors mitigate against this interpretation: 1) the rhomboidal teeth have no articular facets on their short margins, as they should if they were aligned in a row, short edge to short edge; 2) the posterolateral margins of
the gibbous teeth exhibit no articular facets; 3) the "twisted" orientation of the tooth base of the rhomboidal teeth indicates the orientation of these teeth on the jaw margin—this orientation would be impossible if these teeth were articulated in a position lateral to the gibbous teeth.

An alternative, and preferred, interpretation of these rhomboidal teeth is that they were aligned in a labiolingually successional row along each jaw margin in the jaws opposite those containing the gibbous teeth. These rhomboidal teeth are represented in the collection by both right and left specimens, as are the gibbous teeth, and when the rhomboidal teeth are arranged in a successional row, the asymmetrical aboral surfaces of the tooth bases align in a row that would fit over a jaw ramus. In this interpretation, these teeth would be at an angle of about 35 degrees to the long dimension of the jaw ramus.

Additionally, this arrangement—the rhomboidal teeth in one set of jaws and the gibbous teeth in the opposing jaws—provides a plausible interpretation for tooth occlusion. The convex surfaces of the slightly angled rhomboidal teeth fit in the "saddle" on the central part of the surface of the gibbous teeth (Fig. 43). If the gibbous teeth were also in opposing jaws, a plausible
manner of occlusion is not apparent with the specimens at hand. The postulated arrangement of the dentition of *Lagarodus angustus* is illustrated in Figure 43.

![Diagram of occlusion of teeth of *Lagarodus angustus*](image)

**Fig. 43.** Postulated manner of occlusion of teeth of *Lagarodus angustus*. A, presumed lower tooth; B, presumed upper tooth.

In this model of arrangement of the dentition of *Lagarodus angustus*, it is difficult to determine which tooth morphotype was in the upper jaws and which morphotype was in the lower jaws. Perhaps some analogous information can be inferred from the dental arrangement of cochliodonts. In this group, flattened tooth plates are commonly associated with the upper jaws and ridged tooth plates are commonly associated with the lower jaws (see Zangerl, 1981, Fig. 21). It is obviously speculative to infer a similar arrangement in *Lagarodus angustus*; however, such an organization may have been advantageous in durophagy. A ridged or gibbous surface on the lower
teeth would tend to hold shelled invertebrates in place as the lower jaws closed, bringing the lower dentition and the prey against the flattened upper teeth.

These interpretations of the orientation and arrangement of the dentition of *Lagarodus angustus* involve considerable speculation and inference based on a relatively small sample size. The evidence presented by this sample does not suggest equally plausible alternative arrangements. There is a possibility that another tooth morphotype, as yet undiscovered, may have been present in a symphysial position. There is also the possibility that the labial and lingual sides of these teeth are reversed from the above interpretation. If that is the case, the gibbous prominence on the presumed lower teeth would have been in the posterolateral position rather than the anteromedial one. This study clearly demonstrates that psammodont dentitions are in great need of re-evaluation.

**Paleoecology.**—Psammodont teeth, including those of *Lagarodus angustus*, are known only from carbonate rocks deposited in shallow water in bank or shelf environments. The thick, platelike teeth of psammodonts, which commonly show evidence of considerable wear, were most certainly adapted for crushing hard-shelled invertebrates. The thick layer of tubular dentine on the tooth crowns is indicative of this durophagous adaptation.
At their zenith in the Mississippian, psammodonts must have exerted influential predation pressure on the shelly benthos and, as Signor and Brett (1984) have recently speculated, such pressures from chondrichthyans may have been significant factors in extinctions and adaptive strategies of benthic organisms. Few invertebrate shells would have been sufficiently robust to resist crushing by teeth of psammodonts.

The acme of psammodont diversity and abundance was apparently reached during the mid-Mississippian and began to decline by Chesterian time. *Lagarodus angustus* was the last psammodont, surviving into the Pennsylvanian with greatly reduced abundance compared to its mid-Mississippian progenitors. Certainly, because of its rarity, *L. angustus* was not a prominent member of the chondrichthyan fauna that fed on benthic organisms during the Pennsylvanian. The reason for the decline of the psammodonts is uncertain at this stage of analysis but it was probably related to the diversification and abundance of competitive chondrichthyan groups such as the petalodonts and cochliodonts.

**Stratigraphic and geographic distribution.** - *Lagarodus angustus* is best known from Lower and particularly Middle Carboniferous (Myachkovian) rocks of the Russian platform. Specimens from these beds have been described and
illustrated by Romanowsky (1864), Trautschold (1874), Ivanova (1958), and Obruchev (1967). A specimen described as *Psammmodus angustus* by de Koninck (1878), from Tournaisian rocks of Belgium, appears to be referable to this species.

An additional specimen of *Lagarodus angustus* was assigned to *Lagarodus* sp. by Bendix Almgreen (1975). This specimen is from the Upper Carboniferous Lower Marine Group (Wedekindellina zone) of Amdrup Land, northeast Greenland. This sequence of rocks is apparently correlative to the Middle Carboniferous of the Moscow basin and the Upper Allegheny-Lower Conemaugh of the Appalachian Basin.

The Appalachian Basin specimens of *Lagarodus angustus* are from the Putnam Hill and Vanport limestones (Allegheny Group). A small, incomplete specimen from the Ames limestone is tentatively assigned to this species.

These data suggest that *Lagarodus angustus* may be most typical of Middle Carboniferous rocks; however, the number of reported specimens is so small that it is difficult to establish a precise stratigraphic range for this species at this time.

**Occurrence.**—Putnam Hill, Ty-3, (1); Vanport, Jmi-2, (1); PA-9, (1); ?Ames, MUMu-5, (1); Minturn, CO-1, (16).
Table 9.—Dimensions of teeth of *Lagarodus angustus* from Pennsylvanian rocks of Ohio and Colorado. Am-pl/l-1 ratio for gibbous teeth averages 2.30; for rhomboidal teeth this ratio averages 2.38. UC-D specimens F-H are rhomboidal teeth; the remainder of teeth in the table are of the gibbous morphology. Abbreviations: am-pl, anteromedial-posterolateral; l-1, labio-lingual.

<table>
<thead>
<tr>
<th>Repository</th>
<th>Unit</th>
<th>Loc.</th>
<th>Am-pl</th>
<th>L-l</th>
<th>Am-pl/l-l</th>
</tr>
</thead>
<tbody>
<tr>
<td>OSU 35066</td>
<td>Vanport</td>
<td>Jmi-2</td>
<td>11.0</td>
<td>5.0</td>
<td>2.20</td>
</tr>
<tr>
<td>OSU 35352</td>
<td>Putnam Hill</td>
<td>Ty-3</td>
<td>8.0</td>
<td>3.0</td>
<td>2.67</td>
</tr>
<tr>
<td></td>
<td>Vanport</td>
<td>PA-9</td>
<td>16.0</td>
<td>8.0</td>
<td>2.00</td>
</tr>
<tr>
<td>UC-D (A)</td>
<td>Minturn</td>
<td>C0-1</td>
<td>26.0</td>
<td>12.0</td>
<td>2.17</td>
</tr>
<tr>
<td>UC-D (B)</td>
<td>&quot;</td>
<td>&quot;</td>
<td>22.0</td>
<td>9.0</td>
<td>2.44</td>
</tr>
<tr>
<td>UC-D (C)</td>
<td>&quot;</td>
<td>&quot;</td>
<td>20.0</td>
<td>8.0</td>
<td>2.50</td>
</tr>
<tr>
<td>UC-D (D)</td>
<td>&quot;</td>
<td>&quot;</td>
<td>15.0</td>
<td>6.0</td>
<td>2.50</td>
</tr>
<tr>
<td>UC-D (E)</td>
<td>&quot;</td>
<td>&quot;</td>
<td>15.0</td>
<td>8.0</td>
<td>1.88</td>
</tr>
<tr>
<td>UC-D (F)</td>
<td>&quot;</td>
<td>&quot;</td>
<td>15.0</td>
<td>7.0</td>
<td>2.14</td>
</tr>
<tr>
<td>UC-D (G)</td>
<td>&quot;</td>
<td>&quot;</td>
<td>20.5</td>
<td>8.0</td>
<td>2.56</td>
</tr>
<tr>
<td>UC-D (H)</td>
<td>&quot;</td>
<td>&quot;</td>
<td>13.5</td>
<td>5.5</td>
<td>2.45</td>
</tr>
</tbody>
</table>
Tooth "A"

Pl. VI, Fig. 10

Characterization.- Small crushing-type tooth with a rectangular crown that is narrowest in the labiolingual dimension. Crown surface relatively flat with slight depression and peaks on the lingual edge. Tooth base large, labially extended, and flattened basally. Nutrient foramina irregularly distributed on labial margin of base.

Referred Specimens.- OSU 35167, Washingtonville, location Car-2; OSU 35168, Columbiana, location Ss-4.

Distribution.- Columbiana and Washingtonville shales (Allegheny Group) of the Appalachian Basin.

Description.- The following description is based on the two specimens in the OSU collection, each of which has a crown width of about 2 mm. The crown is rectangular to slightly peaked medially and globose, with relatively high, rounded margins. The occlusal surface of the crown forms a flat, comparatively broad surface that is relatively smooth but slightly punctate. OSU 35167 exhibits a slight medio-lingual groove on the crown (Fig. 44). The lingual margin of the crown slightly overhangs the tooth base.
The tooth base is as wide as the crown and slightly higher than the height of the crown. Labially, the base extends forward and narrows, forming a labially extended shelf. Lingually, the tooth base is nearly vertical but has a slightly scooped out area. Basally, the tooth base is slightly concave and smooth. Several large foramina are present on the sloping labial surface of the tooth base and some of them are accompanied by a deep groove that traverses this sloping surface and connects with the foramen. Foramina may also be present lingually.

Fig. 44.- Tooth "A" (OSU 35167) from the Washingtonville shale, location Car-2. A, labial; B, lateral; C, lingual. Bar scale represents 1 mm.

DISCUSSION

Only two specimens of this tiny tooth are in the OSU collection and oddly both are from Allegheny units that yielded only a few other chondrichthyaū remains. There
appears to be little doubt that these specimens are indeed teeth rather than dermal or mucous membrane denticles. One specimen (OSU 35167) exhibits significant wear on the oral-lingual surface of the tooth crown, suggesting that the lingual edge of the tooth acted as a broad crushing ridge rather than the entire crown acting as a broad crushing plate.

The taxonomic affinities of this tooth are very uncertain at this time. These specimens do not closely resemble teeth of cochliodonts or petalodonts nor are they like teeth of hybodonts. It is possible that they belong with a group of Carboniferous chondrichthians that is as yet undefined. Such definition will have to await additional material for study.

As noted previously, these teeth appear to have functioned in crushing prey and it appears that they were organized in labiolingually successional rows. The slight depression on the lingual surface of the tooth base appears to have accommodated the labial margin of the crown of the succeeding tooth.

Characterization.— Small tooth with a flat crown that is subcircular and with a basolabial projection. Crown surface punctate. Tooth base elongate, labially projecting and narrowed basally. Lingually, tooth base hollow and scooped out. Several irregularly distributed foramina present labially.

Referred Specimen.— OSU 38615, Vanport limestone, location Lw-2.

Distribution.— Vanport limestone of the Appalachian Basin.

Description.— This tiny tooth measures about 1 mm in crown width and is less than 2 mm in maximum dimension. OSU 38615 (Fig. 45) is the only specimen of this morphology in the collection. The crown is subcircular when viewed orally with a narrow labial projection that curves basally across the labial surface of the tooth base. The crown is relatively high above the tooth base and has rounded, turned-under edges. The crown surface is punctate although relatively smooth and flat.

The tooth base is very elongate and projects labially. At the crown junction, the tooth base is just slightly narrower than the crown but basally it becomes narrowed. A
slightly raised area is present on the basolabial portion of the tooth base. Lingually, the tooth base is scooped out throughout most of its length. Several relatively large nutrient foramina are present labially on either side of the basolabial projection of the crown. No foramina are visible lingually, although this surface appears to be slightly damaged.

Fig. 45.- Tooth "B" (OSU 38615) from the Vanport limestone at location Lw-2. A, labial; B, lateral. Bar scale represents 0.5 mm.

DISCUSSION

This tooth appears to be of the crushing variety and the punctate surface would seem to indicate the presence of tubular dentine, an adaptation for durophagy. However,
tooth "B" is unlike teeth of well-known groups of Carboniferous durophagous chondrichthyans and cannot be placed with any known genus or even order at present. This tooth has a general resemblance to tooth "A" because of its size and the presence of a flattened crown surmounting an elongate tooth base; however, the two forms of teeth differ in a number of details including the basolabial projection of the crown on "B" and the more elongate tooth base of this specimen. Both tooth forms are so poorly known, however, it would be premature to rule out the possibility that they were derived from the dentition of the same species of chondrichthyan. The high degree of symmetry of tooth "B" suggests that it may have been a medial or even symphyseal tooth.

It is probable that these teeth nested in labiolingually successional rows as is indicated by the scooped out lingual surface of the tooth. This hollow area would accommodate the convex surface of the successional tooth behind it. The basolabial projection of the crown and the slightly raised area at the basal end of the tooth base may have functioned as spacers between successional teeth.

Occurrence.—Vanport, Lw-2, (1).
Tooth? "C"

Characterization.- Chondrichthyan tooth with a crown nearly circular in outline, at a high angle to base, and with a gently convex, pock-marked surface. Base flaring, subcircular, and deeply concave basally.

Referred Specimen.- OSU 38616, Skelley limestone, location Nbu-3.

Distribution.- Skelley limestone of the Appalachian Basin.

Description.- This specimen is about 1 mm in maximum dimension and appears to have suffered postmortem abrasion (Fig. 46). The crown is nearly circular when viewed orally and is gently convex with the highest part in the center. The edge of the crown is delineated by a sharp undercut to the base. The crown surface is smooth except for large, deep pits which are irregularly distributed but most apparent near the left anterior edge. The crown is at a high angle, about 50 degrees, to the base. The posterior crown edge, which is the highest part of the specimen, appears to be highly abraded.

The base is comparatively small in relation to the size of the crown and has a peculiar twist or corkscrew pattern whereby the right side of the base descends lower
than does the left side. A deep concavity is present on the undersurface. Nutrient foramina are not visible on the specimen.

![Fig. 46.- Tooth? "C", OSU 38616, Skelley limestone, location Nbu-3. A, labio-oral; B, lateral; C, aboral. Bar scale represents 0.5 mm.](image)

**DISCUSSION**

This unique specimen is one of the more enigmatic examples of chondrichthyan remains in the OSU collection. The size, robustness, and possible antemortem wear on the specimen suggest that it is a small dentition tooth from a durophagous chondrichthyan; however, it could just as easily, perhaps, be interpreted as a dermal denticle, particularly in regard to the characteristics of the base. Obviously, additional specimens will be necessary in order to make a more detailed analysis of this presumed tooth form.
Assuming that the interpretation of this specimen as a tooth is correct, it quite obviously could be interpreted as designed for durophagy. The broad, convex oral surface is reminiscent of a common morphology seen in other Carboniferous durophagous chondrichthyans. The deep pock marks on the surface of the crown are not punctae marking the distal ends of osteons in tubular dentine. Their origin is, however, uncertain at this time.

Occurrence.— Skelley, Nbu-3, (1).
MICROSCOPIC CHONDRICHTHYAN REMAINS FROM
PENNSYLVANIAN MARINE ROCKS OF OHIO
AND ADJACENT AREAS
VOLUME II

DISSERTATION

Presented in Partial Fulfillment of the Requirements for
the Degree Doctor of Philosophy in the Graduate
School of the Ohio State University

By
Michael C. Hansen, B.S., M.S.

* * * * *

The Ohio State University
1986

Reading Committee:
Stig M. Bergstrom
Ted M. Cavender
James W. Collinson
Walter C. Sweet

Approved By:
Stig M. Bergstrom
Adviser
Department of
Geology and Mineralogy
# TABLE OF CONTENTS

**LIST OF TABLES** ................................................................. xvii
**LIST OF FIGURES** ............................................................... xviii
**LIST OF PLATES** ................................................................. xxi
**DERMAL DENTICLES** ............................................................. 307

Subclass, Order, Family *Incertae Sedis*

- Cooperella *typicalis* ....................................................... 308
- Cooperella *striatula* ......................................................... 321
- Kirkella *typicalis* ............................................................ 328
- Moreyella *typicalis* .......................................................... 339
- Nebraska *kella ossiani* ..................................................... 351
- Ohioella *merrilli* ............................................................. 359
- Sturgeonella *quinqueloba* ................................................ 377
- Twayella *zideki* .............................................................. 390
- Williamsella *typicalis* ..................................................... 397
- Williamsella *striata* ........................................................ 406
- Dermal denticle "A" ............................................................ 411
- Dermal denticle "B" ............................................................ 417
- Dermal denticle "C" ............................................................ 423
- Dermal denticle "D" ............................................................ 430
- Dermal denticle "E" ............................................................ 434
- Dermal denticle "F" ............................................................ 438
# LIST OF TABLES

<table>
<thead>
<tr>
<th>TABLES</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>10. Occurrence and frequency of morphotypes of Cooperella typicalis denticles</td>
<td>320</td>
</tr>
<tr>
<td>11. Occurrence and frequency of morphotypes of Cooperella striatula denticles</td>
<td>327</td>
</tr>
<tr>
<td>12. Occurrence and frequency of morphotypes of Moreyella typicalis denticles</td>
<td>350</td>
</tr>
<tr>
<td>13. Occurrence and frequency of morphotypes of Ohioella merrilli denticles</td>
<td>376</td>
</tr>
<tr>
<td>14. Occurrence and frequency of symmoriid mucous membrane denticles</td>
<td>455</td>
</tr>
</tbody>
</table>
## LIST OF FIGURES

<table>
<thead>
<tr>
<th>FIGURE</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>47. Morphotypes I, II, and III of <em>Cooperella typica</em>lis</td>
<td>311</td>
</tr>
<tr>
<td>48. Holotype of <em>Cooperella typica</em>lis Gunnell 1933</td>
<td>312</td>
</tr>
<tr>
<td>49. Holotype of <em>Cooperella subsulcata</em> Gunnell 1933</td>
<td>313</td>
</tr>
<tr>
<td>50. Holotype of <em>Cooperella striata</em> Gunnell 1933</td>
<td>314</td>
</tr>
<tr>
<td>51. Gunnell's (1933) species assigned to <em>Cooperella striata</em></td>
<td>323</td>
</tr>
<tr>
<td>52. Morphotypes assigned to <em>Cooperella striata</em></td>
<td>324</td>
</tr>
<tr>
<td>53. Cotypes of <em>Kirkella typica</em>lis Gunnell 1933</td>
<td>331</td>
</tr>
<tr>
<td>54. Holotype of <em>Kirkella elliptica</em> Gunnell 1933</td>
<td>332</td>
</tr>
<tr>
<td>55. Cotypes of <em>Hammondella globosa</em> Gunnell 1933 and holotype of <em>H. globosa</em> Gunnell 1933</td>
<td>333</td>
</tr>
<tr>
<td>56. Morphotypes of <em>Moreyella typica</em>lis</td>
<td>343</td>
</tr>
<tr>
<td>57. Holotype of <em>Moreyella typica</em>lis Gunnell 1933</td>
<td>346</td>
</tr>
<tr>
<td>58. Holotype of <em>Moreyella aviculiformis</em> Gunnell 1933</td>
<td>347</td>
</tr>
<tr>
<td>59. Holotype of <em>Nebraskella ossiani</em></td>
<td>352</td>
</tr>
<tr>
<td>60. <em>Nebraskella ossiani</em> denticles</td>
<td>354</td>
</tr>
<tr>
<td>61. Holotype of <em>Ohioella merrilli</em></td>
<td>361</td>
</tr>
</tbody>
</table>
FIGURE

62. Morphotype I of *Ohioella merrilli* .................. 362
63. Morphotype II of *Ohioella merrilli* ................. 363
64. Morphotype IV of *Ohioella merrilli* ................. 366
65. Morphotype III of *Ohioella merrilli* ................. 367
66. Morphotype IV of *Ohioella merrilli* ................. 368
67. Holotype of *Sturgeonella (Cooleyella) quinqueloba* ................. 381
68. Holotype of *Cooleyella spatulata* .................. 381
69. Holotype of *Cooleyella quadriloba* .................. 382
70. Holotype of *Cooleyella simplex* .................... 382
71. Holotype of *Cooleyella cuspidata* .................. 384
72. Morphological variation of *Sturgeonella quinqueloba* .......... 387
73. Holotype of *Twayella zideki* ...................... 392
74. Morphological variation of *Twayella zideki* .......... 393
75. Holotype of *Williamsella typicalis* ................. 399
76. Holotype of *Williamsella striata* ................. 407
77. Dermal? denticle "A" .................................. 412
78. Denticles assigned to *Hybodus allegheniensis* ......... 414
79. Dermal denticle "B" .................................. 418
80. Scales of *Deltoptychius armigerus* ................. 421
81. Dermal denticle "C" .................................. 424
82. Denticles of *Fortscottella gigantea* and *F. gemmicula* .......... 427
83. Dermal denticle "D" .................................. 431

xix
<table>
<thead>
<tr>
<th>FIGURE</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>84. Dermal denticle &quot;E&quot;</td>
<td>435</td>
</tr>
<tr>
<td>85. Dermal denticle &quot;F&quot;</td>
<td>439</td>
</tr>
<tr>
<td>86. Single-cusped symmoriid denticles</td>
<td>444</td>
</tr>
<tr>
<td>87. Varieties of multicusped symmoriid denticles</td>
<td>445</td>
</tr>
<tr>
<td>88. Denticles of <em>Gunnellodus bellistriatus</em> and <em>G. cameratus</em></td>
<td>449</td>
</tr>
<tr>
<td>89. Holotype of <em>Gunnellodus trispinousus</em></td>
<td>450</td>
</tr>
<tr>
<td>90. Mucous membrane denticle &quot;A&quot;</td>
<td>458</td>
</tr>
<tr>
<td>91. Distribution of productive collecting localities in Ohio</td>
<td>482</td>
</tr>
</tbody>
</table>
**LIST OF PLATES**

<table>
<thead>
<tr>
<th>PLATE</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>I.</td>
<td>Xenacanthus tridentatus</td>
</tr>
<tr>
<td>II.</td>
<td>Zangerlodus williamsi</td>
</tr>
<tr>
<td>III.</td>
<td>Lissodus duffini, L. zideki, Maiseyodus johnsoni</td>
</tr>
<tr>
<td>IV.</td>
<td>Denaea saltsmani, D. meccaensis, Cobelodus aculeatus, Stehacanthus aitonensis, Symmorium reniforme</td>
</tr>
<tr>
<td>V.</td>
<td>Coolevella peculiaris</td>
</tr>
<tr>
<td>VI.</td>
<td>Hybodont tooth &quot;A&quot;, uncertain hybodonts, Venustodus argutus, Dentition tooth &quot;A&quot;, Dentition tooth &quot;B&quot;, Phoebodus heslerorum, Lagarodus angustus</td>
</tr>
<tr>
<td>VII.</td>
<td>Cooperella striatula, C. typicalis, Nebraskella ossiani, Kirkella typicalis</td>
</tr>
<tr>
<td>VIII.</td>
<td>Moreyella typicalis, Twayella zideki</td>
</tr>
<tr>
<td>IX.</td>
<td>Ohioella merrilli</td>
</tr>
<tr>
<td>X.</td>
<td>Sturgeonella quinqueloba, Williamsella striata, W. typicalis</td>
</tr>
</tbody>
</table>
SYSTEMATIC PALEONTOLOGY

- DENTICLES
Genus *Cooperella* Gunnell 1933

**Characterization.**—Small placoid denticles with an elongate, posteriorly-directed blade that is ornamented with several parallel to subparallel keels. Pedicel constricted. Basal plate oval to quadrangular, with several neck canals and a large basal foramen.

**Type Species.**—*Cooperella typicalis* Gunnell 1933.

*Cooperella typicalis* Gunnell 1933

Pl. VII, figs. 5-8

*Cooperella typicalis*, Gunnell 1933, p. 292-293, Pl. 32, fig. 37.

*Cooperella striata*, Gunnell 1933, p. 293, Pl. 33, figs. 20, 21.

*Cooperella subsulcata*, Gunnell 1933, p. 292, Pl. 31, fig. 72.

Subtype No. 062, Tway and Zidek, 1982, figs. 4a-e.
Subtype No. 199, Tway and Zidek, 1982, figs. 10a-e.
Subtype No. 224, Tway and Zidek, 1982, figs. 13a-d.
Subtype No. 229, Tway and Zidek, 1982, figs. 15a-c.
?Subtype No. 237, Tway and Zidek, 1982, figs.17a-d.
Subtype No. 031, Tway and Zidek, 1982, figs. 24a-d.

**Characterization.**—Small (less than 0.5 mm) placoid dermal denticles with a posteriorly elongated, blade-like crown that tapers to a sharp, posteriorly-directed point in the
median portion. Posteriorly directed and pointed lateral lobes may be present. Crown surface ornamented with five or more keels that traverse the length of the crown. A median ridge and lateral sulci may be present. Pedicel constricted below crown with neck canals present basally. Base ovate to quadrate with a single, large basal foramen.

**Distribution.**—Pennsylvanian of Appalachian and Midcontinent Basins.

**Referred Specimens.**—OSU 38625, 38653.

**Description.**—The following description is based on three separate variants or morphotypes that are herein grouped under Gunnell's (1933) type species *Cooperella*, *C. typicales*. Descriptions are based on specimens in the collection and, where possible, on observations of Gunnell's original specimens.

All denticles assigned to this species are characterized by a long, posteriorly-overhanging crown that is at a high angle (> 50 degrees) to the pedicel. The posterior margin of the crown is extended in its median portion to a sharp-pointed blade and may have secondary lateral lobes. The surface of the crown has from 5 to 8 keels, some of which may be united, on some specimens, into a median ridge. Deep sulci may be present on one or both sides of specimens with a median ridge.
The pedicel is constricted just below the crown/pedicel junction and flares basally into a basal plate. The basal portion of the pedicel may have longitudinal ridges and indentations. Commonly, neck canals are present in the indentations and may be present both anteriorly and posteriorly. The basal surface of the basal plate is slightly concave, subcircular to quadrangular in outline, and has a centrally located, comparatively large foramen.

The first morphotype (I; Fig. 47, A-E) includes specimens that appear to be similar to Gunnell's (1933) description and illustration of his type specimen of C. typicalis (see Discussion). These denticles, as typified by a specimen (OSU 35443) from the Ames Limestone at location PA-4, have six keels on the crown and slight development of distinct, groove-like sulci. The holotype of Cooperella striata Gunnell (1933) (UM 517-5) falls within this morphotype and differs only in the possession of eight keels on the crown and a single sulcus.

The second morphotype (II; Fig. 47, F-I) included in this species appears to be identical to Cooperella subsulcata Gunnell 1933. These denticles are characterized by a prominent median ridge, which is widest anteriorly and converges posteriorly, and has a weak keel on either margin. One or two keels may be present laterally. A
relatively deep sulcus separates the median ridge from the lateral keels. The posterior margin of the crown is divided into three prominent lobes, the longest of which is the median lobe. The pedicel is short in many specimens. The base is similar to that of morphotype I.

Fig. 47.—Morphology of morphotypes I, II, and III of denticles assigned to *Cooperella typicalis*. A–E, morphotype I, similar to *C. typicalis* Gunnell, in anterior, lateral, posterior, apical, and basal views; F–I, morphotype II, similar to *C. subsulcata* Gunnell, in anterior, lateral, posterior, and basal views; J–M, morphotype III, in anterior, lateral, posterior and basal views. Bar scales represent 0.5 mm.
A third morphotype (III, Fig. 47, J–M), which appears to be transitional between the other two morphotypes placed in this species, has well-developed lobes on the posterior margin of the crown and at least six keels on the crown surface. Deep sulci, such as those that are found in morphotype II, are absent. These denticles have very short pedicels and a base similar to that of the other morphotypes.

DISCUSSION

Cooperella was established by Gunnell (1933) for isolated dermal denticles from Pennsylvanian rocks of Missouri and Kansas. Denticles assigned to this genus by Gunnell all bear in common a posteriorly elongated crown, which has on its surface a series of parallel to subparallel keels.

Gunnell (1933) assigned seven species to Cooperella: C. striatula, C. selluliformis, C. subsulcata, C. eroda, C. rectistriata, C. typica/is, and C. striata. Gunnell (1933) designated C. typica/is as the type species. The holotype of C. typica/is (UM 508–5) is badly broken and little morphological information can derived from this specimen (Fig. 48). In addition, the holotypes of C. subsulcata (Fig. 49) and C. rectistriata are irretrievably lost (R. L. Ethington, personal communication, 1982).
Therefore, for these two species and, in effect, the type species of the genus, morphological determinations must depend upon Gunnell's brief descriptions and figures.

Fig. 48. Holotype (UM 508-5) of Cooperella typicallis in anterior view. This specimen is now badly damaged. Redrawn from Gunnell (1933). Bar scale represents 0.5 mm.

The denticles assigned to species of Cooperella by Gunnell (1933) and those in the collection that fit this general morphotype are the most perplexing ones in the entire suite of dermal denticles from Pennsylvanian rocks of the Appalachian Basin. Although Gunnell's species of Cooperella all have a common morphology of a keeled crown, they do not form an obvious morphological transition series. Similarly, specimens in the collection do not depict an obvious transition series, although there are clear morphological similarities.
Fig. 49.—Holotype of Cooperella subsulcata in anterior view. This specimen is now lost. Redrawn from Gunnell (1933). Bar scale represents 0.5 mm.

The most expedient procedure in dealing with these denticles at this stage of knowledge appears to be to divide them into species, which represent two broadly separate morphological groups. The first group is united with Gunnell's (1933) type species of the genus, Cooperella typicalis. The second group, which consists of short-crowned, weakly keeled specimens, is placed in Gunnell's (1933) species, C. striatula. An obvious and direct morphological transition between the two groups and, to some degree within each group, is not apparent in the collection at hand. Cooperella denticles are not abundant in any sample and occurred in only 21 samples; it is therefore not surprising that such transition series, if they exist, are not readily apparent.
Fig. 50.—Holotype (UM 517-5) of Cooperella striata Gunnell 1933. A, anterior; B, posterior; C, apical; D, lateral; E, basal. Bar scale represents 0.5 mm.

The small, posteriorly elongated, keeled denticles of the Cooperella morphotype are typical of modern sharks which are fast swimmers and generally live in offshore habitats (Reif and Goto, 1979). Such denticles commonly form a closely spaced pavement over the body surface of the shark and have a principal function of channeling water across the body surface in order to reduce friction.

It is very possible that all of the denticles herein united under two species of Cooperella, C. typicalis and C. striata, were derived from a single species of shark. The more elongate denticles referred to C. typicalis may represent trunk denticles, whereas the shortened, weakly keeled denticles referred herein to C. striata, may be from snout regions of the shark.
Alternatively, the similar but distinct morphotypes of denticles united in *Cooperella typicalis* may represent more than one species of shark (Table 9). Those of *C. subsulcata* (morphotype II) are particularly suspect in this regard. This possibility is reinforced by the relatively small number of distinct types of dermal denticles in the collection when compared to the number of species in the collection defined by teeth.

Denticles similar in general morphology to those placed herein in *Cooperella typicalis* have been illustrated by Gazdzicki (1974) and Duffin and Gazdzicki (1977) from Rhaetian strata in the Tatra Mountains of Poland. The crowns of these denticles resemble closely the crowns of Gunnell's species, *Cooperella subsulcata*, herein assigned to *C. typicalis*. The presence of secondary keels immediately lateral to the median ridge in the Rhaetian denticles is a minor difference from denticles of *Cooperella typicalis*. The basal plate is larger in comparison to the crown in the Rhaetian specimens and this structure has many more vertical ridges and depressions. In addition, the Triassic denticles are nearly twice as large as the Pennsylvanian ones.

Pomesano Cherchi (1967) described five species of a new genus, *Nurrella*, from the Muschelkalk (M. Triassic) of Sardinia. These specimens, which were interpreted by this
author to be conodonts, are undoubtedly chondrichthyan dermal denticles. Four of these five species, *N. costata*, *N. maxiai*, *N. vardabassoii*, and *N. maccagnoae*, are keeled and bear some similarity to *Cooperella* denticles. These two genera are not, however, congeneric.

The only Pennsylvanian chondrichthyan groups that survived into the Triassic were the hybodonts and neoselachians. Of the hybodonts in the fauna, only teeth of *Maiseyodus johnsoni* occur in sufficient abundance to be considered for evaluation of mutual occurrence. Only 11 localities (19 percent) yielded both *Cooperella typicalis* denticles and *Maiseyodus johnsoni* teeth. A total of 48 localities (81 percent) yielded one or the other but not both. These data are not convincing evidence that *C. typicalis* denticles were derived from the same shark that bore *M. johnsoni* teeth. However, the frequency and abundance of *C. typicalis* denticles is so low that credible comparisons are difficult. A similar lack of correlation is apparent also for *C. typicalis* denticles and the neoselachian in the fauna, *Cooleyella peculiaris*.

In general, the placoid scales of *Cooperella* are similar to some of those attributed to hybodonts by Reif (1979, fig. 9). A specimen illustrated by Reif (1978, fig. 10a), from an unidentified hybodont from Triassic rocks of Spitsbergen, has morphological similarities to those
denticles placed in *Cooperella typicalis*. A dentine from a hybodont, *Synechodus jurensis*, from Upper Jurassic rocks of Germany, illustrated by Reif and Goto (1979, fig. 2e) is very similar to Gunnell's (1933) specimens of *Cooperella subsulcata* (herein assigned to *C. typicalis*). A number of denticles illustrated by Tway and Zidek (1982) are referable to *Cooperella typicalis*. Subtype 031 appears similar to the holotype of *C. typicalis* and to *C. striata* (Morphotype I). Subtypes 062, 199, 224, and 229 are similar to *C. subsulcata* (Morphotype II). Subtype 237 is questionably referred to Morphotype III.

**Stratigraphic Distribution and Paleoecology.**—The denticles herein grouped in *Cooperella typicalis* range through nearly the entire marine sequence in the Appalachian Basin, being absent only in samples from the Columbiana and Washingtonville (Allegheny Group). They are present, in some comparative abundance, in the Putnam Hill limestone suggesting that their absence in these Allegheny units is due to either environment or, perhaps more likely, limited sampling of these units. These denticles are also, surprisingly, rare in the Ames limestone and other Conemaugh units. None were noted in samples from the Gaysport and Skelley limestones; however, these units were sampled at only a few localities.
The units that yielded denticles of *Cooperella typicalis* all appear to represent normal marine environments. There is little evidence, at this stage of understanding, to suggest that these localities represent "far" offshore environments. As noted previously in the Discussion, streamlined, keeled denticles similar to those of *Cooperella* suggest a fast-swimming shark. It can be inferred that the shark that bore these denticles may have been an active predator on other fast-swimming prey—probably other chondrichthyans and perhaps paleoniscoids. Tentative evidence presented above indicates that these denticles may have been borne by a hybodont shark.

**Occurrence.**—"Lower Mercer", Vc-8, (1); Vc-9, (2); Vel-7, (8); Vel-34, (3); Boggs, Sb-4, (3); Lower Mercer, CSj-3, (1); CSj-1, (1); MUF-3, (1); Upper Mercer, Mp-3, (14); Putnam Hill, CSO-2, (1); MUm-4, (1); Pmc-4, (1); Td-4, (14); Tt-1, (4); Tt-1, (1); Vanport, Ld-1, (1); Brush Creek, Aw-47, (8); Cambridge, Nn-13, (1); Portersville, Aw-47, (2); Noble, Nbu-1, (1); Ames, PA-3, (2); PA-4, (2).
Table 10.- Occurrence and frequency of morphotypes I, II, and III of *Cooperella typicais* in the Appalachian Basin sample.

<table>
<thead>
<tr>
<th>UNIT</th>
<th>LOCALITY</th>
<th>I</th>
<th>II</th>
<th>III</th>
</tr>
</thead>
<tbody>
<tr>
<td>&quot;L. Mercer&quot;</td>
<td>Vc-8</td>
<td>–</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Vc-9</td>
<td>–</td>
<td>2</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Ve1-7</td>
<td>–</td>
<td>8</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Ve1-34</td>
<td>–</td>
<td>3</td>
<td>–</td>
</tr>
<tr>
<td>Boggs</td>
<td>Sb-4</td>
<td>–</td>
<td>3</td>
<td>–</td>
</tr>
<tr>
<td>L. Mercer</td>
<td>CSj-3</td>
<td>–</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>CS1-1</td>
<td>–</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Muf-3</td>
<td>–</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td>U. Mercer</td>
<td>Mp-3</td>
<td>1</td>
<td>10</td>
<td>–</td>
</tr>
<tr>
<td>Putnam Hill</td>
<td>CSo-2</td>
<td>–</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>MUpu-4</td>
<td>–</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Pmc-4</td>
<td>–</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Td-4</td>
<td>–</td>
<td>14</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Tf-1</td>
<td>–</td>
<td>4</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Tl-1</td>
<td>–</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td>Vanport</td>
<td>Ld-1</td>
<td>–</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td>Brush Creek</td>
<td>Aw-47</td>
<td>2</td>
<td>7</td>
<td>–</td>
</tr>
<tr>
<td>Cambridge</td>
<td>Nn-13</td>
<td>–</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td>Portersville</td>
<td>Aw-47</td>
<td>–</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Noble</td>
<td>Nbu-1</td>
<td>–</td>
<td>–</td>
<td>1</td>
</tr>
<tr>
<td>Ames</td>
<td>PA-3</td>
<td>1</td>
<td>1</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>PA-4</td>
<td>–</td>
<td>–</td>
<td>2</td>
</tr>
</tbody>
</table>
Cooperella striatula Gunnell 1933

Pl. VII, Figs. 1-4, 9-10

Cooperella striatula, Gunnell, 1933, p. 293, Pl. 31, fig. 69.

Cooperella selluliformis, Gunnell, 1933, p. 291, Pl. 31, fig. 70.

Cooperella eroda, Gunnell, 1933, p. 291, Pl. 31, figs. 73-75.

Cooperella rectistriata, Gunnell, 1933, p. 292, Pl. 31, figs. 76-77.

?Cooperella sp., Gunnell, 1933, p. 292, Pl. 32, fig. 20.

Subtype No. 026, Tway and Zidek, 1982, figs. 21a-e.

Subtype No. 029, Tway and Zidek, 1982, figs. 23a-d.

?Subtype No. 157, Tway and Zidek, 1982, figs. 38a-e.

Subtype No. 195, Tway and Zidek, 1982, figs. 42a-d.

Subtype No. 225, Tway and Zidek, 1982, figs. 44a-d.

Subtype No. 138, Tway and Zidek, 1982, figs. 59a-e.

Subtype No. 141, Tway and Zidek, 1982, figs. 60a-e.

Subtype No. 145, Tway and Zidek, 1982, figs. 61a-d.

Subtype No. 215, Tway and Zidek, 1982, figs. 68a-d.

Characterization.—Small placoid denticles with a short (anterior-posterior dimension) posteriorly projecting crown. Crown surface ornamented with six or more faint keels that commonly do not reach the posterior margin. Crown slightly elevated in median portion and lacking
distinct lateral lobes. Pedicel constricted and relatively long. Base subcircular with neck canals and a large basal foramen.

Holotype.—University of Missouri UM 502-5.

Distribution.—Pennsylvanian of Appalachian and Midcontinent Basins.

Referred Specimens.—OSU 38649, 38650, 38653.

Description.—Denticles referred to a morphotype I (Fig. 52, A-D) are similar in morphology to the denticles of Cooperella striatula, C. selluliformis, C. eroda, and C. rectistriata described by Gunnell (1933) (see Fig. 51). The crown is oval to quadrate and at a relatively low angle to the pedicel. From five to eight or more relatively weak keels originate on the anterior margin, at the crown/pedicel junction, and continue parallel to one another across the anterior portion of the crown. In most specimens the keels weaken posteriorly and do not reach the posterior margin of the crown.

The pedicel is short and constricted beneath the crown. The base is oval to quadrate and has a large basal foramen. Several neck canals may be present on the lower portion of the pedicel of denticles of morphotype I.
An additional morphotype (II, Fig. 52, E-L), which has some variation, is provisionally placed with this species. The crown of this morphotype is at an angle of about 40 degrees with the pedicel. The crown tapers apically to a sharp point that projects only a short distance posteriorly. The crown surface is ornamented with four to six keels that are most prominent anteriorly and weaker posteriorly. The pedicel is constricted and bears several neck canals. The base is flared and has a single basal foramen.

Fig. 51.- Gunnell's (1933) species herein assigned to Cooperella striatula. A-C, holotype (UM 502-5) of Cooperella striatula in anterior, basal, and lateral views. D-F, holotype of Cooperella eroda (UM 503-4) in anterior, posterior and lateral views. G-I, holotype (UM 503-1) of Cooperella selluliformis in anterior, posterior, and lateral views. Bar scales represent 0.5 mm.
DISCUSSION

Four of Gunnell's (1933) species assigned to Cooperella are similar in having a short crown with only weakly developed keels. Cooperella striatula is herein chosen as the senior synonym because it was the first species of this morphotype to be described by Gunnell (1933) and because the holotype (UM 502-5) is extant and relatively well preserved. The type specimen of C. rectistriata is lost (R. L. Ethington, personal communication, 1982). Unfortunately, the base of the holotype of C. striatula is broken. An anonymous note on the slide indicates that it was "broken during study". However, the crown morphology appears to be the most diagnostic character of these denticles (Fig. 51, A-C).

Gunnell's (1933) four species herein united in Cooperella striatula have sufficient similarity to be provisionally interpreted as a morphological transition series (morphotype I, Fig. 52). The second morphotype (II, Fig. 52) appears to have sufficient similarity to those grouped in morphotype I to be included with them in C. striatula; however, this grouping is tentative and provisional. Unfortunately, the sample of specimens herein grouped in C. striatula is so small that it is difficult to adequately assess the range of morphological variation in these denticles.
As indicated in the discussion of Cooperella typicalis, denticles assigned to this genus are perhaps the most perplexing of any in the collection, in part because so few specimens are available for study. There is considerable uncertainty as to whether the morphotypes described for each species of Cooperella represent an imperfect morphological transition series for each species or whether they represent distinct species. The procedure followed here for both C. typicalis and C. striatula appears to be the most expedient one with present knowledge and available specimens. It should not be surprising that such uncertainties would arise during initial studies of dermal denticles of Paleozoic sharks. Nevertheless, Cooperella, as now constituted, provides a workable taxonomic unit.

Stratigraphic Distribution and Paleoecology.—Morphotypes I and II occur in low frequency throughout most of the Pennsylvanian marine rock sequence in the Appalachian Basin. The only units that did not yield denticles of Cooperella striatula were the Putnam Hill, Columbiana, and Washingtonville (Allegheny Group), and the Brush Creek, Gaysport, and Skelly (Conemaugh Group). It is probable that these denticles will eventually be recovered from these units also. Cooperella striatula denticles were present at 12 localities representing 11 stratigraphic
units. At 4 of the 11 localities (36 percent) both morphotypes were present (Table 11). At only one locality did more than 2 denticles of each morphotype occur. Denticles of *Cooperella striatula* do not appear to be of significant biostratigraphic value.

Fig. 52.—Denticle morphotypes from the Appalachian Basin sample herein assigned to *Cooperella striatula*. A–D, morphotype I, similar to the holotype, in anterior, lateral, posterior, and basal views ("Lower Mercer", Vel-7). E–H, morphotype II, in anterior, lateral, posterior, and basal views ("Lower Mercer", Vel-7). I–L, another variation of morphotype II, in anterior, lateral, posterior, and basal views (Upper Mercer, Mp-3). Bar scale represents 0.5 mm.
Taxonomic Affinities and Functional Morphology.—The functional design of Cooperella striatula denticles, which are small, compact, streamlined structures with subparallel keels, suggests that they were derived from a fast-swimming shark. This denticle design channels water across the body surface and reduces the coefficient of friction. Reif (1979) indicated that denticles of this general form are typical of hybodonts.

Occurrence.—"Lower Mercer", Vel-7, (4); Boggs, Sb-4, (1); Lower Mercer, MUmu-3, (1); PA-10, (1); Upper Mercer, Mp-3, (1); Vanport, Ld-1, (2); Brush Creek, Aw-47, (7); Cambridge, Nn-13, (1); Portersville, Acn-31, (1); Noble, Nbu-1, (2); Ames, PA-3, (3); PA-4, (3).

Table 11.—Distribution and frequency of morphotypes I and II of Cooperella striatula.

<table>
<thead>
<tr>
<th>UNIT</th>
<th>LOCATION</th>
<th>I</th>
<th>II</th>
</tr>
</thead>
<tbody>
<tr>
<td>&quot;L. Mercer&quot;</td>
<td>Vel-7</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Boggs</td>
<td>Sb-4</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>L. Mercer</td>
<td>MUmu-3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>&quot;</td>
<td>PA-10</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>U. Mercer</td>
<td>Mp-3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Vanport</td>
<td>Ld-1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Brush Creek</td>
<td>Aw-47</td>
<td>7</td>
<td>-</td>
</tr>
<tr>
<td>Cambridge</td>
<td>Nn-13</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Portersville</td>
<td>Acn-31</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Noble</td>
<td>Nbu-1</td>
<td>2</td>
<td>-</td>
</tr>
<tr>
<td>Ames</td>
<td>PA-3</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>&quot;</td>
<td>PA-4</td>
<td>2</td>
<td>1</td>
</tr>
</tbody>
</table>
Genus *Kirkella* Gunnell 1933

Characterization.—Dermal denticles in which the crown is rounded to subellipsoidal in outline, bulbous, commonly with minor buttresses and indentations on basal portion. Pedicel elongate, with deep vertical indentations within which are neck canals. Base slightly flared, concave basally, with a single foramen.

Type Species.—*Kirkella typicalis* Gunnell 1933.

*Kirkella typicalis* Gunnell 1933

Pl. VII, Figs. 14-19

*Kirkella typicalis* Gunnell, 1933, p. 294, Pl. 33, figs. 14-16.


*Hammondella globosa* Gunnell, 1933, p. 293, Pl. 33, figs. 42-43.

*Hammondella crassa* Gunnell, 1933, p. 293, Pl. 33, fig. 47.

*Janassa* sp., Schultze, 1985, Fig. 2, no. 9.

Subtype No. 008, Tway and Zidek, 1982, figs. 57a-d.

Subtype No. 111, Tway and Zidek, 1982, figs. 65a-d.

Subtype No. 103, Tway and Zidek, 1983, figs. 67a-b.

Subtype No. 109, Tway and Zidek, 1983, figs. 68a-c.

Subtype No. 134, Tway and Zidek, 1983, figs. 69a-c.
Subtype No. 144, Tway and Zidek, 1983, figs. 71a-c.
Subtype No. 192, Tway and Zidek, 1983, figs. 72a-b.
Subtype No. 206, Tway and Zidek, 1983, figs. 74a-b.
?Subtype No. 201, Tway and Zidek, 1983, figs. 73a-b.

Distribution.—Pennsylvanian of the Appalachian and Midcontinent Basins; Lower Permian of Kansas.

Referred Specimens.—OSU 38644, 38646, 38647, 38651.

Description.—Denticles of *Kirkella typicalis* are generally less than one millimeter in maximum dimension although those assigned by Gunnell to *Hammondella* are slightly larger than those which he assigned to *Kirkella*. The crowns have a subcircular to quadrangular to an irregular outline when viewed apically. The crown margin on some specimens is indented and buttressed. The crown forms a flattened to bulbous cap that overhangs the pedicel. In some specimens the crown is compressed and elongated, with one margin overhanging the pedicel more than the other margins. The enameloid of the crown may join the pedicel abruptly, with a narrow ridge serving as a demarcation between the two structures, or the enameloid may form raised lobes between which are indentations. On some specimens, particularly those with relatively flat crowns, faint keels may be present along the edges of the crown.
The pedicel is relatively long and constricted in most specimens and has longitudinal ridges and intervening indentations. Neck canals are commonly present in the indentations. The base flares slightly and may be approximately the same diameter as the crown. The basal surface is slightly concave and bears a single basal foramen.

Determination of anterior-posterior orientations on these denticles is difficult. A few specimens are triangular in outline with keels on two sides (cf. Tway and Zidek, 1983, figs. 69a–c). Denticles of this morphology suggest moderate streamlining with the apex of the triangle being anterior. Most specimens, however, are devoid of any features that would suggest preferred orientation. Denticles referred by Gunnell (1933) to Hammondella, and provisionally included herein with Kirkella typicalis, exhibit definite anterior and posterior surfaces.

DISCUSSION

Kirkella typicalis was named by Gunnell (1933) for blunt-crowned denticles from Pennsylvanian rocks of Kansas and Missouri. He named three species, of which the type species was designated as K. typicalis. Gunnell designated two specimens (UM 517-1, UM 517-2), from the same horizon
and locality, as cotypes of this species (Fig. 53). These specimens are very similar to one another in having subcircular (in apical view) somewhat flattened crowns. Specimen UM 517-2 is herein designated the lectotype of this species, although the other specimen (UM 517-1) could equally well serve in this capacity. The two additional species named by Gunnell, *K. indentata* and *K. elliptica*, were based upon specimens with minor variations in the crown morphology. The holotype of *K. elliptica* (UM 518-3) has a globose crown, in contrast to the more flattened crown of *K. typicalis* (Fig. 54). The holotype of *K. indentata* (UM 516-4) is an incomplete specimen that is broken sagittally (Fig. 54). However, this specimen is similar to the holotype of *K. typicalis* except for indentations on the lateral margins of the crown. The morphological variations of *K. elliptica* and *K. indentata* are, however, very minor when compared to the type species of the genus, *K. typicalis*. Indeed, Orvig (1966) has illustrated as much or more variation in similar denticles from a single specimen of *Janassa bituminosa*. There can be little question, therefore, that these taxa are part of a morphological transition series and that they should be included in a single species.
Fig. 53.—Cotypes of Kirkella typica lis Gunnell 1933. I, UM 517-2, herein designated as the lectotype of K. typica lis. A, apical; B, lateral; C, lateral. II, UM 517-1. A, apical; B, lateral; C, basal. Bar scales represent 0.5 mm.

Fig. 54.—I, holotype of Kirkella elliptica Gunnell 1933 (UM 518-3). A, apical; B-D, lateral views. II, holotype of Kirkella indentata Gunnell 1933 (UM 516-4). A, apical; B, lateral; C, lateral; D, broken edge revealing pulp cavity. Bar scales represent 0.5 mm.
Similar, although slightly larger, denticles were described by Gunnell (1933) as *Hammondella globosa* and *Hammondella crassa*. These denticles have an elevated crown, particularly *H. crassa*, and exhibit apparent anterior and posterior surfaces (Fig. 55). Such denticles, of which there are no examples in the OSU collection, are provisionally included with *Kirkella typicalis*. They may represent specialized denticles that occurred with low frequency on the chondrichthyan that bore *K. typicalis* denticles. Alternatively, there is the possibility that *Hammondella* denticles are from a species closely related to *K. typicalis*. Larger collections of both *K. typicalis* and *Hammondella* denticles may clarify this uncertainty.

![Fig. 55.- I, UM 521-4, cotype of *Hammondella globosa* Gunnell 1933. A-C, lateral views; D, apical view. II, UM 522-3, holotype of *Hammondella crassa* Gunnell 1933. A-B, lateral views; C, apical view. Bar scale represents 0.5 mm.](image-url)
Should it be determined in future studies that *Hammondella globosa* denticles are distinct from those of *Kirkella typicalis*, then UM 521-4 should be designated as the lectotype of *H. globosa*. This specimen was designated by Gunnell (1933), along with UM 521-3, as a cotype of *H. globosa*. However, UM 521-3 is badly broken and part of the specimen is missing; it is therefore unsuitable as a lectotype. The holotype of *H. crassa* (UM 522-3) is well preserved and was derived from the same locality in the Americus Limestone as were Gunnell's (1933) specimens of *H. globosa*.

Orvig (1966), in his studies of denticles associated with a specimen of a petalodont, *Janassa bituminosa*, from the Upper Permian (Lower Zechstein) of northern Germany, concluded that these denticles were identical to those described by Gunnell (1933) as species of *Kirkella* and *Hammondella*. Orvig's (1966) illustrations leave little doubt as to the similarity of *J. bituminosa* denticles to those of *Kirkella*. None of the denticles illustrated by Orvig is identical to the holotype of *Hammondella crassa*. Orvig's (1966) illustrations of specimens prepared by acetic acid techniques are far superior to those illustrations of *Janassa bituminosa* denticles by Hancock and Howse (1870), Weigelt (1930), Malzahn (1968), and
Schaumberg (1977). Most of these illustrations are insufficient for proper identification of similar denticles from microsamples.

There is a strong temptation to place Kirkella and Hammondella denticles in synonomy with Janassa on the basis of Orvig's (1966) evidence that similar or perhaps identical placoid denticles are found in association with an Upper Permian specimen of this petalodont. Indeed, Schultze (1985) followed this procedure by illustrating a denticle of this morphology, from the Lower Permian of Kansas, as Janassa sp. The uncertainty in this procedure, from a parsimonious perspective, is that there is a possibility that similar or perhaps even identical denticles occur in other petalodont species that lived contemporaneously with Janassa throughout its persistent history (Late Mississippian through Late Permian). Woodward (1920) presented tantalizing although inconclusive evidence that appears to warrant this conservatism. He described and illustrated the dentition and some denticles of a petalodont which he referred to Climaxodus wisei (now placed in Tanaodus St. John and Worthen 1875; Hansen, 1985). Orvig (1966) referred this specimen to Janassa. Woodward's (1920) description is too brief and his figures are too small in order to determine if the denticles of Tanaodus wisei are identical to those
of Kirkella; however, there is little doubt that they are similar to the Kirkella morphotype and thus suggest that this denticle form may be typical of several or perhaps many petalodonts. In addition to Janassa, the petalodonts Peripristis semicircularis, Petalodus ohioensis, Polyrhizodus carbonarius and Cholodus (= Fissodus) inaequalis are present in marine Pennsylvanian rocks of the Appalachian Basin. Unfortunately, no specimens of any of these petalodonts have been found with biologic associations of teeth and denticles.

Orvig (1966) stated, names such as Kirkella "can only be ascribed temporary status for general use." Undoubtedly, Kirkella typicalis is a junior synonym of a species founded on isolated teeth, probably those of a petalodont and perhaps those of Janassa; however, until that correlation can be definitely be made for Pennsylvanian denticles, it seems best to retain Gunnell's species, Kirkella typicalis. It should be noted that the low frequency of specimens of K. typicalis in the collection (23 specimens from 14 localities) appears to be consistent with their probable assignment to Janassa. Teeth of both Petalodus ohioensis and Peripristis semicircularis are abundant in the macroscopic collection (probably the two most abundant species in the OSU collection) and are known from nearly every marine unit.
It would appear probable that denticles from either of these petalodonts would be more abundant and more widely distributed than are those from the collection herein assigned to \textit{K. typicalis}.

Tway and Zidek (1982, 1983) illustrated denticles of \textit{Kirkella typicalis} as nine separate subtypes. The morphological variations of these denticles, although comparatively minor and consistent with the variation that would be expected in a single species, have resulted in the large number of separate subtypes with the Scripps system of artificial taxonomy.

**Stratigraphic Distribution and Paleoeology.**—Denticles of \textit{Kirkella typicalis} occur throughout nearly the entire Pennsylvanian marine sequence of the Appalachian basin. They are absent only from the Boggs (Pottsville Group), Columbiana and Washingtonville (Allegheny Group), and Gaysport and Skelley (Conemaugh Group). All of these units were sampled at relatively few localities. In all samples the frequency of these denticles was low (see Occurrence).

Surprisingly, the Ames limestone yielded only two denticles of \textit{Kirkella typicalis}. Denticles of this species are robust in comparison to denticles of most other species in the collection; it is therefore unlikely that this paucity is a result of postmortem destruction by wave agitation. This circumstance does not appear to be
entirely consistent with the contention that *K. typicalis* denticles were derived from *Janassa* or perhaps another petalodont as petalodont teeth are more abundant in the Ames limestone than in any other marine unit in the Pennsylvanian of the Appalachian Basin.

*Kirkella typicalis* denticles are of the form indicated by Applegate (1967) and Reif and Goto (1979) to be typical of shallow-water, bottom-dwelling chondrichthians. The broad, flattened crowns of these denticles appear to have functioned in protecting the skin from abrasion by bottom sediments. Indeed, some *K. typicalis* denticles in the collection exhibit considerable abrasion of the crowns. Functionally, these denticles are consistent with the mode of life interpreted from specimens of *Janassa* from the Upper Permian of Germany. These dorsoventrally flattened sharks have been found with remains of brachiopods, foraminifers, and crabs in the gut (Malzahn, 1968, 1972). It is probable that *Kirkella typicalis* denticles were derived from a durophagous, bottom-dwelling chondrichthyan that lived in shallow, normal-marine waters.

**Occurrence.**—"Lower Mercer", Vel-7, (3); Vel-34, (1); Lower Mercer, MUmu-3, (1); Upper Mercer, Mp-3, (1); Putnam Hill, Td-4, (2); Vanport, Jmi-2(1); Ld-1, (1); Brush Creek, At-5, (1); Aw-47, (5); Cambridge, Gca-5, (1); Portersville, Aw-47, (3); Noble, Nbu-1, (4); Ames, Cma-10, (1); PA-4, (1).
Genus Morevella Gunnell 1933

Characterization.—A genus of chondrichthyans characterized by small, variable dermal denticles that can be assigned to four morphotypes within a morphological transition series. The crown consists of a blade ranging from a broad, posteriorly lobate form with a median ridge and small ridges on the lateral edges of each lobe (I); to a lobate blade with a prominent median ridge bordered by a deep sulcus and lateral lobes with a prominent ridge (II); to a blade that lacks distinct lobes posteriorly and with a subdued median ridge (III); to a blade that is thin and spikelike without lateral lobes (IV). Pedicel short and constricted. Base cruciform with a prominent basal cavity.

Type Species.—Morevella typicalis Gunnell 1933

Morevella typicalis Gunnell 1933

Pl. VIII, Figs. 1-16

Morevella typicalis Gunnell, 1933, p. 295, Pl. 31, fig. 53.

Morevella aviculiformis Gunnell, 1933, p. 295, Pl. 31, fig. 63.

Morevella trilobita Gunnell, 1933, p. 295-296, Pl. 32, fig. 24.

Staurognathus caltrop Mendenhall, 1951, p. 31, Pl. 1, figs. 1-3.
Subtype 005, Tway and Zidek, 1982, figs. 2a-e.
Subtype 066, Tway and Zidek, 1982, figs. 5a-e.
Subtype 089, Tway and Zidek, 1982, figs. 8a-f.
Subtype 213, Tway and Zidek, 1982, figs. 11a-c.
Subtype 220, Tway and Zidek, 1982, figs. 12a-c.
Subtype 227, Tway and Zidek, 1982, figs. 14a-c.
Subtype 002, Tway and Zidek, 1982, figs. 20a-e.
Subtype 118, Tway and Zidek, 1983, figs. 16a-e.
Subtype 119, Tway and Zidek, 1983, figs. 17a-d.

Characterization.—As for the genus, which is monotypic.

Referred Specimens.—OSU 38620, 38635a-c, 38654, 38655, 38656, 38657.

Distribution.—Pennsylvanian of the Appalachian basin, Upper Pennsylvanian and Lower Permian of the Midcontinent basin.

Description.—Four distinct morphotypes, which appear to form a disjunct morphological transition series, are provisionally assigned to this species. All of these placoid denticles are relatively small, with maximum dimensions of 0.5 to 1.0 mm.

The first morphotype (I, Fig. 56, A-D) is includes the holotype of Moreyella typicalis. These denticles have a relatively large, posteriorly overhanging crown blade.
dominated by a median ridge that is robust at its beginning on the anterior part of the base. The median ridge tapers posteriorly to a sharp point and forms the median lobe of the denticle. Laterally, the median ridge is bordered on either side by a shallow, broad sulcus. The distal portion of the sulcus forms a shallow, U-shaped lobe. The lateral margins of the crown blade exhibit ridges that, distally, form sharp peaks, each of which is shorter than the median lobe.

The posterior portion of the crown blade is slightly concave and has a weak median ridge that extends from the base to near the tip of the median lobe. The pedicel is short, both anteriorly and posteriorly. The denticle base is small in comparison to the remainder of the denticle, has an ovoid to cruciform outline, and is concave basally.

The second morphotype (II, Fig. 56, E-G) is trilobed and similar to morphotype I, but is more compressed laterally and less compressed in the antero-posterior dimension. A prominent median ridge is robust basally, where it forms the anterior portion of the pedicel/base. Distally, the median ridge tapers to a sharp point, forming the apex of the median lobe. Lateral to the median ridge are deep sulci that form the lateral lobes. A slight ridge is present on the lateral edge of each lateral lobe.
Posteriorly, the crown has a prominent median ridge that, in conjunction with the prominent anterior ridge, gives these denticles a deep antero-posterior dimension. Shallow sulci border the median ridge. The pedicel is short and formed partially by the median anterior and posterior ridges and by short ridges beneath each lateral lobe. These ridges form the "spokes" of the cruciform base. Basally, the denticle is deeply concave with a single, large basal foramen.

The third morphotype (III, Fig. 56, H-K) is questionably included in this transition series; however, it appears to be transitional between morphotypes I and II and has several features in common with all denticles assigned to this species. The crown blade is leaf-shaped, that is, it is narrower basally, widens in the medial portion, and then tapers to a sharp median point. The distal portions of the blade, on the lateral edges, show slight notches that appear to be incipient lateral lobes. A narrow, prominent, anterior median ridge runs from the base of the denticle to about midpoint, where it fades into a broad, raised area distally. Laterally, the median ridge is bordered by shallow sulci.
Fig. 56.- Morphotypes I-IV of the morphological transition series of *Moreyella typicalis* denticles. A-D, morphotype II in anterior, lateral, and posterior views; E-G, morphotype II in anterior, lateral, and posterior views; H-K, morphotype III in anterior, lateral, posterior, and basal views; L-O, morphotype IV in anterior, lateral, posterior, and basal views. Bar scale represents 0.5 mm.
Posteriorly, these denticles are concave with a prominent median ridge that runs from the base to near the distal portion of the blade. The pedicel is moderately long with an upwardly imbricated ridge that marks the junction between the pedicel and the crown. This ridge is prominent anteriorly and less prominent posteriorly. The base is cruciform in shape and deeply concave basally with a single basal foramen.

The fourth morphotype (IV, Fig. 56, L-0) assigned to this species has a long, spikelike, posteriorly directed crown blade that is subcircular in cross section and unornamented. The spikelike crown blade may be inclined slightly to the right or left and some specimens exhibit a shortened spike and a pronounced flattening of the anterior surface. The base is cruciform with a deep basal cavity in which there is a large basal foramen. Each leg or spoke of the cruciform base is marked, on many specimens, by a surface ridge. A thin band of "webbing" connects each spoke of the base, resembling the foot of an aquatic bird.

**DISCUSSION**

*Moreyella* was erected by Gunnell (1933) with *M. typicalis* as the type species. The holotype (UM 500-1), from the Winterset Limestone, is relatively well preserved (Fig. 57) and is similar to specimens from the Appalachian
Basin placed in morphotype I (Fig. 56, A-O). *Moreyella aviculiformis* Gunnell (1933) is represented by UM 501-4 and is also well preserved (Fig. 58). This species is placed in synonymy with *M. typicalis*. *Moreyella trilobita* Gunnell (1933) has grooves on the crown ridges, a characteristic which Gunnell (1933) determined to be of specific distinction. Unfortunately, the holotype is irretrievably lost (R. L. Ethington, personal communication, 1982). The illustration of this specimen (Gunnell, 1933, Pl. 32, fig. 24) suggests that it differs from *M. typicalis* only in minor morphological details; therefore, *M. trilobita* is placed in synonymy with *M. typicalis*.

![Fig. 57.- Holotype (UM 500-1) of Moreyella typicalis Gunnell 1933. A, anterior; B, posterior; C, lateral. Bar scale represents 0.5 mm.](image-url)
The denticles herein assigned to *Moreyella typicalis* represent one of the most diverse morphological transition series in the OSU collection. It appears that the provisional placement of these four morphotypes in *M. typicalis* is warranted on the basis of a suite of common morphological features exhibited by the 147 specimens of this species in the OSU collection.

All of these specimens bear in common a well-developed median ridge, or as in morphotype IV, the median ridge constitutes the entire denticle crown, and a cruciform, deeply excavated base. Mutual occurrence data (Table 12) suggest that the derivation of these four morphotypes was from a single species of shark. Twelve localities, of a total of 21, yielded two or more morphotypes (57 percent); seven localities (33 percent) yielded three or more morphotypes; and two localities (10 percent) yielded all four morphotypes. To a degree, these figures are influenced by the relative rarity of some denticle forms. Only 6 percent of the collection of this species consists of morphotype I, and only 12 percent consists of morphotype III. Of this assemblage united in *Moreyella typicalis*, 45 percent are of morphotype II and 39 percent are assigned to morphotype IV.
A specimen of morphotype IV, from Virgilian rocks of Nebraska, was illustrated in a thesis by Mendenhall (1951). He interpreted it to be a conodont and placed the specimen in *Staurognathus* Branson and Mehl (1941) as a new species, *S. caltrap*. This manuscript species did not receive formal designation.

Schultze (1985, Fig. 2, no. 1) illustrated a denticle from Lower Permian rocks (Chase Group, Gearyan) of Kansas that appears to be referable to *Moreyella typicalis*. This specimen is of the form placed in morphotype I. Reif and Goto (1979, Fig. 1) illustrated two denticles from Middle Permian rocks of Japan that are similar to those of *M. typicalis*, morphotype I. The pedicels and bases and minor features of the crowns of these Permian denticles differ from those derived from Pennsylvanian rocks of the Appalachian Basin.
Tway and Zidek (1982, 1983) illustrated nine specimens from Virgilian rocks of the Midcontinent which are herein interpreted to be morphotypes of *Morevella typicalis*. Subtypes 089 and 002 are interpreted to be morphotype I; Subtype 005 is assigned to morphotype II; Subtypes 066, 213, 220, and 227 are assigned to morphotype III; Subtypes 118 and 119 are referred to morphotype IV.

Denticles of morphotypes I, II, and III appear to have functioned in channeling water across the body surface of the shark that bore them. These denticles are sharply inclined posteriorly and probably were positioned so that the posterior tip of one denticle overlapped the anterior margin of the denticle behind it. The ridges on morphotypes I and II and to a degree, morphotype II, must have functioned as keels to channel water across the body surface. The abundance of specimens of morphotype II suggests that this denticle form covered broad surfaces of the body such as the flanks and back.

The denticles of morphotype IV are more perplexing. These spikelike denticles are streamlined and show right and left asymmetry. These features suggest that they channeled water and that they were derived from right, left, and median positions on the body. There is a possibility that they were branchial denticles.
Stratigraphic Distribution and Paleoecology.—Denticles of all morphotypes of *Moreyella typicalis* are widely distributed throughout the Pennsylvanian marine sequence of the Appalachian Basin. Only the Boggs, Lower Mercer, Columbiana, Washingtonville, and Gaysport did not yield at least one morphotype of these denticles. All of these units, except the Lower Mercer, were sampled at relatively few localities. Conemaugh units yielded the largest numbers of *M. typicalis* denticles (Table 2; Table 12).

Tway and Zidek's (1982, 1983) specimens were derived from Virgilian rocks of the Midcontinent as was the specimen illustrated by Mendenhall (1951). The specimen illustrated by Schultze (1985) was derived from Lower Permian rocks of the Midcontinent. Gunnell's (1933) specimens were from Pennsylvanian rocks of the Midcontinent. All of these units appear to indicate a normal marine environment.

Occurrence.—"Lower Mercer", Vel-7, (3): Upper Mercer, Mpu-3, (3); Putnam Hill, CSo-2, (1); MUm-4, (5); Td-4, (3); Vanport, Ld-1, (7); Lw-2, (4): Brush Creek, Aw-47, (22): Cambridge, GAp-4, (1); GAs-1, (20); Gca-5, (21); Nn-13, (4): Portersville, At-45B, (20); Aw-47, (19): Noble, Nbu-1, (3): Ames, Aa-64, (1); Gwi-3, (1); Nbu-4, (2); Pb-4, (1); PA-3, (4): Skelley, Nbu-3, (2).
Table 12.- Distribution and frequency of morphotypes I-IV of *Moreyella typicalis*.

<table>
<thead>
<tr>
<th>UNIT</th>
<th>LOCALITY</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>&quot;L. Mercer&quot;</td>
<td>Vel-7</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>U. Mercer</td>
<td>Mp-3</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Putnam Hill</td>
<td>CS0-2</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>&quot;</td>
<td>MUm-4</td>
<td></td>
<td>4</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Td-4</td>
<td></td>
<td>2</td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Vanport</td>
<td>Ld-1</td>
<td></td>
<td>4</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>&quot;</td>
<td>Lw-2</td>
<td></td>
<td>1</td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>Brush Creek</td>
<td>Aw-47</td>
<td>1</td>
<td>16</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Cambridge</td>
<td>Gap-4</td>
<td></td>
<td></td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>GAs-1</td>
<td></td>
<td>12</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>&quot;</td>
<td>Gca-5</td>
<td></td>
<td>15</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>&quot;</td>
<td>Nn-13</td>
<td></td>
<td></td>
<td></td>
<td>4</td>
</tr>
<tr>
<td>Portersville</td>
<td>At-45B</td>
<td></td>
<td>2</td>
<td>1</td>
<td>17</td>
</tr>
<tr>
<td>&quot;</td>
<td>Aw-47</td>
<td>1</td>
<td>6</td>
<td>1</td>
<td>11</td>
</tr>
<tr>
<td>Noble</td>
<td>Nbu-1</td>
<td></td>
<td>1</td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>Ames</td>
<td>Aa-64</td>
<td></td>
<td></td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Gwi-3</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Nbu-4</td>
<td></td>
<td></td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Pb-4</td>
<td></td>
<td></td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>PA-3</td>
<td></td>
<td>1</td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>Skelley</td>
<td>Nbu-3</td>
<td></td>
<td></td>
<td></td>
<td>2</td>
</tr>
</tbody>
</table>
Genus *Nebraskella* n. g.

Characterization.—A genus of chondrichthyan that is characterized by greatly modified, spine-like, dermal denticles that attain a size of 10 mm or more. Crown elongate, resembling a feather, with a tapering shaft that may bifurcate distally. Shaft tear-drop shaped in cross section. Posterior portion of shaft laterally compressed and modified distally into several small, hooklike projections. Basal part of shaft marked by longitudinal ridges and sulci which are short anteriorly and elongate posteriorly. Crown at an angle of about 70 degrees to the base. Base small, triangular to oval, and concave.

**Type Species**.—*Nebraskella ossiani* n. sp.

*Nebraskella ossiani* n. sp.

Pl. VII, Figs. 11-13

"Listracanthus"-type spine, Ossian, 1974, p. 135-138, Pl. 6, fig. 13.

Subtype 128, Tway and Zidek, 1983, figs. 18a-b.

Characterization.—As for the genus, which is monotypic.

Holotype.—TMM 41647.92 (Texas Memorial Museum), Indian Cave Sandstone (Upper Pennsylvanian), Site 2 (Ossian, 1974, p. 315), Peru, Nemaha County, Nebraska.

**Referred Specimens**.—OSU 35449, Portersville, At-45B; OSU 35450a-c, Ames, Acn-31.
Distribution.- Upper Conemaugh of the Appalachian basin, Virgilian of the Midcontinent basin.

Etymology.- The genus is named for the state of Nebraska, where the holotype was collected, and the species is named in honor of Dr. Clair R. Ossian, who collected the holotype and first studied the Peru fauna.

Description.- Specimens in the collection are in the range of one to two millimeters in length, although the specimen illustrated by Ossian (1974, Pl. 6, fig. 13; see Fig. 59,), designated herein as the holotype, is approximately 10 mm in length. It is probable that most specimens are in the smaller size range.

Fig. 59.- Holotype of *Nebraskella ossiani* (TMM 41647.92) in lateral view. Posterior is to the left. Bar scale represents 1 mm. Redrawn from a photograph in Ossian (1974).
The crown consists of a long, tapering shaft that is set at an angle of about 70 degrees to the base. In cross section, the shaft is tear-drop shaped being wider anteriorly and becoming thin and compressed posteriorly. This shape and particularly the thin, compressed posterior part of the denticle gives it a superficial resemblance to a primary wing feather of a bird in which the vanes are developed principally on one side of the shaft. Distally, the shaft narrows to a sharp point but on one specimen in the collection (OSU 35449; Fig. 60. Pl. VII, Fig. 12), it bifurcates to form two short prongs. Posteriorly, the shaft is very compressed, forming a thin, sheetlike posterior extension to the main portion of the shaft. This compressed portion is widest basally and becomes reduced distally, disappearing about two-thirds of the distance from the base to the tip of the shaft. Distally, the posterior, compressed portion forms three or more hooklike projections. The shaft is ornamented with ridges and sulci that are short anteriorly but longer posteriorly, especially along the compressed portion.

The base is triangular to slightly oval in outline, widest anteriorly, and is concave on the underside. Several small nutrient foramina were noted on the underside of the base in some specimens in the collection.
Fig. 60.—Incomplete specimen (OSU 35449, Portersville, At-45B) of *Nebraskella ossiani* in A, lateral; B, anterior views. Bar scale represents 0.5 mm.

DISCUSSION

These comparatively large denticles are reminiscent of chondrichthyan median fin spines; however, like *Listracanthus*, they are actually highly modified dermal denticles. This fact is confirmed by the base of the denticle which lacks any structure for deep insertion into the integument. It is also apparent that they are complex, compound denticles that are the product of fusion of individual elements. In particular, the posterior portion of the denticle appears to be comprised of individual fused shafts.
Denticles herein assigned to a new species, *Nebraskella ossianii*, were first illustrated and briefly described by Ossian (1974). He reported a total of 303 specimens from two localities in Upper Virgilian strata of Nebraska. The specimen illustrated by Ossian (1974, Pl. 6, fig. 134, TMM 41647.92) is the best preserved example of this species and is designated as the holotype. The large sample of these denticles reported by Ossian merits restudy as does the remainder of his abundant chondrichthyan fauna.

Tway and Zidek (1983, figs. 18a-b) figured a specimen of *Nebraskella ossianii* that lacks the distal portion of the shaft. Tway (1982) reported these denticles in 17 samples from Virgilian strata of the Midcontinent. These specimens should also be examined in future studies of this species.

Ossian (1974) referred to these denticles as "Listracanthus"-type spines and suggested that they were derived from a cochliodont, *Deltodus*. He based this proposed association on a suggested synonymy in Romer (1966, p. 351) in which *Listracanthus* was questionably listed as a junior synonym of a Lower Carboniferous cochliodont, *Deltoptychius*. Romer's listing was derived from the work of Patterson (1965) in which compound denticles, that somewhat resemble *Listracanthus*, were
described in association with *Deltoptychius armigerus*. Ossian (1974) described these denticles in his discussion of *Deltodus*, teeth of which were abundant in the Peru fauna.

Neither the denticles of *Deltoptychius armigerus* described by Patterson (1965) nor the denticles herein assigned to *Nebraskella ossiani* are identical with those of *Listracanthus*, although all three of these denticles are similar in structure and function. Spinelike denticles of *Deltoptychius armigerus* resemble those of *Listracanthus* more closely than they do the denticles herein referred to *N. ossiani* although all three denticles differ sufficiently to leave little doubt that they were derived from different species of chondrichthyans. True *Listracanthus* "spines" are considerably larger than those of *N. ossiani* and occur primarily in Pennsylvanian black shales as a component of the Mecca fauna. Chorn and Reaves (1978) recently described a partial, articulated squamation of a Pennsylvanian chondrichthyan from the Midcontinent basin in which *Listracanthus* "spines" are associated with *Petrodus*-like denticles. The *Listracanthus* elements formed longitudinal rows on the back of this chondrichthyan. Zangerl (1981) noted that *Listracanthus* elements are indeed greatly modified dermal denticles rather than true spines.
It is probable that *Nebraskella ossiani* denticles formed a portion of the defensive armament of a chondrichthyan; very likely a cochliodont. Certainly, the direct association of similar denticles with a cochliodont, *Deltoptychius armigerus* (Patterson, 1965), is strong evidence in this regard. The fact that such denticles appear to have functioned as a spiny, protective covering of a bottom-dwelling (or at least bottom-feeding) chondrichthyan suggests that they may have been derived from a cochliodont, a group which probably was dominant among durophagous bottom feeders in Pennsylvanian seas. *Deltodus* would be a likely candidate for association with *N. ossiani* denticles; however, the relative abundance of teeth of *Deltodus* throughout the Pennsylvanian marine section and the apparent restriction of these denticles to Upper Conemaugh rocks would appear to suggest that they were derived from another cochliodont, the identity of which is uncertain at this time. Ossian (1974) reported large numbers of both *Deltodus* teeth and *N. ossiani* denticles in his Peru fauna. It is likely that *N. ossiani* denticles will not only be eventually correlated with teeth but also with another dentine form as well. Evidence presented by Patterson (1965) for *Deltoptychius armigerus* and the
evidence presented by Chorn and Reaves (1978) for Listracanthus suggests that these additional forms will prove to be Petrodus-like denticles.

Stratigraphic Distribution and Paleoecology.—Nebraskella ossiani denticles have been recovered in samples from seven localities in the Appalachian Basin. Five of these localities are in the Ames limestone and the other two localities are in the Portersville and Noble, respectively. It is probable that the stratigraphic distribution of these denticles is somewhat greater and future sampling may produce them from other units. Until such evidence is forthcoming, however, the distribution is restricted to the Upper Conemaugh of the Appalachian Basin, a distribution which agrees, in general, with the occurrence of denticles referable to this species reported by Tway (1982) and Ossian (1974) from Upper Virgilian rocks of the Midcontinent. All of these localities indicate normal marine conditions.

Occurrence.—Portersville, At-45B, (1); Noble, Nn-12, (1); Ames, Acn-31, (3); Gwi-3, (2); Gv-1, (1); MOm-1, (1); Nbu-4, (1).
Genus Ohioella n. g.

Characterization.- A genus of chondrichthyan characterized by comparatively large, compound denticles that exhibit considerable morphological variation and fusion of odontodes. Principal morphotype with a distally elongated crown that is compressed laterally. Anterior crown surface marked by several prominent ridges and sulci. Posteriorly, crown marked by less conspicuous ridges, especially along distal margin. Pedicel short and constricted. Base conical and marked by faint radiating ridges. Basal surface concave with concentric growth rings. Denticles of this morphotype may be fused in aggregates with a common base.

Another common morphotype consists of equidimensional denticles with short crowns and ridges radiating from a central point or central apical ridge. Distinct pedicel absent and base short and only slightly wider than the lateral dimension of the crown. Anterior and posterior surfaces not apparent on most specimens. A less common morphotype consists of greatly asymmetrical denticles that bear prominent ridges on one side and a smooth, deeply concave surface on the opposite side. Base very small.

Type Species.- Ohioella merrilli n. sp.
**Ohioella merrilli** n. sp.

Pl. IX, Figs. 1-17

Subtype 002, Tway and Zidek, 1982, figs. 18a-e.
Subtype 236, Tway and Zidek, 1983, figs. 66a-b.
Elasmobranchii denticles, Schultze, 1985, Fig. 2, nos. 4, 5, 6?, 8, 10, 11a-b, 12.
?Multidentodus gracilis, Harlton, 1933, p. 13-14, Pl. 3, figs. 5a-b.
?Subtype 098, Tway and Zidek, 1982, figs. 64a-e.

**Characterization.**—As for the genus, which is monotypic.

**Distribution.**—Pennsylvanian of the Appalachian Basin; Morrowan?, Virgilian, and Gearyan (Lower Permian) of the Midcontinent.

**Holotype.**—OSU 35446, "Lower Mercer" limestone, location Vel-34.

**Referred Specimens.**—OSU 35447a-h, 38659a-b, 38660, 38661, 38662.

**Etymology.**—The generic designation is in recognition of the state of Ohio. The specific name is in recognition of the work of Dr. Glen K. Merrill on the Pennsylvanian conodont fauna of the Appalachian Basin.
Description.- The holotype (OSU 35446, Fig. 61) is relatively small, about 0.9 mm in maximum dimension, in comparison to other specimens of this morphotype, some of which range to about 1.5 mm in maximum dimension. The crown is elongate, narrowed laterally, and possesses weakly developed lateral lobes. The anterior surface of the crown is marked by a prominent median keel and slightly smaller lateral keels or ridges. Deep sulci are present between the keels. The distal margin of the crown blade is marked laterally by two weakly developed notches or lobes. Posteriorly, the crown has a median ridge from which the surface slopes to the junctions with the lateral margins.

The pedicel is short and constricted. The base is conical and flares outward beyond the maximum lateral extent of the crown. Faint sulci and ridges form a radiating pattern on the base. The undersurface of the base is deeply concave and its margin is marked by a relatively thick ridge. A single, small foramen is present in the center of the base.

Other specimens of this morphotype (I) may exhibit additional ridges and sulci on the anterior surface and more serrations on the distal margins of the crown (Fig. 61). Some of these specimens also exhibit prominent, concentric growth rings on the under surface of the base.
Posteriorly, some specimens exhibit short, faint ridges and sulci near the distal margin. Additional specimens assigned to this morphotype appear to represent two or more fused denticles (Fig. 62). This appears to be a simple fusion along the lateral margins. The base commonly appears to be that of a single denticle.

Fig. 61.—Holotype of Ohioella merrilli (OSU 35446) from the "Lower Mercer" limestone at location Vel-34 and another specimen (OSU 35447) from the same locality in A and E, anterior; B and F, lateral; C and G, posterior; D and H, basal views. Both specimens are morphotype I. Bar scales represent 0.5 mm.
A second morphotype (II, Fig. 63), provisionally included with this species, has an elongate, pointed crown with only a single anterior median ridge and no development of lateral lobes. Posteriorly, the crown surface is smooth with only a median ridge. The pedicel is marked by only a slight constriction. The base is conical, flaring, and considerably broader than the width of the denticle crown. The base is marked by faint, spokelike, radiating ridges. The undersurface of the base is deeply concave.

Fig. 62.- Additional specimens of morphotype I of Ohioella merrilli. A, Fused denticles in anterior view, Skelley, location Nbu-3. B, Concentric growth rings on underside of denticle base, (OSU 35447), "Lower Mercer", location Vel-34. Bar scale represents 0.5 mm.
A third morphotype (III, Fig. 64) includes several varieties that appear to be variations on a theme. These denticles are nearly equidimensional, although a few specimens are slightly higher than they are wide. The crown consists of riblike ridges that radiate from a central axis and traverse the entire crown to the platelike base. Some of these ridges may exhibit a single bifurcation and many ridges, on unworn specimens, may have slight serrations or bumpy prominences. Many specimens are nearly circular in horizontal section whereas others are elongated and the ridges emanate from an apical ridge rather than from a central point. The simplest variety of this morphotype consists of two ridges that intersect at
right angles, forming a cross pattern when viewed apically. Anterior, posterior and lateral orientations are impossible to discern in most specimens, but a few exhibit a smooth, concave surface that is interpreted to be posterior (Fig. 64). A distinct pedicel is not discernable in most specimens. The base is thin and only slightly wider than the breadth of the denticle crown. The under surface of the base is concave and a foramen is evident on some specimens.

A fourth morphotype (IV, Fig. 66) is distinguished by a high degree of asymmetry. One surface of the crown is marked by prominent ridges and sulci that originate near the base and curve distally towards a prominent (posterior?) projection. The opposing crown surface is deeply concave and relatively smooth, except for faint ridges that may be present distally. The presumed posterior surface of the denticle is narrow basally and flares distally into a weakly pointed leaf shape. The basal two-thirds of this surface is marked by a prominent longitudinal ridge. When viewed apically, the crown ridges emanate from a longitudinal ridge. These denticles are asymmetrical to either right or left. The very thin base is concave on the under surface and relatively small in comparison to the size of the denticle.
Fig. 64.- Three examples of morphological transition within morphotype III of *Ohioella merrilli*. A, lateral; B, apical: Brush Creek limestone, location Aw-47. C, lateral; D, apical: Vanport limestone, location Ld-1. E, lateral; F, apical: "Lower Mercer" limestone, location Vel-34. Bar scale represents 0.5 mm.

DISCUSSION

The denticles included herein in *Ohioella merrilli* exhibit the greatest variation of any morphological transition series in the collection. It is probable that this transition series would not have been recognized if a relatively large collection of specimens had not been available. These facts demonstrate the difficulty in working with small collections of specimens and the possibilities that can be realized with relatively large collections.
Fig. 65.- Morphotype III of *Ohioella merrilli*. Note concave (posterior?) surface, which suggests a morphological transition between morphotypes I and III. Skelley limestone, location Nbu-3. A, anterior; B, lateral; C, posterior; D, apical; E, basal. Bar scale represents 0.5 mm.

There is some uncertainty in the grouping of all of these morphotypes in a single species. Morphological features common to all of these denticles include size, robust keels or ridges, and a blending of characteristics from one morphotype to another. In addition, the mutual occurrence of morphotypes contributes to the credibility of this grouping. Of the 33 localities that produced specimens (including one Oklahoma locality from which R. H. Mapes provided specimens) eight (25 percent) produced three morphotypes. Fourteen localities (44 percent) produced two or more morphotypes. No locality yielded all four morphotypes. Four localities, Vel-34 ("Lower
Mercer"), OK-2 (Atoka Formation), PA-3 (Ames), and Nbu-3 (Skelley), yielded a comparatively large number of specimens that suggest the proposed morphological transition series. In particular, location Nbu-3, a bone bed that contains specimens which have suffered postmortem abrasion, yielded a total of 68 specimens of *Ohioella merrilli*. These specimens exhibit a logical transition between morphotypes, except for morphotype II, which did not occur at this locality. It should be noted that at most of these localities (Table 13) specimens of *O. merrilli* occurred in low frequency— it is not surprising that not all morphotypes were represented.

The proposed morphological transition series for *Ohioella merrilli* is logical on the basis of mutual-occurrence data and particularly on the basis of morphological similarities of the denticles assigned to this species. Added evidence is derived from the variety of denticles of a Carboniferous chondrichthyan, *Helodus simplex*, illustrated by Patterson (1965). Although the denticles of *H. simplex* are not identical to those of *Ohioella merrilli*, they exhibit comparable variation and some of them bear a general resemblance to the latter species.
Fig. 66. - Morphotype IV of *Ohioella merrilli*. Skelley limestone, location Nbu-3. A, ridged lateral surface; B, concave lateral surface; C, presumed posterior; D, apical; E, basal. Bar scale represents 0.5 mm.

Specimens of morphotype I range from relatively simple forms to relatively complex ones that represent fusion of at least two and up to four denticles (each of which is composed of several odontodes) on a common base. Some specimens from Vel-34 ("Lower Mercer", OSU 35447) exhibit concentric growth rings on the underside of the base, thus confirming that they are fused denticles.

Morphotype II, of which only eight specimens were recovered, is the most uncertain in assignment to this species; they are provisionally placed here. The crowns of these specimens are relatively simple cones with only one
or two ridges on the anterior surface. They are interpreted to be relatively simple denticles that represent fusion of only a few lepidomoria. The bases of these denticles are relatively large in comparison to the crown. There is a possibility that these denticles were derived from a chondrichthyan species other than the one that bore denticles of *Ohioella merrilli*.

Morphotype III includes specimens with the greatest variability of any morphotype included in this species. These specimens, which are organized on a radial plan with spokelike ridges radiating from a central point or central axial ridge, include short, equidimensional varieties and higher, elongated varieties. The more equidimensional specimens resemble the common Carboniferous denticles known as *Petrodus*, but these two denticles are not identical. *Petrodus* denticles have fewer radiating ridges, have a thicker, convex (basally) base, and are considerably larger, up to 15 mm in maximum dimension (Zidek, 1973).

Chorn and Reaves (1978) have noted a biological association of *Petrodus* denticles with spinelike denticles of *Listracanthus*. Zangerl (1981) has also noted an association of *Petrodus* denticles with teeth of *Carcharopsis* cf. *C. prototypus* Davis 1883 in the Upper Mississippian Fayetteville Shale of Arkansas. Denticles
assigned to Petrodus have been reported from numerous units in Mississippian and Pennsylvanian rocks but it is uncertain at this time if they all belong to this precise denticle form as defined by Moy Thomas (1935). It is very possible that a wide variety of denticles of this general morphology have been incorrectly assigned to this genus. Noteworthy in this regard are specimens of Calopodus apicalis St. John and Worthen 1875 recently excavated by Dr. Rainer Zangerl from the Mecca fauna in Indiana. In addition to the teeth of C. apicalis, the slabs bear associated denticles of the Listracanthus form and denticles that resemble, but are not identical to, Petrodus. It is possible also that denticles of the general form of Petrodus occurred in several chondrichthyan species. Such robust denticles were probably excellent protection for the skin of bottom-dwelling chondrichthyans and, indeed, many denticles of the Petrodus form show strong abrasion (Zidek, 1973).

True Petrodus denticles are uncommon in Pennsylvanian rocks of the Appalachian Basin. None were recovered from the microscopic samples and about 20 specimens are in the macroscopic collection; all from either the Putnam Hill limestone or the Columbiana shale. In the Midcontinent and Eastern Interior Basins, Petrodus denticles are abundant (Zidek, 1973), and particularly in the black shales as
part of the Mecca fauna. Such black shales have not been recognized in the Appalachian Basin and the apparent associate of Petrodus, the spinelike denticles of Listracanthus, are also rare in the Appalachian basin. No specimens are in the OSU collection, although Newberry (1875) reported two specimens of Listracanthus, one of which was derived from the Washingtonville shale in Perry County, Ohio.

Denticles of morphotype IV are similar to the short-crowned ones of morphotype III except that they are compressed and asymmetrical. One side of these denticles, opposite the ridged surface, is nearly smooth and deeply concave (Fig. 66). This side of the denticle is interpreted to be a lateral side and suggests that such denticles were nested together in rows. The relatively low frequency of morphotype IV denticles and their right and left asymmetry suggests that they served a specialized function on opposite sides of the midline.

Of the great diversity of Pennsylvanian chondrichthyan denticles illustrated by Tway and Zidek (1982, 1983), only two specimens appear to be, with certainty, referable to Ohioella merrilli. Subtype 002 (1982, figs. 18a–e) is referable to morphotype I and subtype 236 (1983, figs. 66a–b) is referable to morphotype III. Subtype 098 (1982, figs. 64a–e) is a compound denticle that may possibly belong with this species.
Schultze (1985) illustrated several denticles from Gearyan (Lower Permian) rocks of Kansas that are probably referable to Ohioella merrilli. His specimens in Fig. 2, nos. 5, 8, and 11a-b, are referable to morphotype III. Specimens in Fig. 2, nos. 4, 10, and 12 appear to represent morphotype I. The specimen in no. 6 of this figure is questionably refered to this species.

Harlton (1933) illustrated a denticle, which he named Multidentodus gracilis, from Morrowan rocks of the Midcontinent, that has some general similarity to the denticles of morphotype I of Ohioella merrilli. If M. gracilis should prove to be conspecific with O. merrilli, then Multidentodus would be unavailable for these denticles because Harlton's (1933) type species of the genus, M. johnsvalleyensis, is a symmoriid branchial denticle.

The probable higher taxonomic affinities of Ohioella merrilli are uncertain at this time. These complex, compound denticles are, in part, of the general type that Reif (1978) referred to ctenacanths but, in my opinion, it is probable that they were derived from some other chondrichthyan group. As noted by Patterson (1965), these growing scales are relatively common in Paleozoic elasmobrachs. Dr. Rainer Zangerl (personal communication, 1985) suggested to me that the fused denticles of
morphotype I resemble those of eugeneodontids from the Mecca fauna. I am doubtful of this assignment, however, because teeth of eugeneodontids are extremely rare in the macroscopic collection from the Appalachian Basin. Certainly, careful comparison of eugeneodontic denticles with those of Ohioella merrilli is in order.

The large size of Ohioella merrilli denticles, the robustness of some morphotypes (especially morphotype III), and their obvious function as protection from abrasion, suggest that these denticles were derived from a durophagous chondrichthyan, possibly a cochliodont or a petalodont. Indeed, denticles of this species have a general resemblance to those of modern bottom-dwelling batoids (see Reif, 1979) and it is likely that similar modes of life were involved. Ohioella merrilli denticles and teeth of cochliodonts and petalodonts range through the entire Pennsylvanian marine sequence of the Appalachian Basin. The relative abundance of O. merrilli denticles, particularly in the Ames and Skelley limestones, suggests that they may have been derived from a cochliodont, Deltodus angularis, or a petalodont, Petalodus ohioensis, both of which are relatively common (as isolated teeth) in the Ames. They are also known from most other Pennsylvanian marine units.
Stratigraphic Distribution and Paleoecology.—Denticles of *Ohioella merrilli* range through the entire Pennsylvanian marine sequence of the Appalachian Basin; they were absent in samples from only the Boggs, Washingtonville, and Gaysport. It is likely that continued sampling would produce them in some, if not all, of these units also. As noted previously, these denticles have been illustrated from Virgilian rocks of the Midcontinent (Tway and Zidek, 1982, 1983) and from Gearyan (Lower Permian) rocks of Kansas (Schultze, 1985). Specimens of *O. merrilli* from Atokan rocks of Oklahoma have been provided by R. H. Mapes and are included in the OSU collection. Harlton's specimen of *Multidentodus gracilis*, possibly referable to *Ohioella*, is from Morrowan rocks. All of these units appear to represent normal marine conditions.

Occurrence.—Lowellville, Tfr-1, (1): "Lower Mercer", SCve-2, (1?); Vel-34, (8): Lower Mercer, MUm-3, (1); Sb-4, (2); T1-7, (4): Upper Mercer, Mbe-1, (1); Mp-3, (1); Ts-5, (1): Putnam Hill, Vel-15, (1): Vanport, Ld-1, (4); Td-4, (1); Vel-34, (1?): Brush Creek, Aw-47, (14): Cambridge, GAg-3, (1): Portersville, At-45B, (1): Noble, Go-1, (1): Ames, Aa-63, (1); Aam-19, (3); Acn-31, (8); At-45B, (2); Aw-58, (2); CAc-2, (4); Cma-10, (1); Gwi-3, (2); Gv-1, (9); HAr-1, (1): M0m-1, (1?); Nbu-4, (7); Pb-4, (3); PA-3, (13); PA-5, (1): Skelley, Nbu-3, (68): Atoka, OK-3, (13).
Table 13.— Frequency and distribution of morphotypes I, II, III, and IV of *Ohioella merrilli* denticles.

<table>
<thead>
<tr>
<th>UNIT</th>
<th>LOCALITY</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lowellville</td>
<td>Tfr-1</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>&quot;L. Mercer&quot;</td>
<td>SCve-2</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1?</td>
</tr>
<tr>
<td>&quot;</td>
<td>Vel-34</td>
<td>5</td>
<td>-</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>L. Mercer</td>
<td>MUm-3</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>Sb-4</td>
<td>2</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>T1-7</td>
<td>1</td>
<td>-</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>U. Mercer</td>
<td>Mbe-1</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>Mp-3</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>Ts-5</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Putnam Hill</td>
<td>Vel-15</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Vanport</td>
<td>Ld-1</td>
<td>-</td>
<td>-</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>&quot;</td>
<td>Td-4</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>Vel-34</td>
<td>1?</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Brush Creek</td>
<td>Aw-47</td>
<td>2</td>
<td>-</td>
<td>9</td>
<td>3</td>
</tr>
<tr>
<td>Cambridge</td>
<td>GAg-3</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Portersville</td>
<td>At-45B</td>
<td>-</td>
<td>1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Noble</td>
<td>Go-1</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Ames</td>
<td>Aa-63</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>&quot;</td>
<td>Aam-19</td>
<td>-</td>
<td>-</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>&quot;</td>
<td>Acn-31</td>
<td>1</td>
<td>-</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>&quot;</td>
<td>At-45B</td>
<td>-</td>
<td>1</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>Aw-58</td>
<td>-</td>
<td>-</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>&quot;</td>
<td>CAc-2</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>&quot;</td>
<td>Cma-10</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>Gwi-3</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>&quot;</td>
<td>Gv-1</td>
<td>1</td>
<td>-</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>&quot;</td>
<td>HAr-1</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>MOm-1</td>
<td>1?</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>Nbu-4</td>
<td>2</td>
<td>-</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>&quot;</td>
<td>Pb-4</td>
<td>3</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>PA-3</td>
<td>8</td>
<td>5</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>PA-5</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Skelley</td>
<td>Nbu-3</td>
<td>23</td>
<td>-</td>
<td>40</td>
<td>5</td>
</tr>
<tr>
<td>Atoka</td>
<td>OK-2</td>
<td>9</td>
<td>1</td>
<td>8</td>
<td>-</td>
</tr>
</tbody>
</table>
Genus *Sturgeonella* n. g.

Characterization.—A chondrichthyan genus characterized by small dermal denticles with a leaf-shaped blade that is at a high angle to the pedicel. Blade terminates distally in an acute median point. Anterobasal portion of blade lobate, divided into one to five ridges and intervening sulci; otherwise devoid of keels or other ornamentation. Pedicel short and developed only posteriorly. Pedicel/base subcircular and commonly multilobate with neck canals and a single basal foramen.

Type Species.—*Sturgeonella quinqueloba* (Gunnell 1933).

Etymology.—Named in honor of Dr. Myron T. Sturgeon, professor emeritus of geology at Ohio University, for his lifelong work on Pennsylvanian paleontology of the Appalachian Basin.

*Sturgeonella quinqueloba* (Gunnell 1933)

Plate X, Figs. 1-13

*Cooleyella quinqueloba*, Gunnell, 1933, p. 290, Pl. 33, Fig. 38.

*Cooleyella spatulata*, Gunnell, 1933, p. 290, Pl. 31, Fig. 64.

*Cooleyella quadrilobata*, Gunnell, 1933, p. 290, Pl. 32, Fig. 23.

*Cooleyella simplex*, Gunnell, 1933, p. 290-291, Pl. 33, Figs. 22-23.
Cooleyella cuspidata, Gunnell, 1933, p. 291, Pl. 32, Fig. 22.

Subtype 028, Tway and Zidek, 1982, Fig. 22a-e.
Subtype 054, Tway and Zidek, 1982, Fig. 26a-e.
Subtype 060, Tway and Zidek, 1982, Fig. 27a-e.
Subtype 064, Tway and Zidek, 1982, Fig. 28a-e.
Subtype 065, Tway and Zidek, 1982, Fig. 29a-e.
Subtype 072, Tway and Zidek, 1982, Fig. 30a-e.
Subtype 147, Tway and Zidek, 1982, Fig. 36a-d.
Subtype 158, Tway and Zidek, 1982, Fig. 39a-e.
Subtype 164, Tway and Zidek, 1982, Fig. 40a-e.
Subtype 190, Tway and Zidek, 1982, Fig. 41a-e.
Subtype 245, Tway and Zidek, 1982, Fig. 46a-b.

Distribution.- Pennsylvanian of the Appalachian and Midcontinent basins.

Referred Specimens.- OSU 38619, 38663a-b, 38664a-c, 38665a-b.

Description.- Denticles of this species range in size from slightly less than 0.5 mm to about 1 mm in maximum dimension. They are highly variable in morphology; however, these variations conform to a well-developed morphological transition series (Fig. 72).

The crowns are leaf-shaped when viewed anteriorly, are widest near the base, and taper apically and posteriorly to a sharp, narrow point. Approximately one-third of the
posterior part of the crown length overhangs the pedicel. The crown blade is at an acute angle to the plane of the base. The central portion of the anterobasal portion of the crown is characterized by one to at least five prominent, anteriorly projecting, longitudinal ridges. Between each ridge is a deep sulcus. Specimens with a greater number of ridges tend to be wider, more squat, and robust than those specimens with only one or two ridges. These ridges and their intervening sulci form the anterior base of the denticle. The distal half of the anterior crown blade is smooth and unornamented. Short, robust denticles with more numerous anterior ridges and sulci commonly exhibit either right or left asymmetry.

Posteriorly, the crown blade is concave and smooth except for a median ridge that extends from the apex of the blade to the base of the crown and onto the pedicel/base. The junction of the posterior part of the crown with the pedicel/base is marked by a sharp line that represents a change in angle from the undercut crown to the outflaring pedicel base.

The pedicel is very short and is well-developed only posteriorly where it is inseparable from the base. Commonly, the pedicel/base is subdivided into a series of longitudinal ridges and sulci—these features form a stellate pattern along the posterobasal margin of the
dentine. Neck canals may be present in the sulci of the posterior pedicel/base. The base is deeply concave and has a single basal foramen.

DISCUSSION

Gunnell (1933) described six species of Coolevella, and interpreted them all to be chondrichthyan dermal denticles. However, the type species of the genus, C. peculiaris, is herein recognized as a tooth of a neoselachian shark. The remaining species that Gunnell placed in this genus are all dermal denticles of uncertain higher taxonomic affinities and they appear to be part of a morphological transition series. Coolevella should not, therefore, be used for these denticles (unless it should be demonstrated that these denticles are from the same shark that bore C. peculiaris teeth). Sturgeonella, is therefore proposed for those dermal denticles formerly placed in Coolevella.

![Fig. 67.- Holotype of Coolevella quinqueloba Gunnell 1933 (UM 520-4), herein designated as the type species of Sturgeonella. A, anterior; B, posterior; C, lateral; D, apical. Bar scale represents 0.5 mm.](image-url)
Of Gunnell's (1933) species assigned to *Cooleyella*, other than *C. peculiaria*, any of them could equally well serve as the type species of *Sturgeonella*. *Cooleyella spatulata*, the first species described by Gunnell (1933, p. 290) is represented by a holotype (UM 501-5) that is badly fractured and therefore impossible to manipulate on the microslide for observation of various perspectives (Fig. 68). This specimen is unsuitable, therefore, to represent the type species of the genus. The next species to be described by Gunnell (1933), other than *C. peculiaria*, was *C. quinqueloba*. The holotype of this species (UM 520-4), from the Americus Limestone, is therefore designated as type species of *Sturgeonella* (Fig. 67).

Fig. 68.- Holotype of *Cooleyella spatulata* Gunnell 1933 (UM 501-5), designated herein as a synonym of *Sturgeonella quinqueloba*. The specimen, depicted here in anterior view, is badly fractured (note black areas) and cannot be manipulated for additional perspectives. Bar scale represents 0.5 mm.
Gunnell's (193) holotypes of Coolevella quadrilobata (UM 508-1), Fig. 69, C. simplex (UM 518-1), Fig. 70, and C. cuspidata (UM 507-5), Fig. 71, are well-preserved denticles that appear to vary from C. quinqueloba only in
the number of ridges on the anterior portion of the crown. They form a well-developed and clearly discernible morphological transition series and without question they are placed in synonymy with *Sturgeonella quinqueloba*.

The Appalachian Basin sample of *Sturgeonella quinqueloba* denticles is comparatively large (332 specimens); and several samples produced multiple examples that demonstrate morphological transition from those with a single basal-median ridge on the blade to those with five basal-median ridges on the blade (Fig. 72). There is considerable morphological variation within each step of this transition series, including examples that are asymmetrical to either right or left. However, all of these denticles exhibit sufficient morphological similarity to suggest that they doubtlessly represent a single chondrichthyan species.

This morphological variation and transition is well illustrated by a variety of denticles figured by Tway and Zidek (1982) that are herein placed in synonymy with *Sturgeonella quinqueloba*. Additional denticles illustrated by these authors (Subtypes 003, 090, 116, and 219) may also possibly belong to this species. *S. quinqueloba* denticles illustrate, perhaps as well as any others, the difficulties with the artificial taxonomic system employed by Tway and Zidek (1982, 1983).
Fig. 71.- Holotype of Cooleyella cuspidata Gunnell 1933 (UM 507-5), herein designated a synonym of Sturgeonella quinqueloba. A, anterior; B, posterior; C, lateral; D, apical. Bar scale represents 0.5 mm.

Sturgeonella quinqueloba scales are of a placoid design and are similar in general morphology to those of some neoselachian sharks (see Bigelow and Schroeder, 1948). The only neoselachian shark identified in the fauna on the basis of isolated teeth is Cooleyella peculiaris. Occurrence data for Cooleyella peculiaris teeth and Sturgeonella quinqueloba denticles indicate that 22 localities (37 percent) yielded both these teeth and denticles. A total of 37 localities (63 percent) yielded either one or the other but not both. Such figures do not indicate a strong correlation between the mutual occurrences of these denticles and teeth; however, most samples yielded only a few specimens of either one, suggesting that large samples may exhibit a stronger correlation. Nevertheless, at the current level of understanding of denticle designs associated with various
groups of Paleozoic chondrichthyans, it would be premature to assign Sturgeonella quinqueloba denticles to Cooleyella pecularia.

Additional evidence on possible affinities of Sturgeonella quinqueloba denticles was provided, inadvertently, by Pomesano Cherchi (1967) who described five new species of presumed conodonts of the new genus Nurrella from Middle Triassic rocks of Sardinia. All of these specimens are, without doubt, chondrichthyan dermal denticles and some of them bear a superficial resemblance to Pennsylvanian denticles herein assigned to Sturgeonella or Cooperella. In particular, Nurrella citae resembles Sturgeonella quinqueloba. Denticles of Nurrella differ from those of Sturgeonella in the shape of the base, which bears an anterior projection, the presence of a well-defined pedicel, particularly anteriorly, and in details of the anterobasal ridges.

There is little question that Sturgeonella and Nurrella denticles are generically distinct; however, their overall similarity suggests, perhaps, that they were derived from the same group of chondrichthyans. Of the Pennsylvanian chondrichthyan groups known from the Appalachian Basin only hybodonts and neoselachians survived into the Triassic, suggesting, therefore, that Sturgeonella quinqueloba denticles may have been derived
from a hybodont or a neoselachian. Mutual-occurrence data have been presented above for *Sturgeonella quinqueloba* and *Coolevella peculiaris*. Similar comparisons between the mutual occurrence of *S. quinqueloba* and the most abundantly represented hybodont in the fauna, *Maisevodus johnsoni*, yielded identical results. A total of 24 localities (37 percent) yielded both *S. quinqueloba* denticles and *M. johnsoni* teeth. A total of 41 localities (63 percent) yielded either one or the other but not both. Obviously, these data are of little assistance in determining if *S. quinqueloba* denticles were derived from *Coolevella peculiaris* or *Maisevodus johnsoni*. Based upon present knowledge and information, it is probable that these denticles represent one or the other of these species as defined by teeth. Larger samples may perhaps shed light on this problem.
Fig. 72.- Morphological transition series of *Sturgeonella quinqueloba* denticles as illustrated by specimens (USU 35444) from location Mp-3, Upper Mercer limestone. A-C, dentele similar to the holotype of *S. quinqueloba* in apical, anterior, and lateral views. D-F, dentele similar to the morphotype named *Cooleyella simplex* by Gunnell, in apical, anterior, and lateral views. H-J, dentele similar to the morphotype named *Cooleyella cuspidata* by Gunnell, in apical, anterior, and lateral views. Bar scale represents 0.5 mm.
Stratigraphic Distribution and Paleoecology.—*Sturgeonella quinqueloba* denticles occur throughout the Pennsylvanian marine section, only being absent from samples from the Boggs, Columbiana, Washingtonville, and Gaysport. All of these units were sampled at only a few localities, suggesting that more extensive sampling would yield *S. quinqueloba* denticles from these units also.

All of the rocks that yielded *Sturgeonella quinqueloba* denticles suggest deposition in a normal marine environment. The morphology of *S. quinqueloba* denticles indicates streamlining for effective channeling of water over the body surface while also protecting the skin from parasites and abrasion. The relatively short, robust denticles may have been derived from snout regions, whereas the more elongate ones were probably derived from flank areas. In general, these denticles do not suggest a shark with swimming abilities as rapid as do those denticles assigned to *Cooperella*. Indeed, the shark that bore *S. quinqueloba* denticles may have been a bottom feeder capable of short, rapid bursts of speed.
Occurrence.— "Lower Mercer", Vel-7, (73); Vc-9, (1): Lower 2, (3); Sb-4, (2): Upper Mercer, Mp-3, (38): Putnam Hill, CSo-2, (3); MUsp-1, (1); Td-4, (14); Tg-6, (4); Sc-6, (1): Vanport, Ld-1, (10); Lw-2, (6); SCve-3, (1); Vel-31, (1); Vr-2, (1): Lower Brush Creek, At-9, (5); Aw-47, (15): Cambridge, Gca-5, (5); GAgr-2, (16); GAgr-3, (3); GAP-4, (5); GAs-1, (13); Nn-13, (6): Portersville, Acn-31, (9); At-45B, (3); Aw-47, (14): Noble, Nbu-1, (14); Nn-12, (4): Ames, Aam-19, (3); Acn-31, (9); At-45B, (1); Cma-10, (4); Gwi-3, (11); HAr-1, (1); Nn-3, (6); Pb-4, (5); PA-3, (17); PA-4, (2).
Genus *Twayella* n. g.

Characterization.—A genus of chondrichthyan characterized by comparatively large, composite denticles with a laterally compressed, elongate crown that is commonly concave anteriorly and marked by elongate, overlapping elements. Posteriorly, crown smooth with a prominent median ridge. Base prominent posteriorly, triangular to lobate, with a robust median ridge. Posterolateral sides of base slightly to strongly concave with one or two small neck canals on each side. Undersurface of base concave, with irregular surface and one or more foramina.

Type Species.—*Twayella zideki* n. sp.

*Twayella zideki* n. sp.

Pl. VIII, Figs. 18-22

Shark dermal denticle I, Ossian, 1974, p. 147, Pl. 8, figs. 5, 6.

Subtype 230, Tway and Zidek, 1982, Figs. 45a-d.

Holotype.—OSU 35448, Ames limestone, location Acn-31.

Referred Specimens.—OSU 38627, Portersville, At-45B.

Distribution.—Conemaugh of the Appalachian Basin; Virgilian of the Midcontinent.
Etymology. - Named in recognition of the work of Drs. Linda E. Tway and Jiri Zidek on microscopic chondrichthyan remains from Pennsylvanian rocks.

Description. - The holotype (OSU 35448, Fig. 73; Pl. VIII, Figs. 18-20) is 1.3 mm in length and 0.5 mm in maximum width. This specimen, as are nearly all examples of this species in the collection, is incomplete. It lacks the distal portion of the crown tip and a portion of the base.

The crown of the holotype exhibits at least five separate fused elements anteriorly, the most prominent of which form robust, anteriorly-projecting lateral margins. The central elements are the smallest and are overlapped by lateral ones. The anterior surface is deeply concave, particularly basally. The anterior crown elements, particularly the lateral ones, exhibit fine, slightly sinuous ridges or cristae. Posteriorly, the crown surface is smooth and dominated by a median ridge that becomes more prominent basally.

Most of the posterior part of the denticle base is missing on the holotype but this specimen exhibits part of a posterior projection and a relatively deep, broad, concave area on either side of the median ridge of the base. Two small neck canals (nutrient foramina) are
present on the left side of the posterior part of the denticle, in the concave area. One canal opening is present on the right side.

Fig. 73.- Holotype of *Twayella zideki* (OSU 35448) from the Ames limestone at location Acn-31. A, anterior; B, lateral; C, posterior. Bar scale represents 0.5 mm.

Additional specimens in the collection yield information on the variation exhibited by these denticles. The simplest forms have crowns with a central elongate element and two lateral elements that converge apically to form a sharp point (Fig. 74; Pl. VIII, Figs. 21-22). Some specimens exhibit a relatively short, broad crown.

The base of OSU 38627 is triangular, projects posteriorly, and has a prominent median ridge. On most specimens, the posterolateral edges of the base are
relatively straight; however, on some specimens these portions of the base exhibit one or two lobes on each side. The denticle base of some specimens is visible on the anterior portion as a short, anteriorly flaring, sometimes slightly lobate, structure. The underside of the base is shallowly concave, sometimes roughened and irregular, and may have one or more foramina.

Fig. 74.- Specimen of *Twayella zideki* illustrating simple fusion of only a few odontodes. OSU 38627, Portersville, At-45B. A, anterior; B, lateral; C, posterior. Bar scale represents 0.5 mm.

**DISCUSSION**

Denticles placed in *Twayella zideki* are distinctive composite denticles. Some short, squat specimens of *T. zideki* have a general, superficial resemblance to some specimens of *Sturgeonella quinqueloba*; however, those of the latter species are considerably smaller and are placoid denticles, not composite denticles as are those of *Twayella zideki*. 
Denticles of *Williamsella typicalis* Gunnell 1933 have a general resemblance to some of those of *Twayella zideki* in that both are compound denticles composed of elongate elements and both are compressed in the anteroposterior dimension. They differ greatly, however, in size, configuration of the base, and in gross morphology. There is a possibility, however, that the specimen assigned to *Williamsella?* sp. by Gunnell (1933, p. 296, Pl. 32, fig. 25) is referable to *T. zideki*. A specimen assigned by Gunnell (1933, p. 296, Pl. 33, fig. 29) to *Williamsella typicalis* may also belong with *T. zideki*.

The compound nature of the denticles of *Twayella zideki* is illustrated by the specimen figured by Tway and Zidek (1982, Fig. 45a-d), especially in their figures 45c-d in which a central core element can be discerned. At least four other elements surround this central core element. Several broken specimens in the collection exhibit features similar to the specimen illustrated by Tway and Zidek.

Ossian (1974) illustrated a perfect specimen of a *Twayella zideki* denticle from the Indian Cave Sandstone of Nebraska. This specimen illustrates the commonly lobate, posterior projecting base of these denticles.

*Twayella zideki* denticles are robust and would have provided protection to the skin of the chondrichthyan that bore them. Many *T. zideki* denticles in the collection
exhibit abrasion along their distal portions. This abrasion is apparently antemortem as judged by the fact that denticles and teeth from other species in the same sample appear fresh and unabraded. Although T. zideki denticles are moderately streamlined, they do not suggest a fast-swimming chondrichthyan.

There is little evidence at this time with which to speculate on the identity (as based on teeth) of the chondrichthyan that bore T. zideki denticles. Likely candidates for this association are petalodonts or cochliodonts. The apparent restriction of these denticles to Conemaugh rocks is excellent evidence for comparison with similarly restricted teeth; however, at this time no teeth are known to be so restricted in their stratigraphic distribution.

Stratigraphic Distribution and Paleoecology.—A total of 54 denticles of T. zideki were recovered in samples from 13 localities representing five stratigraphic units. All of these units are in the Conemaugh Group. Only the Brush Creek and Gaysport limestones in the Conemaugh did not produce specimens. Most localities produced only a few specimens, although 22 denticles of this species were recovered from the Skelley limestone bone bed at location Nbu-3. Owing to the low frequency of these denticles in the samples there is a possibility that they will
eventually be recovered from older marine units. At this time, however, it appears that *T. zideki* denticles are indicative of Conemaugh strata.

The specimen illustrated by Tway and Zidek (1982) and the specimen illustrated by Ossian (1974) are from Virgilian rocks of the Midcontinent, an occurrence that does not contradict the apparent limited stratigraphic range of these denticles in the Appalachian Basin. Denticles of *Twayella zideki* may be of biostratigraphic value, although their relatively low frequency of occurrence would be a limitation in this regard. All units that produced these denticles appear to represent deposition under normal marine conditions.

**Occurrence.**—Cambridge, Nn-13, (2); Portersville, At-45B, (1); Aw-47, (5); Noble, Nbu-1, (4); Ames, Acn-31, (2); Aw-58, (1); CAc-2, (1); Cma-10, (2); Gwi-3, (1); Nbu-4, (2); PA-4, (3); Skelley, Gv-1, (8); Nbu-3, (22).
Genus *Williamsella* Gunnell 1933

Characterization.- A genus of chondrichthyans characterized by complex, composite denticles with an antero-posteriorly compressed and posteriorly overhanging crown blade that is composed of fused odontodes. Dentine base small, oval, and concave with concentric growth rings.

Type Species.- *Williamsella typicalis* Gunnell 1933

*Williamsella typicalis* Gunnell 1933

Pl. X, Figs. 16-17

*Williamsella typicalis*, Gunnell, 1933, p. 296, Pl. 32, fig. 21; Pl. 33, fig. 28.

?*Williamsella typicalis*, Gunnell, 1933, p. 296, Pl. 33, fig. 29.

*Williamsella*? sp., Gunnell, 1933, p. 296, Pl. 32, fig. 25.

Subtype 082, Tway and Zidek, 1982, figs. 63a-c.

?Subtype 230, Tway and Zidek, 1982, figs. 45a-d.

Characterization.- *Williamsella* denticles which are laterally compressed and with a small number (less than 7) of coarse, interwoven, overlapping odontodes.


Distribution.- Pennsylvanian of the Appalachian Basin; Missourian and Virgilian of the Midcontinent.
Description.- The following description is based on observations of the holotype, specimens in the Appalachian basin collection, and specimens illustrated by Tway and Zidek (1982). The crown is relatively narrow in the lateral dimension, distally elongate, and compressed in the antero-posterior dimension. The crown is greatly extended, posteriorly, over the base, is convex anteriorly, and concave posteriorly. The anterior surface of the crown is marked by several large, coarse, smooth ridges (odontodes) that commonly overlap one another distally. In particular, the outermost lateral ridges appear to overlap those located in medial positions. Commonly, the central ridge or odontode is visible only near the base.

The denticle base is circular to elliptical in shape, concave on the basal surface, and commonly exhibits one or more small basal foramina. Some specimens exhibit several concentric, partially overlapping growth rings on the base. A foramen may be associated with each growth ring.

DISCUSSION

Gunnell (1933) described two species of Williamsella, W. typicalis and W. striata. The former was designated as the type species of the genus. The holotype of W. typicalis (UM 507-4, Fig. 75) is from the Cherryvale Shale
at Kansas City, Missouri. This specimen is well-preserved; however, it lacks the distal portion of the crown. The holotype does not exhibit complex overlapping of the crown ridges--these structures are relatively straight and parallel to one another. As only the basal portion of this denticle is preserved, it is possible that the ridges, of which there are only three visible on the specimen, overlapped in the distal (and missing) part of the denticle. The specimen assigned to *Williamsella* sp. by Gunnell (1933) does exhibit the overlapping ridges and is herein assigned to *W. typicalis*. This specimen lacks the denticle base.

![A B C](image)

**Fig. 75.** Holotype (UM 507-4) of *Williamsella typicalis* Gunnell 1933, from the Cherryvale Shale (Virgilian) at Kansas City, Missouri. A, anterior; B, posterobasal; C, lateral. Bar scale represents 0.5 mm.

Two additional specimens referred by Gunnell (1933, Pl. 33, figs. 28-29) to *Williamsella typicalis* deserve further comment. The specimen in Gunnell's figure 28, illustrated with the denticle base to the left, appears to
with the denticle base to the left, appears to exhibit the coarse-ridges that are characteristic of this species. The specimen in Gunnell's figure 29 appears to have only two coarse ridges, on the lateral margins, and a relatively broad base. This specimen is questionably included in this species.

Tway and Zidek (1982, figs. 63a-c) illustrated a denticle referable to *Williamsella typicalis* (subtype 082). This specimen clearly exhibits concentric and overlapping growth rings on the basal surface. In addition, two other scales illustrated by these authors may be referable to this species. Subtypes 098 and 210 (Tway and Zidek, 1982, figs. 64a-c; figs. 67a-b) appear to be of the general form of *Williamsella* denticles; however, the anterior ridges are considerably less robust and these specimens bear ridges on the posterior part of the crown blade. Subtype 230 (Tway and Zidek, 1982, figs. 45a-d) appears to be a composite scale with robust anterior ridges or odontodes, but it has an expanded base quite unlike that seen in typical scales of *Williamsella*. It is probable that this specimen belongs in another species.

Complex, composite denticles of the general morphology of *Williamsella typicalis* and *W. striata* have been assigned by Reif (1978) to ctenacanthid sharks, principally on the basis of their occurrence on an Early
Carboniferous ctenacanthid, *Ctenacanthus costellatus* Traquair 1884. Such scales are known by isolated examples from rocks ranging in age from Middle Devonian through Triassic. The stratigraphic range of these denticles appears to coincide, in general, with the stratigraphic range of median fin spines of the *Ctenacanthus* morphotype (see Maisey, 1984, for a review of these spines).

The composite scales of ctenacanths are of the growing or composite type, as defined by Reif (1978), and increase in size and complexity by addition of new elements to the lateral margins of the scales. These individual elements are termed odontodes in the terminology of Orvig (1977). According to Reif (1978) there is no positive evidence that these scales were shed.

The oldest known scales of the general ctenacanth morphotype were named *Cladolepis gunnelli* by Wells (1944) and are well known from Middle Devonian rocks of the central United States. They were also illustrated by Gross (1973). These scales have a general resemblance to those of *Williamsella striata* but are certainly not identical to this species. Scales illustrated by Reif (1978), from ctenacanths or presumed ctenacanths, have a general resemblance to scales of *Williamsella* but, again, they are not identical. *Phoebodus heslerorum*, a Pennsylvanian
ctenacanth described by Williams (1985), has composite scales of the *Williamsella* morphotype (see below) as does another ctenacanth, *Bandringa rayi* Zangerl 1969.

It should by noted that composite scales also occur in other groups of Paleozoic chondrichthians. Zangerl (1966, 1968) has noted this general morphotype in *Orodus* and in a eugeneodontid. Detailed comparisons of these scales with those from ctenacanths may reveal morphological differences between the groups but at present it appears that some caution is in order in higher taxonomic assignments.

Young (1982) illustrated scales of the general ctenacanth morphotype that were derived from *Antarctilamna prisca*, a shark which he interpreted to be a xenacanth on the basis of diplododont teeth. As noted in the Discussion of *Xenacanthus tridentatus*, *A. prisca* could alternatively be interpreted as a ctenacanth or perhaps as a primitive xenacanth that retained a number of plesiomorphous characters.

The scales of an Early Carboniferous xenacanth, *Diplodoselache woodi* Dick 1981, are of the composite type and bear a general resemblance to scales of *Orodus* described by Zangerl (1968). These scales are less like those of the ctenacanth-scale morphotype as defined by Reif (1978) than are the scales of *Antarctilamna prisca*.
The only teeth in the OSU collection, either macroscopic or microscopic, that appear to be assignable to ctenacanth sharks are *Phoebodus heslerorum* Williams 1985 and *Zangerlodus williamsi* n.g., n.sp. The two specimens of *Williamsella typicalis* in the collection did not occur at the same localities as did either of these ctenacanth species defined by teeth. *Phoebodus heslerorum* can be eliminated from consideration as the bearer of the denticles of either species of *Williamsella*. Although the exact morphology of *P. heslerorum* scales is unclear in Williams' (1985) photographs, he has indicated to me (personal communication, 1985) that the figures of *W. typicalis* and *W. striata* scales in Tway and Zidek (1982) are unlike the denticles of *P. heslerorum*. Williams indicated that the denticles of *P. heslerorum* consist of odontodes attached to one another near the denticle base but, in the distal portion of the denticle, the odontodes are separate, fingerlike structures.

With present data, therefore, the most parsimonious procedure appears to be to retain *Williamsella typicalis* as a distinct species. The scales of *W. striata*, as discussed more fully in the Discussion of that species, may have been derived from the shark that bore *Zangerlodus williamsi* teeth.
Additional possibilities to be considered are that the scales of Williamsella were derived from the xenacanth in the fauna, Xenacanthus tridentatus, or from an orodontid or eugeneodontid. It is improbable that X. tridentatus bore these scales, as the teeth of this species do not occur at localities yielding Williamsella denticles. Denticles of both species of Williamsella occur stratigraphically higher than do teeth of X. tridentatus. Teeth of orodontids and eugeneodontids are very rare in Pennsylvanian rocks of Ohio; only a few specimens are known from the OSU macroscopic collection. In addition, denticles of Orodus and Eugeneodus illustrated by Zangerl (1968, 1981) differ considerably from those of either species of Williamsella.

Stratigraphic Distribution and Paleoecology.—Scales of Williamsella typicalis are rare in the OSU collection, with only two examples known. Ironically, these two specimens occurred at opposite ends of the Pennsylvanian sequence of marine rocks, one specimen being derived from the "Lower Mercer" at location Vc-8 and the other specimen being derived from the Skelley at location Nbu-3. It is apparent from these data and from the record for Gunnell's holotype of W. typicalis, from the Cherryvale Shale (Kansas City Group, Virgilian), and from the Virgilian
specimens of Tway and Zidek (1982), that the shark that bore these denticles ranged through the entire Pennsylvanian.

Interestingly, the two localities that yielded *W. typicalis* denticles did not yield denticles of *W. striata*; however, the frequency of both of these denticles is relatively low in most samples examined in this study.

Williamsella striata Gunnell 1933
Pl. X, Figs. 14-15

*Williamsella striata*, Gunnell, 1933, p. 296, Pl. 33, fig. 48.

Subtype 049, Tway and Zidek, 1982, figs. 58a-c.

Elasmobranchii scale, Schultze, 1985, fig. 2, no. 7.

Characterization.- Denticles of *Williamsella* that are characterized by quadrangular to laterally elongate crowns that bear fused, triangle-shaped, complexly overlapping odontodes on their anterior surfaces. Dentine base oval to ellipsoidal with concentric, overlapping growth rings.

Refered Specimens.- OSU 38617, Upper Mercer, Ty-7; OSU 38626, Aw-47.

Distribution.- Pennsylvanian of the Appalachian and Midcontinent Basins; Lower Permian of the Midcontinent.

Description.- These denticles range in shape from quadrangular to very laterally elongate specimens. The crown blade is compressed in the antero-posterior dimension, convexo-concave, and overhangs the base in a posterior direction. The anterior surface of the crown is composed of numerous fused, triangle-shaped, overlapping odontodes. Each odontode has a shallow vertical sulcus in its median portion and may be marked by two or three faint vertical ridges. The odontodes appear to be compressed in
an antero-posterior dimension and are fused throughout
their lengths. The posterior surface of the crown is
concave, smooth, and lacks any ornamentation or indication
of fused odontodes. Several neck canals may be present
posteriorly at the junction of the base and crown.

The denticle base is oval to ellipsoidal, concave
basally, and on some specimens exhibits well-developed,
concentric, overlapping growth rings. A basal canal may be
associated with each growth ring. Anteriorly, the denticle
base may not be visible or only slightly so, whereas
posteriorly, the base forms a small shelf.

DISCUSSION

Gunnell (1933) named Williamsella striata as a second
species of this genus; W. typicalis was designated as the
type species. The holotype of W. striata (UM 522-4, Fig.
76) is a well-preserved specimen from the Americus
Limestone (Wabaunsee Group, Virgilian) near Bellvue,
Kansas.

Williamsella striata denticles are clearly of the
tenacanth morphotype (sensu stricto) as defined by Reif
(1978) and exhibit nearly complete fusion of numerous
odontodes. This species is retained in Williamsella for
convenience at this stage of knowledge because these
denticles have a general similarity to those of W.
The possibility cannot be ruled out at this time that *W. typicalis* and *W. striata* were derived from the same shark species.

Fig. 76.—Holotype (UM 522-4) of *Williamsella striata* Gunnell 1933, from the Americas Limestone (Wabaunsee Group, Virgilian). A, anterior; B, posterior; C, posterobasal; C, lateral. Bar scale represents 0.5 mm.

Tway and Zidek (1982, figs. 58a-c) illustrated an excellent example of a *Williamsella striata* denticle from Virgilian rocks of the Midcontinent basin. Schultze (1985) figured another example from Lower Permian (Gearyan) rocks of Kansas.

Based on the assumption that Reif (1978) was correct in assigning this denticle morphotype to ctenacanth sharks, the search for the probable bearer of *Williamsella striata* denticles is narrowed considerably. One ctenacanth in the fauna, *Phoebodus heslerorum*, can be ruled out as a
candidate on the basis of lack of mutual occurrence of these teeth with *W. striata* denticles and, more importantly, by the observations of Michael Williams (personal communication, 1985) who indicated to me that *W. striata* denticles are unlike those he described in association with other skeletal material of *P. heslerorum*. The only other teeth in the fauna that can be construed as being derived from a ctenacanth are those of *Zangerlodus williamsi* n. g., n. sp. The stratigraphic ranges of these teeth and *W. striata* denticles agree in general and 47 percent (7 of 15) of the localities that yielded *Williamsella striata* denticles also yielded teeth of *Zangerlodus williamsi*. The evidence is not overwhelming that *W. striata* denticles were derived from the shark that bore *Z. williamsi* teeth; however, I have strong suspicions that this was the case.

**Stratigraphic Distribution and Paleoecology.** - A total of 15 localities yielded *Williamsella striata* denticles in low frequencies except for location PA-3, from which 19 specimens were recovered. These denticles are most abundant in Conemaugh rocks; every unit except the Noble and Gaysport yielded examples. Only the Putnam Hill limestone yielded examples from the Allegheny Group and only the Upper Mercer limestone of the Pottsville Group produced specimens. All of these localities appear to represent normal marine conditions.

Characterization.—A chondrichthyan that is characterized by relatively large, robust, compound denticles with a crown consisting of several stout, ridged, tapering, posteriorly projecting elements that are largest laterally and smaller medially, forming a bilobed crown. Base quadrangular, convex, and smooth. Neck canals (nutrient foramina) present on posterior portion of crown just above base/crown junction.

Referred Specimens.—OSU 35190a, Cambridge, Ale-19; OSU 38604, Skelley, Nbu-3.

Distribution.—Conemaugh of the Appalachian Basin.

Description.—These denticles are about 2 mm or less in maximum dimension. The crown consists of up to five, or possibly more, fused elements. Each element is broad basally, and tapers apically to a sharp, posteriorly projecting point. The anterior surface of each element is marked by two or three coarse, longitudinal ridges, between which are broad, shallow sulci. Posteriorly, the crown elements are relatively smooth. The medial crown elements are the smallest and are overlapped laterally by larger elements. This circumstance gives a bilobed appearance to many specimens (Fig. 77).
The base is quadrangular in outline and broader than the crown, forming a shelf around the base of the crown. The undersurface of the crown is highly convex anteriorly and commonly concave along the posterior margin. The surface of the base is very smooth and polished with no evidence of foramina or other irregularities. Several irregular neck canals (nutrient foramina) are present on the posterior portion of the crown, just above the base/crown junction.

**DISCUSSION**

These denticles are of the compound variety, consisting of several fused elements. It is obvious that the larger lateral elements were added later and that the smaller medial elements were the first formed.
The smooth, quadrangular, highly convex bases of these denticles are reminiscent of those found on scales of acanthodians and on a Pennsylvanian chondrichthyan, "Holmsella". As noted by Orvig (1966) and Zangerl (1968), "Holmsella" scales are truly those of chondrichthyans, as is demonstrated by their compound nature. The same evidence applies to the denticles under consideration here, which are quite obviously compound denticles of a chondrichthyan. These denticles are distinct from those of "Holmsella" and differ from the latter taxon by the presence of much larger and fewer crown elements. Scales of precisely this morphology were not reported by Orvig (1966) in the articulated squamation of "Holmsella". These denticles have a general resemblance to those of Maplemillia costata Gross 1973, from Upper Devonian rocks of Iowa.

A denticle very similar to those under discussion was figured and described by Lund (1970) as a denticle of a nonmarine hybodontid, Hybodus allegheniensis. I have examined Lund's specimens and can see no particular difference between them and dermal denticle "A"; they are conspecific. Lund's (1970) species was defined by a fragmentary median fin spine associated with isolated teeth and denticles in residues obtained by acid treatment of samples of the Duquesne limestone (Conemaugh) from
Pittsburgh, Pennsylvania. There does not appear to be any reason to doubt that the scale figured by Lund (1970; Fig. 78 herein) was derived from a nonmarine limestone, although there is no compelling reason to associate these denticles with the hybodontid teeth and spines, other than mutual occurrence at this one locality.

Fig. 78.- Dentine (CM 19136) from the nonmarine Duquesne limestone at Pittsburgh, Pennsylvania assigned by Lund (1970) to Hybodus allegheniensis. A, anterior; B, lateral. From Lund (1970, fig. 5). Bar scale represents 1.0 mm.

Specimens of dermal denticle "A" in the OSU collection were derived from undoubted marine units except, possibly, those from locations Ale-19 and Nbu-3. The former locality contains a mixture of both marine and nonmarine chondrichthyan remains whereas the latter locality is less certain in this regard. Twenty denticles of this morphotype were obtained from location Ale-19 ("Buffalo"
sandstone; Cambridge equivalent according to Carothers, 1976) bone bed, which contains a mixture of marine chondrichthyan elements (petalodonts, cochliodonts, symmoriids) and nonmarine chondrichthyan remains (Orthacanthus compressus). There is also the possibility that the chondrichthyan that bore these scales was euryhaline and able to move freely between marine and brackish or nonmarine environments. Denticles, teeth, and median fin spines similar to those described by Lund (1970) from the Duquesne limestone have not been found in samples of nonmarine limestones processed during this study (not formally considered as part of this report). A third possibility would be that specimens of dermal denticle "A" were emplaced in marine sediments by postmortem transport. Nevertheless, dermal denticle "A" appears to be conspecific with those assigned to Hybodus allegheniensis by Lund (1970), whether or not they were derived from this hybodont. It is of interest to note also that similar denticles have not been reported from well-known Mesozoic hybodonts, although denticles in these chondrichthyans are extremely variable (see Reif, 1978). These occurrence data reinforce the statement that both caution and detailed study are necessary in order to determine the environmental origin of any particular chondrichthyan remains.
These denticles have a general resemblance to the complex, multirow mucous membrane denticles of symmetricids, although they differ from the latter in the robustness of the crown elements and by the extremely convex base. There is a possibility that specimens of dermal dentine "A" were derived from mucous membrane tissues, probably those covering branchial arches. On the other hand, the general resemblance of these denticles to the scales of "Holmsella" suggests that they are dermal denticles.

Stratigraphic Distribution.— Specimens of dermal dentine "A" have been recovered in samples from five localities in Conemaugh marine units. Only the Noble and Gaysport in the Conemaugh did not yield specimens. Owing to the low frequency of these denticles in the samples, it is not inconceivable that they may occur lower in the Pennsylvanian section.

DERMAL DENTICLE "B"
Pl. XI, Figs. 1-2
Subtype 148, Tway and Zidek, 1983, figs. 49a-b.

Characterization.- A chondrichthyan that is characterized by small to medium-sized compound denticles with a crown consisting of two or more principal cusps and commonly two or three secondary cusps, all of which are aligned in a single, anterior-posterior row. Each cusp is markedly compressed laterally and tapers to a sharp, recurved point. The cusps are fused throughout two-thirds or more of their lengths. The denticle base is short, roughly oval in outline, weakly lobate along its margins, and concave basally. Neck canals (foramina) are present along the crown/base junction. Relatively large nutrient foramina are present basally.

Referred Specimens.- OSU 38608, Lower Mercer, location Hfg-5; OSU 38607, Portersville, location Aw-47.

Distribution.- Pottsville and Conemaugh of the Appalachian Basin; Virgilian of the Midcontinent.

Description.- These denticles measure about 1 mm or slightly less in maximum dimension (Fig. 79). The crown consists of up to six, and perhaps more, laterally compressed cusps organized in a longitudinal row. Three or more of the cusps are relatively large, becoming
progressively larger posteriorly. Two or more of the comparatively small secondary cusps are located posterior to and in line with the principal cusps. Each cusp is relatively wide basally and narrows apically to a pointed, recurved, narrow ridge. The cusps are fused throughout two-thirds or more of their lengths. Prominent grooves, that may extend onto the base, mark the points of fusion between the individual cusps. Commonly, the cusps appear to be smooth, with no ornamentation; however, some specimens exhibit no signs of wear (OSU 38608) bear very weak, widely spaced ridges or cristae near the bases of the cusps.

Fig. 79.- Dermal denticle "B" (OSU 38608), Lower Mercer limestone, location Hfg-5. Unfortunately, the crown of this denticle was broken from the base during manipulation after this illustration had been prepared. A, lateral; B, apical. Bar scale represents 0.5 mm.
The base of the denticle is approximately oval in outline. Shallow, irregular lobes, which mark the zones of fusion of individual denticle elements, are present along the margin of the base. These zones of fusion are marked by sulci on the surface of the sloping platform of the denticle base. Very tiny foramina (neck canals) are present on each side of the denticle just above the junction of the crown and base. The concave underside of the denticle base may exhibit one or more relatively large basal foramina.

DISCUSSION

Specimens of dermal denticle "B" could be interpreted to be mucous membrane denticles because of the alignment of the cusps in a longitudinal row; however, they are most likely to be dermal denticles that armored the skin of a bottom-dwelling or bottom-feeding chondrichthyan, perhaps a cochliodont. Patterson (1965, fig. 32; see Fig. 80, herein) illustrated scales of a Lower Carboniferous cochliodont, Deltoptychius armigerus, that bear similarity to the scales under discussion.

The scales illustrated by Patterson (1965) consist of three to four laterally compressed principal cusps and several smaller secondary cusps fused in a longitudinal row. These cusps do not appear to be as sharply pointed as the denticles from the Appalachian Basin and the bases of
the *Deltopychius armigerus* denticles are wider and more lobate than are those of dermal denticle "B". Nevertheless, the similarities between the two denticles are sufficient to indicate that the OSU specimens may have been derived from a chondrichthyan that was similar phylogenetically (a cochliodont) or one that was similar in regard to mode of life. Although the cochliodonts (consisting of isolated, or in one case associated, teeth) in the macroscopic fauna have not been studied in detail, it is plausible that these denticles may have been derived from either *Deltodus* or *Cochliodus*. The relative rarity of these denticles in the microscopic fauna suggests that a less common cochliodont such as *Cochliodus* would have been the likely source for these denticles. It is possible that a dermal spine in the fauna, *Nebraskella ossiani*, might have also been derived from the same chondrichthyan that bore dermal denticle "B". In addition, the denticles described elsewhere in this report as dermal denticle "C" may have been associated with dermal denticle "B". Unfortunately, all of these dermal denticles and spines occur in such low frequency that mutual-occurrence data yield no significant relationships between any of these forms.
Fig. 80.—Scales of *Deltopychius armigerus* from the Lower Carboniferous of Britain. From Patterson (1965). A, apical (top) and basal (bottom); B, lateral; C, lateral; D, lateral (top) and apical (bottom). Abbreviations: a.c., accessory cusp; b.c., basal canal; n.c., neck canal; p.c., pulp cavity. Bar scale represents 0.25 mm.

Tway and Zidek (1983, figs. 49a-b) illustrated a denticle (their subtype 143) that appears to be referable to dermal denticle "B". This specimen, from the Shawnee Group (Virgilian) of Kansas, possesses two principal cusps and one secondary cusp. Very small neck canals (foramina) are clearly visible on this specimen at the junction of the crown and base.
Stratigraphically, these denticles are widespread, being present in the Pottsville and Conemaugh Groups of the Appalachian Basin. However, samples from only six localities yielded specimens. These data suggest that specimens of dermal denticle "B" will probably be found eventually in marine units throughout the Pennsylvanian section.

Occurrence.—Lower Mercer, Hfg-5, (1); Upper Mercer, Mp-3, (2); Portersville, At-45B, (4); Aw-47, (1); Ames, Cma-10, (1); Pb-4, (1).
DERMAL DENTICLE "C"

Pl. XI, Figs. 3-4

Subtype 019, Tway and Zidek, 1983, figs. 37a-b.

Fortscottella gemmicula, Gunnell, 1933, p. 293, Pl. 32, fig., 35.

Characterization.—A chondrichthyan characterized by small to medium-sized, compound denticles that consist of at least four or five, perhaps more, triangular, pointed cusps that are compressed in the anterior-posterior dimension. Base oval in outline, short, marginally lobate, and concave basally.

Referred Specimens.—OSU 38609, Portersville, location At-45B; OSU 38610, Noble, location Nbu-1.

Distribution.—Pennsylvanian of the Appalachian Basin; Virgilian of the Midcontinent.

Description.—These denticles are of small to medium size, ranging to about 1 mm in maximum dimension. The crown consists of up to four or five weakly fused cusps nested together in an anterior-posterior row. Specimens with as few as two cusps are in the OSU collection. The anterior cusp is the smallest; the cusps become progressively larger posteriorly. Each cusp is triangular in shape, when viewed anteriorly, being comparatively wide at the base and tapering rapidly to a sharp point. The anterior baso-
lateral margins of each cusp may bear tiny secondary cusps, one on each side, although this feature is rare. Some specimens exhibit a lateral ridge or carinae along the lateral sides of the cusps. Each cusp is concave anteriorly and convex posteriorly; however, the lateral dimension of the cusp is greater than is the anterior-posterior dimension, giving an overall anterior-posterior compression to the cusp. Other than the lateral carinae, the cusps are smooth and bear no cristae or other ornamentation. A typical specimen is illustrated in Figure 81.

Fig. 81.- Dermal denticle "C", OSU 38609, Portersville, location At-45B. A, lateral; B, antero-apical. Bar scale represents 0.5 mm.
The base is oval in outline, with the long axis of the oval oriented anterior-posteriorly, and shallowly lobate along its margins. Spokelike ridges and corresponding sulci radiate across the platformlike upper surface of the base. The undersurface of the base is shallowly concave. Very tiny foramina (neck canals) may be present on the posterior side of each denticle element, at the base/crown junction; however, these openings are commonly visible only on the posteriormost element. Larger foramina may be present on the concave undersurface of the base.

**DISCUSSION**

Specimens of dermal denticle "C" have a general similarity to those designated as dermal denticle "B" except that the cusps differ in the axis of compression and denticle "C" has cusps that are more weakly fused. Morphological differences between the two denticles are sufficient to consider them as separate taxa; however, it is possible that they were derived from the same chondrichthyan. Of the 11 localities that yielded one or both denticle types, four localities (36 percent) yielded both denticles "B" and "C". These mutual-occurrence data are not sufficiently convincing to indicate conclusively that these two denticle morphotypes were derived from the same chondrichthyan. Additional sampling may clarify this possibility.
Nevertheless, it is likely that dermal denticle "C" was derived from a cochliodont or similar bottom-feeding chondrichthyan, as probably were the denticles of morphotype "B". The denticles of *Deltoptychius armigerus*, described by Patterson (1965), bear resemblance to denticle "C". Although the cusps of *D. armigerus* denticles are most like those of denticle "B", the base of the former denticle most resembles that of denticle "C". These general similarities would suggest that all three denticle types were perhaps derived from similar chondrichthyan--the similarities may have been phylogenetic, adaptive, or both.

Tway and Zidek (1983) illustrated a single specimen that is referable to dermal denticle "C". This specimen exhibits the very tiny bumptlike secondary cusps on the baso-lateral margins of the principal cusps. Their specimen was derived from the Plattsmouth Limestone (Shawnee Group, Virgilian) of Missouri.

Gunnell (1933) described and illustrated a new species of *Fortscottella, F. gemmicula*, that may be the same taxon as dermal denticle "C". The holotype of *F. gemmicula* (UM 510-3), from the Chanute Shale (Missourian), is a tiny specimen that preserves four triangular, fused, anteriorly–posteriorly compressed cusps (Fig. 82). It is possible that this specimen is the same species as those
those specimens placed herein in dermal denticle "C"; however, re-examination of Gunnell's holotype will be required in order to definitively make this assessment.

Fig. 82.- Holotypes of *Fortscottella gigantea* Gunnell 1931 (UM 489-1), from the Fort Scott Limestone of Missouri, *E. gemmicula* Gunnell 1933 (UM 510-3), from the Chanute Shale of Missouri, and *F. semiserrata* Gunnell 1931 (UM 488-4), also from the Fort Scott Limestone. A, *F. gigantea* in lateral view; B, *E. gemmicula* in antero-lateral view; C, *F. semiserrata* in apical view (anterior at top). Bar scales represent 0.5 mm.

Gunnell's (1931) type species *Fortscottella, F. gigantea*, does not bear close similarity to dermal denticle "C" nor does it appear to have much
morphological similarity to Gunnell's other three species of this genus, *F. serrata* and *F. semiserrata* Gunnell 1931, and *F. gemmicula* Gunnell 1933. The holotype of *F. gigantea* (UM 489-1) is a large compound denticle that consists of prominent lateral ridges with intervening, deep, broad sulci (Fig. 82). Gunnell's (1931) original illustration of the holotype does not convey these features clearly. No specimens in the OSU collection are of this same morphology.

The holotypes of *Fortscottella serrata* (UM 488-5) and *F. semiserrata* (UM 488-4) are more like *F. gemmicula* in their morphologies, consisting of fused, triangular cusps; however, these cusps are strongly fused throughout their lengths, a feature unlike that seen in any specimens assigned to dermal denticle "C". Although the holotypes of *F. serrata* and *F. semiserrata* do not appear to be related to the type species, *F. gigantea*, their relationships to *F. gemmicula* and dermal denticle "C" remain equally uncertain. Nevertheless, if *F. gemmicula*, and perhaps *F. semiserrata* are determined to be conspecific with dermal denticle "C", establishment of a new genus will be required.

It should be noted that the holotypes of all of Gunnell's (1931; 1933) species of *Fortscottella* are not in particularly good condition; *F. gigantea* and *F. serrata*
are so badly cracked that they cannot be manipulated on
the microslides. The holotype of *F. gigantea* is also
missing the apical portion of the crown.

GAp-4, (1): Portersville, At-45B, (2); Aw-47, (1): Noble,
Characterization. - Chondrichthyan dermal denticles that are characterized by specimens that are small to medium-sized, robust, with a short, highly irregular, robust crowns consisting of one or more blunt, highly crenulated peaks. Base very large in comparison to the crown, platelike to bulbous, with a broad rim and a smooth, commonly greatly convex, rounded basal surface.

Referred Specimens. - OSU 38611, Cambridge, Pmo-10; OSU 38612, Portersville, At-45B.

Distribution. - Conemaugh of the Appalachian Basin; Virgilian of the Midcontinent.

Description. - These denticles (Fig. 83) range in size from about 0.5 mm to about 1 mm in maximum dimension. The denticle crown is small in comparison to the base and consists of one or more, rough, highly irregular cones set upon the flat, upper surface of the base. Relatively small specimens exhibit only one or two cusps, which may be arranged in a row and partially fused, or only slightly separated. The cusps have deep, very irregular sulci and ridges and are blunt and rounded apically. In larger
specimens the cusps are more conelike and are strongly fused so that only their apical portions remain separate. In some unworn specimens an imbricated, triangular pattern of very weak ridges is present.

![Image of Dermal denticle](image)

**Fig. 83.** - Dermal denticle "D" in apico-lateral view. OSU 38611, Cambridge limestone, location Pmo-10. Hachured area represents a broken portion of the specimen. Bar scale represents 0.5 mm.

The base in small specimens consists of a round, disclike platform that is relatively thin in the baso-apical dimension. Larger specimens exhibit a very thick, bulbous, basally convex base that is very smooth and polished. The upper surface of the base is flat, smooth, and forms a wide platform that surrounds the diminutive crown. One or more comparatively large foramina may be present on the undersurface of the base.
DISCUSSION

Some specimens of dermal denticle "D" are reminiscent of acanthodian scales because of the rounded, bulbous base exhibited by larger specimens. However, it is obvious that they are compound chondrichthyan denticles that are the result of fusion of individual elements, not unlike those referred to a chondrichthyan, "Holmsella", by Orvig (1966) and Zangerl (1968). The crowns of dermal denticle "D" are, however, very different from those of "Holmsella". In the latter genus the crown consists of ridges on a flat crown surface whereas in dermal denticle "D", the crowns are distinct, raised cones. In addition, these two denticles differ in a number of other morphological details.

It is probable that these denticles functioned as a protective pavement on the skin of a bottom-dwelling/bottom-feeding chondrichthyan. The stout, robust morphology of the denticles appears to be consistent with this interpretation and the crown surface on some specimens appears to exhibit antemortem abrasion as would be expected in a benthic-oriented chondrichthyan. These denticles are so rare in the fauna that it is not possible at this time to refer them to any particular taxon based on teeth. It is possible that the source chondrichthyan may have been a cochliodont.
Tway and Zidek (1983) illustrated two specimens that appear to be referable to this taxon. Their subtype 172 is from the Plattsmouth Limestone (Shawnee Group, Virgilian) of Nebraska and their subtype 240 is from the Stoner Limestone (Lansing Group, Virgilian). The latter specimen possesses relatively large crown cusps in comparison to the size of the base, although it closely follows the morphological scheme exhibited by the Appalachian specimens.

Specimens of dermal dentine "D" appear to be confined to Conemaugh rocks in the Appalachian Basin and have been collected from all of the marine units in this group except from the Noble and Gaysport, each of which was sampled at only a few localities. As with other relatively rare specimens in the OSU collection, this known stratigraphic range remains provisional and subject to revision when additional collections become available.

Occurrence.—Brush Creek, Aw-47, (1); Cambridge, Pmo-10, (1); Portersville, At-45B, (1); Ames, Gv-1, (1); M0m-1, (1); Skelley, Nbu-3, (1).
DERMAL DENTICLE "E"

Pl. XI, Fig. 5

?Subtype 191, Tway and Zidek, 1982, figs. 9a-e.

Characterization.—Chondrichthyan dermal denticles characterized by size small size and a trilobed crown with blunt, unornamented apical spikes surmounting each lobe. Central spike largest of the three. Two crown cusps of similar morphology but different size are fused and share a single base and pedicel. Base subcircular and weakly lobed. Pedicel narrow and comparatively long.

Referred Specimen.—OSU 38613, Putnam Hill limestone, location MUm4-Um4.

Distribution.—Putnam Hill limestone of the Appalachian Basin; ?Virgilian of the Midcontinent.

Description.—Only a single example of this dentine is in the OSU collection; morphological variation cannot, therefore, be assessed. This specimen is comparatively small, about 0.5 mm in maximum dimension, and is of the placoid type, although two dentine crowns are obviously fused (Fig. 84). The crown is compressed in the anterior-posterior dimension and consists of three peaked lobes, the central one of which is the largest. These lobes consist of blunt, rounded spikes that have no ridges, keels, or other ornamentation. Anterior to this large,
trilobed crown is a smaller trilobed crown that mimics its successor in morphology. Basally, the anterior crown element is fused to and indistinguishable from the larger, succeeding denticle element.

The pedicel region of the denticle is relatively long and slightly narrowed. The base flares outward, forming a wide, sloping shelf that is wider than the crown. The underside of the base is shallowly concave. The margins of the base are slightly lobate. Nutrient foramina (neck canals) are not visible on this specimen.

Fig. 84.- Dermal denticle "E" (OSU 38613) from the Putnam Hill limestone at location MUm 4. A, anterior; B, posterior; C, apical. Bar scale represents 0.5 mm.
DISCUSSION

Although this denticle is complete and well-preserved, a single specimen is inadequate for assessing morphological variation or for deciphering possible taxonomic affinities by analysis of mutual-occurrence data. No other specimen in the collection resembles this denticle, either in a fused arrangement, as is this one, or a single, nonfused specimen. The only other denticle in the collection that even approximates the morphology of dermal denticle "E" is a specimen (OSU 36814, dermal denticle "F") from the same Putnam Hill sample. This specimen has three spiked lobes, as does dermal denticle "E", but they are compressed and ornamented, unlike dermal denticle "E". In addition, dermal denticle "F" is considerably larger than the one under discussion and does not appear to have fused elements. As both of these denticles are unique in the collection, it would be premature to rule out the possibility that they represent opposite endpoints in a morphological transition series, although that possibility seems remote with present knowledge.

The most unusual feature of dermal denticle "E" is that it appears to be of the placoid type, with a long, narrow pedicel and a single element crown, except that two denticle crowns are fused together, as would be expected
in a compound denticle. Both denticle crowns share a common pedicel and base, with no observable separation of these structures into two or more elements.

A specimen illustrated by Tway and Zidek (1982, figs. 9a-e) resembles dermal denticle "E" in that the crown consists of three blunt, rounded, spikelike apical lobes and is preceded by another, smaller denticle crown. The smaller, anterior-most denticle crown of this specimen has its own distinct pedicel and base, rather than sharing these structures as in dermal denticle "E". In addition, the denticle illustrated by Tway and Zidek (1983), from the Stoner Limestone (Lansing Group, Virgilian) of Iowa, has a multilobate base with distinct, spokelike ridges and intervening sulci. Owing to these morphological differences, Tway and Zidek's (1983) specimen is provisionally and questionably referred to dermal denticle "E".

Dermal denticle "E" has a very general resemblance to a scale of a Mesozoic hybodont, Hybodus delabechei, illustrated by Reif (1978, fig. 2c). The hybodont scale has more sharply pointed crown cusps and has ornamentation consisting of broadly spaced ridges and sulci; however, it appears to be composed of two or more fused crown elements. There is a possibility, untestable at present, that dermal denticle "E" was derived from a hybodont.

Occurrence.—Putnam Hill, MUMU-4, (1).
DERMAL DENTICLE "F"

Pl. XI, Fig. 6

?Subtype 237, Tway and Zidek, 1982, figs. 17a-d.

Characterization.- Chondrichthyan dermal denticles characterized by a vertical, trilobed crown. Each crown lobe tapers to a sharp point and lateral lobes flare outward from the vertical central lobe. Anterior crown surface ornamented with irregular, vertical ridges. Pedicel narrowed slightly and elongate. Base high and relatively narrow with a deeply concave basal surface. Small foramina (neck canals) present posteriorly.

Referred Specimen.- OSU 38614, Putnam Hill limestone, location MUMu-4.

Distribution.- Putnam Hill limestone of the Appalachian Basin; ?Virgilian of the Midcontinent.

Description.- Dermal denticle "F" is represented by only a single specimen in the collection (Fig. 85). This specimen is relatively small, just slightly under 1 mm in maximum dimension, and is in a nearly vertical plane from base to crown tip. The crown is trilobed and each lobe is triangular, relatively wide at the base, and tapers to a point. The lobes are short in comparison to the length of the crown. The lateral crown lobes are located just
slightly anterior to the medial lobe and overlap it somewhat. The crown is compressed in the anterior-posterior dimension and relatively wide medially in the lateral dimension. The anterior surface of the crown is marked by irregular, relatively prominent ridges and intervening sulci. Posteriorly, the crown is relatively smooth, with only a few irregular indentations on the surface.

The pedicel is relatively long and narrow but is not constricted to a great degree. The base is about as wide as the maximum width of the crown and is high with a steeply sloping margin. The undersurface of the base is deeply concave. A few foramina (neck canals) are visible in the pedicel region.

Fig. 85.- Dermal denticle "F" (OSU 38614) from the Putnam Hill limestone at location MUm-4. A, anterior; B, lateral; C, posterior. Bar scale represents 0.5 mm.
DISCUSSION

The unique specimen of dermal denticle "F" is unusual in that it resembles a placoid denticle but appears to have three fused crown elements, which make up the lobes of the crown. This fusion is not so apparent as in dermal denticle "E", from the same sample. As noted in the discussion of the latter denticle, there is a possibility that the two denticles represent the opposite endpoints in a morphological transition series.

A denticle illustrated by Tway and Zidek (1982, figs. 17a-d; subtype 237) has a general similarity to dermal denticle "F"; however, the crown is more inclined, the lobes do not appear to be separate entities, and the base is not as high as in dermal denticle "F". Because of these differences, Tway and Zidek's specimen is questionably referred to dermal denticle "F". Obviously, additional specimens of both denticles would serve to elucidate potential relationships and clarify morphological details.

Occurrence.—Putnam Hill, MUMU-4, (1).
MUCOUS MEMBRANE DENTICLES

Symmoriid Mucous Membrane Denticles

Pl. XI, Figs. 13-16

Scolopodus ellipticus, Gunnell, 1931, p. 248, Pl. 29, fig. 10.

Idiacanthus bellistriatus, Gunnell, 1933, p. 293, Pl. 31, fig. 60.

Idiacanthus cameratus, Gunnell, 1933, p. 294, Pl. 32, fig. 29.

?Idiacanthus trispinosus, Gunnell, 1933, p. 294, Pl. 33, fig. 46.

Scolopodus striatum, Harlton, 1933, p. 12, Pl. 3, fig. 1.

Scolopodus oklahomensis, Harlton, 1933, p. 12, Pl. 3, fig. 6.

Multidentodus wapanuckensis, Harlton, 1933, p. 13, Pl. 3, fig. 2.

Multidentodus johnsvallevensis, Harlton, 1933, p. 13, Pl. 3, fig. 3.

Multidentodus typicus, Harlton, 1933, p. 13, Pl. 3, fig. 4.

Multidentodus brevis, Harlton, 1933, p. 13, Pl. 3, fig. 7.

Multidentodus irregularis, Harlton, 1933, p. 13, Pl. 3, fig. 8.

Scolopodus sigmoidalis, Harris and Hollingsworth, 1933, pp. 194-195, Pl. 1, fig. 5.
Gunnellodus, Wilimovsky, 1954, substitute name for Idiacanthus (preoccupied).

Subtype 017, Tway and Zidek, 1983, figs. 3a-e.
Subtype 032, Tway and Zidek, 1983, figs. 4a-b.
Subtype 056, Tway and Zidek, 1983, figs. 8a-c.
Subtype 095, Tway and Zidek, 1983, fig. 11.
Subtype 096, Tway and Zidek, 1983, fig. 12.
Subtype 105, Tway and Zidek, 1983, fig. 13.
Subtype 193, Tway and Zidek, 1983, figs. 30a-b.
Subtype 018, Tway and Zidek, 1983, figs. 36a-b.
Subtype 057, Tway and Zidek, 1983, figs. 40a-b.
Subtype 074, Tway and Zidek, 1983, figs. 42a-b.
Subtype 124, Tway and Zidek, 1983, figs. 46a-b.
Subtype 198, Tway and Zidek, 1983, figs. 54a-c.
Subtype 212, Tway and Zidek, 1983, figs. 58a-c.

"Stemmatias" mucous membrane dentine, Schultze, 1985, Fig. 4, no. 2.

Characterization.—Symmoriid mucous membrane denticles that are characterized by being extremely variable and consisting of single denticles or aggregates of denticles that are based on a theme of conical, recurved, commonly cristated cusps set on a bulbous to flattened base. Varieties consist of a single, conical cusp; fused, single rows of cusps; fused, double rows of cusps; and fused, irregular, multiple rows of cusps.
Distribution.- Pennsylvanian of the Appalachian and Midcontinent Basins.

Referred Specimens.- OSU 38602, Brush Creek, Aw-47; OSU 38603, Ames, Pb-4.

Description.- Symmoriid mucous membrane denticles range in size from about 0.5 mm to about 1.5 mm in maximum dimension. They are composed of cusps, or aggregates of cusps, each of which is oval in cross section, tapers to a sharp, recurved point, and is commonly marked by numerous apically converging cristae. The denticle bases are flattened to bulbous, relatively short, and only slightly wider than the crowns. The bases commonly have a roughened appearance. Small nutrient foramina are commonly present at the base/crown junction, particularly on the posterior side. Apparent nutrient foramina are present on the roughened base.

There are four main varieties or morphotypes of symmoriid mucous membrane denticles and considerable variation characterizes each type (Figs. 86, 87). The first morphotype consists of a single, recurved cusp that is set on an oval, sometimes bulbous base. Cristae are closely and evenly spaced on the cusp, except on the anterior portion, where they are weakly developed and sometimes absent. There may be some proximal bifurcation of cristae. Specimens of this morphotype possess
relatively short, stubby cusps; however, there is a
gradation from the stubby forms to long, slender forms set
on a triangular base. These latter specimens probably
represent teeth from the palatoquadrate of Cobelodus
aculeatus.

Fig. 86.- Variation in single-cusped symmoriid mucous
membrane denticles and a tooth from the palatoquadrate of
Cobelodus aculeatus. A, stubby variety of denticle; B, C,
transitional varieties that are probably mucous membrane
denticles rather than teeth; D, tooth from palatoquadrate
of Cobelodus aculeatus. All specimens in lateral view,
anterior to the right. Bar scale represents 0.5 mm. A–C,
Portersville, location Aw-47; D, Ames, location PA-3.

The second morphotype consists of relatively short,
stubby, cristated cusps that are fused at their bases. The
anterior cusp is the smallest and the cusps become
progressively larger posteriorly. The base is arched and
commonly flattened on most specimens. On some specimens the individual fused bases of the denticles can be discerned. Specimens with at least six cusps have been observed in the OSU collection.

Fig. 87.—Varieties of multicusped symmoriid mucous membrane denticles. A, B, single-row variety in anterior and lateral views, respectively. Note fusion of two single-cusped denticles. Cambridge, location GAs-1. C, D, double-row variety in anterior and lateral views, respectively. Brush Creek, location Aw-47. E, F, multirow denticles in anterior and lateral views, respectively. Ames, location Pb-4. Bar scale represents 0.5 mm.
A third morphotype consists of two converging, imbricated, arched rows of cusps set on a single base. These specimens resemble the single-row variety in nearly all morphological details except that the two rows are fused. At least six cusps per row have been observed on specimens in the OSU collection.

A fourth morphotype, which may be restricted only to Symmorium reniforme, consists of numerous, irregular rows of denticles set on a common base. These rows appear to be offset or staggered and the individual cusps increase in size from anterior to posterior. The cusps appear to lack cristae and are relatively smooth.

DISCUSSION

Recent studies by Zidek (1973), Zangerl and Case (1976), Zangerl (1981), and particularly Williams (1985) have cast considerable light on the correct identification and interpretation of mucous membrane denticles of symmoriid sharks. Zangerl and Case (1976) described mucous membrane denticles that were in place on branchial arches of specimens of Cobelodus aculeatus from the Pennsylvanian Mecca fauna. They placed a variety of such denticles described and named by Gunnell (1933) and Harlton (1933) in synonomy with this species. Zidek (1973) had earlier recognized that these previously described, isolated denticles were mucous membrane denticles of cladodontid sharks.
Williams (1985), in a study of Denaea meccaensis, Symmrium reniforme, and Stethacanthus altonesis, recognized that the mucous membrane denticles described by Zangerl and Case (1976) also occurred on the branchial arches of these other symmoriid sharks and suggested that such denticles may be characteristic of the group rather than individual species. Owing to this fact, Williams (1985) considered Stemmatodus (Stemmatias, see below) a nomen dubium.

Williams (1985) and Zangerl and Case (1976) also noted that these denticles are similar to those described by St. John and Worthen (1875) under the names Stemmatodus simplex, for the single-row variety, and Stemmatodus bicristatus, for the double-row variety. Hay (1899) substituted Stemmatias for Stemmatodus (preoccupied). St. John and Worthen's specimens (1875, Pl. 8, figs. 28-38), which include seven species assigned to Stemmatias, were derived from the Upper Burlington Limestone (Osagean) of Iowa, except for a single-row variety, S. compactus, which came from Chesterian rocks of Illinois and S. keokuk, from the Keokuk Limestone. This latter species was not illustrated. Although these Mississippian mucous membrane denticles closely resemble those of symmoriid sharks from Pennsylvanian rocks, they
may not be identical. Of the symmoriid species known from the Pennsylvanian, only Stethacanthus altonensis is known to range as low as the Lower Mississippian.

Restudy of St. John and Worthen's (1875) specimens of Stemmatias may indicate minor morphological differences that permit these mucous membrane denticles to be distinguished from those of Pennsylvanian age. It is also possible that the Mississippian denticles that are most similar to the Pennsylvanian ones were derived from the species common to both geologic systems, Stethacanthus altonensis. Alternatively, such denticles may be plesiomorphous for cladodontid sharks. Nevertheless, it is apparent that the Pennsylvanian specimens are probably referable to symmoriids. Owing to these uncertainties, St. John and Worthen's (1875) species of Stemmatodus (Stemmatias) are not placed in synonomy herein. These species of Stemmatias should, however, be used in an informal sense or, preferably, the designation--"cladodontid mucous membrane denticles of the 'Stemmatias' type."

Symmoriid mucous membrane denticles were described as a variety of species of Idiakanthus (preoccupied; Gunneliodus, substitute name), Multidentodus, and Scolopodus by micropaleontologists in the early 1930's (see synonomy) when conodonts were thought to be remains
of primitive fishes. A strict adherence to form taxonomy prevailed and relatively minor variations in morphology were regarded to be of specific importance. Such an approach prompted Zangerl (1981) to state that naming such isolated chondrichthyan parts was an exercise in futility. Two of Gunnell's holotypes are illustrated in Fig. 88. They are single-cusp varieties of symmoriid mucous membrane denticles.

![Diagram of denticles](image)

Fig. 88.—Gunnell’s (1933) holotypes of Gunnellodus (Idiacanthus) bellistriatus (A-C) and G. cameratus (D-F). Both species are symmoriid mucous membrane denticles. A-C, holotype (UM 501-1) of G. bellistriatus in A, lateral; B, antero-apical; C, posterobasal. D-F, holotype (UM 509-2) of G. cameratus in D, lateral; E, anterior; F, basolateral. Bar scale represents 0.5 mm.
Gunnell's (1933) presumed holotype of *Gunnellodus (Idiacanthus) trispinosus* (UM 522-2) in anterior view. This broken specimen (hachured area) does not appear to be the same one that was illustrated by Gunnell (1933, Pl. 33, fig. 46). See text for discussion. Bar scale represents 0.5 mm.

Gunnell's (1933) species, *Gunnellodus (Idiacanthus) trispinosus*, presents problems in accurate assignment. The specimen illustrated by Gunnell (1933, Pl. 33, fig. 46) and his description of the species indicate that the holotype possesses three cristated cusps. The illustrated specimen is clearly a symmorid mucous membrane dentine of the single-row variety. However, the University of Missouri specimen (UM 522-2) considered to be the holotype does not have three cristated cusps (Fig. 89). Although this specimen is broken and cannot be manipulated on the
microslide, it is apparently not the same specimen illustrated by Gunnell. Although this specimen appears to be a mucous membrane denticle, it does not appear to be that of a symmoriid nor does it resemble closely any other specimens in the OSU collection. Until this discrepancy can be resolved, *Gunnellodus trispinosus* is questionably placed in synonymy.

Tway and Zidek (1983) illustrated 13 subtypes that are referable to symmoriid mucous membrane denticles. Such a long list of separate nonbiological categories indicates a major limitation of the Scripps system.

Zangerl and Case (1976) noted that the single-cusp mucous membrane denticles of *Cobelodus aculeatus* were commonly associated with the anterior branchial arches whereas the single-row variety were associated with posterior branchial arches. They also noted that the single-cusp forms are similar to, and perhaps indistinguishable from, the teeth associated with the palatoquadrate. They suggested, in general, that the teeth of this species are longer and more slender, whereas the branchial denticles are shorter- crowned and stubby. Of the single-cone specimens in the collection, some are quite clearly of the stubby variety whereas others are just as clearly of the elongate, needlelike variety. Each of these morphological endpoints
can accurately be assigned to one category or another (Table 14); however, there are a number of specimens in the OSU collection that are too short to be placed conveniently with *C. aculeatus* palatoquadrate teeth and too long to be placed with certainty with the single-cone variety of branchial denticles. For convenience, these transitional specimens are included in the category of single-cusped denticles (Table 14). It should be noted that Zangerl and Case (1976) did not report any of the double-row variety nor any of the multi-rowed, complex variety denticles from specimens of *Cobelodus aculeatus*.

Williams (1985) indicated that specimens of *Symmorium reniforme* from the Mecca fauna possessed all forms of these mucous membrane denticles; single cone, single row, double row, and multirow. Of the four Pennsylvanian genera of symmoriids, only *S. reniforme* is known to have possessed the complex, multirow form ("*Stemmatias* cheiriformis") and these denticles may prove to be distinctive of this species in Pennsylvanian rocks.

*Stethacanthus altonensis*, according to Williams (1985), also possessed single-cone, single-row, and double-row forms. No complex, multirow forms were reported. A coneshaped dentine with small lateral cusps, described elsewhere in this report as "mucous membrane dentine B", is, according to Rainer Zangerl (personal
communication, 1985), similar to those he has noted (unpublished) on specimens of *S. altonensis* from the Mecca fauna. This observation requires confirmation.

*Denaea meccensis*, teeth of which are as yet not known with certainty from the Appalachian basin, has, according to Williams (1985), only the single-row variety of mucous membrane denticles and an extremely irregular, multicone form. This latter variety of denticle has not been recognized in the Appalachian basin samples. Mucous membrane denticles of the new species of *Denaea*, *D. saltsmanii*, described herein, are as yet unknown; however, it is likely that they will prove to be of one or more of the symmoriid morphotypes described above.

In summary, the mucous membrane denticles described here appear to have been derived from symmoriid sharks. As noted above, the complex, multirow forms may be indicative of *Symmorium reniforme* and the long, needlelike forms are undoubtedly teeth from the palatoquadrate of *Cobelodus aculeatus*. The additional morphotypes, stubby single-cusp and single-row, do not appear to be indicative of a particular species of symmoriid.

**Stratigraphic Distribution.**—Mucous membrane denticles of the varieties described above range through the entire Pennsylvanian marine sequence of Ohio. Only the Boggs and Gaysport did not yield one or more varieties of these
denticles. It is probable that some of the specimens classified as single-cusped denticles (Table 14) are actually palatoquadrate teeth of Cobelodus aculeatus. Complex, multirow forms are relatively rare and occur at only a few localities. Paleoecological data are given in the discussions of individual species of symmoriid sharks.

Occurrence.- Lowellville, MUho-5, (1): "Lower Mercer", Vc-8, (1); Vc-9, (5); Vel-6, (2); Vel-7, (5); Vel-34, (7): Lower Mercer, CS1-1, (1); Hfg-5, (1); Tl-1, (1): Upper Mercer, CSj-3, (2); Ts-5, (1): Putnam Hill, MUm-4, (4); Pmc-4, (1): Vanport, Ld-1, (2); Mp-1, (1); Spk-1, (2); Td-4, (1): Washingtonville, CAr-2, (1); Twa-1, (1): Columbiana, Mg-1, (1): Brush Creek, At-9, (1); At-51, (3); Aw-47, (32); Gca-6, (7): Cambridge, GAs-1, (2); Gca-5, (19); Gwe-1, (9); Nn-13, (17); Pmo-10, (1): Portersville, Acn-31, (34); At-45B, (35); Aw-47, (23): Noble, Nbu-1, (24); Nn-12, (4): Ames, Aa-63, (1); Aa-64, (4); Aam-19, (1); Acn-31, (12); CAc-2, (9); Cma-10, (25); Gv-1, (8); Gwi-3, (18); HAr-1, (5); M0m-1, (4); Nn-3, (6); Nbu-4, (12); Pb-4, (18); PA-3, (4); PA-5, (11): Skelley, Aal-14, (3); Nbu-3, (13).
Table 14.—Distribution of morphotypes of symmoriid mucous membrane denticles, including single-cusped, needlelike teeth of *Cobelodus aculeatus* (see text). Abbreviations: SC, single cusp; SR, single row; DR, double row; MR, multirow; COB, undoubted needlelike teeth of *Cobelodus aculeatus*.

<table>
<thead>
<tr>
<th>UNIT</th>
<th>LOCALITY</th>
<th>SC</th>
<th>SR</th>
<th>DR</th>
<th>MR</th>
<th>COB</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lowellville</td>
<td>MUho-5</td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;L. Mercer&quot;</td>
<td>Vc-8</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Vc-9</td>
<td>1</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Vel-6</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Vel-7</td>
<td></td>
<td>5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Vel-34</td>
<td>5</td>
<td></td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L. Mercer</td>
<td>CS1-1</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Hfg-5</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Tl-7</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>U. Mercer</td>
<td>CSj-3</td>
<td></td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Ts-5</td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Putnam Hill</td>
<td>MUm-4</td>
<td></td>
<td>4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Pmc-4</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vanport</td>
<td>Ld-1</td>
<td>1</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Mp-1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Spk-1</td>
<td></td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Td-4</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wash'tonville</td>
<td>CAr-2</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Twa-1</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Columbiana</td>
<td>Mg-1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brush Creek</td>
<td>At-9</td>
<td></td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>At-51</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Aw-47</td>
<td></td>
<td>7</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Gca-6</td>
<td>7</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cambridge</td>
<td>GAs-1</td>
<td></td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Gca-5</td>
<td>9</td>
<td>8</td>
<td></td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Gwe-1</td>
<td>7</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Nn-13</td>
<td>15</td>
<td></td>
<td></td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Pmo-10</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Portersville</td>
<td>Acn-31</td>
<td>23</td>
<td>9</td>
<td>1</td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>&quot;</td>
<td>At-45B</td>
<td>16</td>
<td>13</td>
<td>1</td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>&quot;</td>
<td>Aw-47</td>
<td>22</td>
<td>7</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Noble</td>
<td>Nbu-1</td>
<td>14</td>
<td>8</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>&quot;</td>
<td>Nn-12</td>
<td>3</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 14.— continued.

<table>
<thead>
<tr>
<th>UNIT</th>
<th>LOCALITY</th>
<th>SC</th>
<th>SR</th>
<th>DR</th>
<th>MR</th>
<th>COB</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ames</td>
<td>Aa-63</td>
<td>-</td>
<td>-</td>
<td>1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>Aa-64</td>
<td>3</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>Aam-19</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>Acn-31</td>
<td>7</td>
<td>2</td>
<td>3</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>CAc-2</td>
<td>6</td>
<td>3</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>Cma-10</td>
<td>19</td>
<td>3</td>
<td>1</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>&quot;</td>
<td>Gv-1</td>
<td>3</td>
<td>3</td>
<td>-</td>
<td>2</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>Gwi-3</td>
<td>11</td>
<td>6</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>&quot;</td>
<td>HAr-1</td>
<td>5</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>M0m-1</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>Nn-3</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>Nbu-4</td>
<td>8</td>
<td>3</td>
<td>-</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>Pb-4</td>
<td>5</td>
<td>12</td>
<td>-</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>PA-3</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>&quot;</td>
<td>PA-5</td>
<td>11</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Skelley</td>
<td>Aal-14</td>
<td>2</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>&quot;</td>
<td>Nbu-3</td>
<td>8</td>
<td>4</td>
<td>-</td>
<td>-</td>
<td>1</td>
</tr>
</tbody>
</table>
Characterization.- A chondrichthyan that is characterized by medium-sized denticles with a prominent, long, spikelike cusp that is flanked laterally and/or anteriorly by very small secondary cusps. Principal cusp weakly cristate; cistae more prominent posteriorly. Base subcircular to triangular, broad, and slightly concave basally. Small nutrient foramina present basally and along lateral margins of base, especially posteriorly.

Referred Specimens.- OSU 38605, Ames, Gv-1; OSU 38606, 38618a-b, Skelley, Nbu-3.

Description.- Specimens of mucous membrane dentine "A" are of medium size, measuring about 1 mm or slightly larger in maximum dimension. The crown is dominated by a prominent, relatively slender, straight cusp that is inclined posteriorly. The cusp is oval in cross section, broad at its base, and tapers rapidly to a sharp point. A lateral carinae may be present on the sides of the cusp and some specimens exhibit weak cistaee, especially on the posterior side of the cusp.

Very small subsidiary cusps are present on either side of the principal cusp and commonly several of these tiny cusps are present anterior to the principal cusp. Some
specimens exhibit slightly larger secondary cusps anterior to and in line with the principal cusp, reminiscent of the single-row mucous membrane denticles of symmoriids.

The base is subcircular to slightly triangular in outline and may exhibit a slightly lobate margin. In most specimens the base is relatively thick and robust. The underside of the base is slightly concave, roughened, and may exhibit one or more irregularly distributed, small foramina. Similarly small and irregular foramina are commonly present along the edges of the base, particularly posteriorly.

Fig. 90.—Specimen of mucous membrane dentine "A" (OSU 38606a) from the Skelley limestone at location Nbu-3. A, antero-apical; B, lateral. This specimen is of the simplest variety of these denticles. Bar scale represents 0.5 mm.
DISCUSSION

Specimens of mucous membrane denticle "A" are reminiscent of teeth of cladodontids; however, they are most probably mucous membrane denticles because they lack specialized nutrient foramina and because the secondary cusps are so irregular and small. In addition, some specimens in the collection, especially some of those in the large assemblage from the Skelley limestone at location Nbu-3 (OSU 38606), exhibit one or more cusps in line with and anterior to the principal cusp, reminiscent of the single-row variety of mucous membrane denticles of symmoriids. Indeed, specimens of mucous membrane denticle "A" can easily be confused with the single-row symmoriid denticles, except that the former possess a subcircular, robust base and the principal cusp is considerably larger than the secondary cusps.

These denticles have a general similarity also to the denticles known as "Cladodus pattersoni" Newberry 1875, referred by Williams (1985) to the posterior dorsal surface of the head and to the spine-brush complex in Stethacanthus altonensis, except that the "C. pattersoni" denticles have only a single cusp and no secondary cusps (Williams, 1985). Dr. Rainer Zangerl (personal communication, 1985) indicated to me that the denticles under discussion appear to be similar to mucous membrane denticles from posterior branchial arches of specimens of
Stethacanthus altonensis from the Pennsylvanian Mecca fauna. Although this observation will require confirmation, it is noteworthy that the Skelley limestone bone bed at location Nbu-3 produced large numbers of S. altonensis teeth and large numbers of mucous membrane denticle "A", as did location Gv-1 in the Ames limestone. Evidence against this association is the absence of these denticles in samples older than the Portersville, whereas, S. altonensis teeth occur throughout the Pennsylvanian marine section, albeit in low frequency. Owing to this low frequency of occurrence of S. altonensis teeth, it is not implausible that specimens mucous membrane denticle "A" would not show up in these samples. It is of interest to note also that neither denticles of "Cladodus pattersoni" nor "Lamodus hamulus" St. John and Worthen 1875, which Williams (1985) referred to the spine-brush complex and anterior portion of the dorsal surface of the head, respectively, in Stethacanthus altonensis, were found in any samples in the collection.

Occurrence.- Portersville, At-45B, (2); Ames, Aam-19, (1); Gv-1, (9); Gwi-3, (1); Skelley, Nbu-3, (71).
REFERENCES CITED


Mapes, R. H. and Hansen, M. C. 1984. Pennsylvanian shark-
cephalopod predation: a case study. Lethaia, 17:175–
183.

M'Coy, Frederick. 1855. Descriptions of the British
Paleozoic fossils in the Geological Museum of the
University of Cambridge. Cambridge, 661 p.

McKee, E. D. and Crosby, E. J. (eds.). 1975. Paleotectonic
investigations of the Pennsylvanian System in the
United States. U. S. Geological Survey Professional

Mendenhall, M. E. 1951. Conodonts and fish remains of the
Douglas and Shawnee Groups of the Virgil Series
(Pennsylvanian) of Nebraska. M. S. thesis, University
of Nebraska, 78 p.

Merrill, G. K. 1972. Pennsylvanian conodont
paleoecology. In F. H. T. Rhodes (ed.), Conodont
paleozoology. Geological Society of America, Special
Paper 141:239-274.

--- 1974. Pennsylvanian conodont localities in
northeastern Ohio. Ohio Geological Survey, Guidebook

--- in manuscript. Tectonically produced marine
transgression and syndepositional tectonics: Ames
Member, West Virginia.

--- and Wentland, E. M. in manuscript. Conodont
determination of the age of the Mill Creek limestone:
Carboniferous, northeastern Pennsylvania.


Morningstar, Helen. 1922. Pottsville fauna of Ohio. Ohio

Morris, D. A. 1967. Lower Conemaugh (Pennsylvanian)
depositional environments and paleogeography in the
Appalachian coal basin. Ph.D. dissertation, University
of Kansas, 521 p.

Morse, W. C. 1931. Pennsylvanian invertebrate fauna.


Oliver, Jack. 1986. Fluids expelled tectonically from orogenic belts: their role in hydrocarbon migration and other geologic phenomena. Geology, 14:99-104.


COLLECTING LOCALITIES

Specimens providing the basis for this report were derived from 14 stratigraphic units at 114 localities in the following Ohio counties: Athens, Carroll, Columbiana, Coshocton, Gallia, Guernsey, Harrison, Hocking, Holmes, Jackson, Jefferson, Lawrence, Mahoning, Morgan, Muskingum, Noble, Perry, Scioto, Stark, Tuscarawas, Vinton, and Washington (Fig. 91). In addition, several localities in Kentucky and Pennsylvania, in the Appalachian Basin, yielded collections that are part of this report. Specimens from selected localities in Carboniferous rocks in Colorado, Montana, and Oklahoma are also described and considered in this report. These productive localities are described in list A-1. Additional localities that either did not produce chondrichthyan remains (list A-2) or did not disaggregate in acetic acid or by other physical or chemical methods (list A-3) are also included in the Appendix. In addition to the Ohio counties listed above, lists A-2 and A-3 include localities in Portage and Wayne Counties.

The Ohio localities are listed in numerical order under the respective counties and civil townships, where the order is alphabetical according to the county and
Fig. 91.—Distribution of productive collecting localities in Pennsylvanian rocks of Ohio.
township names. The capitalized first letter(s) of the locality indicates the county, the lower case letter(s) the civil township, and the number indicates the particular locality within the township. Localities in states other than Ohio are designated by capital letters for the state abbreviation and a number indicating a specific locality. This system of locality designation was developed by Myron T. Sturgeon at Ohio University and has been utilized in previous reports on the Pennsylvanian fauna of Ohio (Sturgeon and Hoare, 1963; Hoare, Sturgeon, and Kindt, 1979). Locality numbers in these publications and other publications by these authors that are identical to those in this report are the same localities. The master file of Pennsylvanian collecting localities in Ohio that are designated with these letters and numbers is maintained at Ohio University by M. T. Sturgeon. Dr. Sturgeon has made provision that at such time as he is no longer willing or able to maintain this file, it be transferred to the permanent record file at the Ohio Division of Geological Survey offices in Columbus.

For each locality, exposures are located by sections and fractions thereof, by reference to various natural or cultural features, and/or by reference to elevation numbers on the pertinent 1:24,000 topographic quadrangle maps, the names of which are indicated in capital letters
on each locality description. This information is followed by the name of the stratigraphic unit(s) at that locality that yielded chondrichthyan remains. Following these data are the file numbers of stratigraphic sections at the locality, if available. These sections, preceded by the designation OGS, are on file in the offices of the Ohio Division of Geological Survey. The names of identified chondrichthyan remains that occurred at a particular locality are listed with the numerical abundance of each species in parentheses. It should be noted that many localities undergo rapid changes in the quality of exposures of some stratigraphic units, particularly those localities in strip mines and some quarries (Sturgeon and Hoare, 1968).

A-1.—LOCALITIES THAT PRODUCED MICROSCOPIC CHONDRICHTHYAN REMAINS

OHIO

ATHENS COUNTY

Alexander Township

Aa1-11. Exposure in ravine, south of U.S. Rte. 50, directly south-southwest of road junction at elev. no. 677 and 0.2 mi. east of Snowden Cem., THE PLAINS. Portersville. OGS 11626. Stethacanthus altonensis (1).

Aa1-14. Exposure in ravine north of road, approximately 1.1 mi. west-southwest of road junction at elev. no. 742, west-northwest of The Plains, THE PLAINS. Skelley. OGS 11226. Maiseyodus johnsoni (1), symmoriid mucous membrane denticle (3).
Ames Township


Athens Township


Aa-64. Exposure on northeast side of U.S. Rte. 50, at north edge of Athens, behind Perkins Pancake House (Brush Creek) and continuing to steep roadcut on northeast side of U.S. Rte. 33 bypass of Athens (Ames), directly north of lower outcrop, ATHENS. Brush Creek. Cooleyella peculiaris (3), Maisyodus johnsoni (2), Moreyella typicallis (1), symmoriid muc. mem. dent. (4). Ames. Maisyodus johnsoni (1).

Canaan Township

Lee Township


Trimble Township

At-9. Exposure on southwest side of Ohio Rte. 13, 0.8 mi. north of Glouster, SE1/4, NE1/4 sec. 10, CORNING. Lower Brush Creek. OGS 6680. Cochliodont indeterminate (1), Maisyodus johnsoni (1), Sturgeonella quinqueloba (5), symmoriid muc. mem. dent. (1).


At-51. Exposure uphill along Athens County Rd. 95, on south side of tributary to Mud Fork, between elev. nos. 745 and 954, N. ctr. sec. 20, JACKSONVILLE. Brush Creek. Kirkella typicalis (1).

At-64. Exposure in east-west ravine and east along east-west trending Trimble Tp. Rd. 345 to hill top at Athens-Morgan County line, S1/2, SW1/4 sec. 1, JACKSONVILLE. Ames. OGS 11648. Maisyodus johnsoni (1), Petalodus ohioensis (1), Symmorium reniforme (2).
Waterloo Township

Aw-47. Exposure in B & O RR cut at northeast edge of New Marshfield, NW1/4, SW1/4 sec. 9, THE PLAINS. Lower Brush Creek. OGS 7617. Cobelodus aculeatus (2), Cooleyella peculiaris (6), Cooperella striatula (7), Cooperella typica lis (10), Deltodus angularis (2), dermal dent. "B" (1), dermal dent. "C" (1), dermal dent. "D" (1), Kirkella typica lis (8), Mais eyodus johnsoni (19), Moreyella typica lis (41), Ohioella merrilli (14), Peripristis semicircularis (1), Sturgeonella quinqueloba (29), symmoriid muc. mem. dent. (55), Symmorium reniforme (1), Twayella zideki (5), Williamsella striata (2), Zangerlodus williamsi (25).

Aw-58. Exposures along Ohio Rte. 56, just east of junction of Ohio Rte. 56 bypass and former Ohio Rte. 56, southwest and west into New Marshfield, SE1/4, SW1/4 sec. 9. THE PLAINS. Ames. Cooleyella peculiaris (1), Ohioella merrilli (2), Peripristis semicircularis (1), Twayella zideki (1).

CARROLL COUNTY

Center Township


Rose Township


COLUMBIANA COUNTY

Madison Township

CMA-10. Exposure on east side of Ohio Rte. 45 at top of hill, on section line between sections 16 and 21, approximately 1.9 miles south of West Point (Merrill loc. 79), NW1/4, NW1/4, NE1/4 sec. 21, WEST POINT. Ames. Dermal dent. "B" (1), Kirkella typica lis (1), Ohioella merrilli (1), Peripristis semicircularis (1), Sturgeonella quinqueloba (4), symmoriid muc. mem. dent. (25), Twayella zideki (2), Williamsella striata (1).
COSHOCTON COUNTY

Jackson Township


Lafayette Township


Oxford Township

CSo-2. Exposure on north side of U.S. Rte. 36, 0.2 miles west of junction of Blue Ridge Run and the Tuscarawas River and 1.6 miles east of Orange, SE1/4 sec. 1, FRENSO. Lower Mercer. Cooleyella peculiaris (1), Cooperella typica (1), Moreyella typica (1), Sturgeonella quinqueloba (3), Symmorium reniforme (1).

GALLIA COUNTY

Green Township

GAg-1. Exposure on east side of Northrup Patriot Rd. opposite sharp southward bend in Raccoon Creek, 1.6 miles east of Ohio Rte. 775 and 0.1 miles south of junction with Ingleside Camp Rd., NE1/4, NW1/4 sec. 26, RODNEY. OGS 12189. Portersville? Cochliodont indeterminate (1), Dermal dent. "A" (5), Lissodus zideki (1), Williamsella striata (2).

GAg-2. Exposure on north side of Taylor Rd., 0.35 miles east of Ohio Rte. 775 and 0.15 miles east of rd. elev. no. 716, NW1/4, NE1/4, NE1/4 sec. 31, RODNEY. OGS 12188. Cambridge. Sturgeonella quinqueloba (16).

GAg-3. Exposure on east side of Pleasant Hill School Rd. at sharp bend, 1.25 miles north of Ohio Rte. 141, SE1/4, NE1/4 sec. 35, RODNEY. Cambridge. Ohioella merrilli (1), Sturgeonella quinqueloba (3), uncertain petalodont (1).
Perry Township

Gap-3. Exposure on east side of Nebo Church Rd. from just north of Nebo Church to top of hill, NW1/4, NE1/4 sec. 17 and SE1/4, SW1/4 sec. 8, PATRIOT. OGS 10354. Brush Creek. Peripristis semicircularis (1).

Gap-4. Exposure in field on south side of Nebo Church Rd., 0.5 miles north of Nebo Church, SE1/4, SW1/4 sec. 8, PATRIOT. Cambridge. Dermal dent. "C" (1), Moreyella typicalis (1), Sturgeonella quinqueloba (5), Williamsella striata (1).

Gap-5. Exposure on north side of Patriot-Cadmus Rd., 0.2 miles west of Patriot (Smyth loc. 154), NE1/4, NW1/4, SE1/4 sec. 34, PATRIOT. OGS 10349. Cambridge. Janassa sp. (1), Maisodus johnsoni (4).

Springfield Township


GUERNSEY COUNTY

Cambridge Township


Gca-6. Exposure on east and west sides of Interstate 77 at milepost 49.9, NE1/4, SW1/4 sec. 22, CAMBRIDGE. OGS 16147. Brush Creek. Cooleyella peculiaris (1), symmoriid muc. mem. dent. (7).

Oxford Township

Go-1. Exposure on south side of Interstate 70, east of junction with Ohio Rte. 513, NE1/4, NW1/4, NW1/4 sec. 25, ANTRIM. Ames. Zangerlodus williamsi (1).
Valley Township

Gv-1. Exposure on east side of Interstate 77 at milepost 37.0, 1.0 miles south of Buffalo and 0.4 miles north of Guernsey/Noble County line, NE1/4, NW1/4, SE1/4 sec. 9, BYESVILLE. OGS 15953. Ames? Cooleyella peculiaris (5), Denaea saltsmani (7), dermal dent. "D" (1), hybodontid tooth "A" (1), muc. mem. dent. "A" (1), Nebraskaella ossiani (1), Ohioella merrilli (9), Stethacanthus altonensis (51), symmoriid muc. mem. dent. (8), Twayella zideki (8).

Westland Township


Wills Township


HARRISON COUNTY

Rumley Township

Har-1. Exposure on north side of Ohio Rte. 151, 0.5 miles west of Jewett, NW1/4, NE1/4, SW1/4 sec. 11, JEWETT. Ames. Cooleyella peculiaris (o), Maiseyodus johnsoni (4), Ohioella merrilli (1), Peripristis semicircularis (1), Sturgeonella quinqueloba (1), symmoriid muc. mem. dent. (5), Zangerlodus williamsi (4).
HOCKING COUNTY

Falls Gore Township


Washington Township

Hwa-1. Exposure on east side of Ohio Rte. 93, 0.3 miles north of Mt. Pleasant and Hocking-Vinton County line, W1/2, SW1/4 sec. 34, NEW PLYMOUTH. Boggs. Dermal dent. "C" (1), Peripristis semicircularis (1), Stethacanthus altonensis (1), Venustodus argutus (1), Xenacanthus tridentatus (3), Zangerlodus williamsi (1).

HOLMES COUNTY

Berlin Township


JACKSON COUNTY

Milton Township

Jmi-2. Exposure on north side of road along Buffer Run, SW1/4, SE1/4 sec. 24, MULGA. Vanport. Cobelodus aculeatus? (1), Kirkella typicalis (1), Lagarodus angustus (1).

JEFFERSON COUNTY

Wayne Township

JEwa-1. Exposure on north side of Pennsylvania RR, east of road junction at elev. no. 985, approximately 1.5 miles north of Bloomingdale, SE1/4 sec. 24, SMITHFIELD. Ames. Venustodus argutus (1).
LAWRENCE COUNTY

Decatur Township


Washington Township

Lw-2. Exposure on east side of Ohio Rte. 93 at 752 (BM) elevation on north side of Brady Run, NW1/4 sec. 23, GALLIA. Vanport. Dentition tooth "B" (1), Moreyella typica lis (4), Sturgeonella quinqueloba (6), uncertain petalodont (1).

MAHONING COUNTY

Berlin Township

Mbe-1. Exposure in valley at junction of Mill Creek and Turkey Broth Creek near Berlin Station Rd. bridge on east side of Berlin Reservoir (Smyth loc. 79), LAKE MILTON. Upper Mercer. Cochlidont indeterminate (1), Cooleyella peculiaris (1), Ohioella merrilli (1).

Green Township


Poland Township

Mp-3. Exposure in valley of Grindstone Run, on west side of road, 0.15 miles south of Lowellville. Type locality of Lowellville limestone, CAMPBELL. OGS 5014, 5029, 10935. Upper Mercer. Cooleyella peculiaris (5), Cooperella striatula (1), Cooperella typicalis (14), dermal dent. "B" (2), dermal dent. "C" (3), hybodontid tooth "A" (1), Kirkella typicalis (1), Maiseyodus johnsoni (5), Moreyella typicalis (3), Ohioella merrilli (1), Sturgeonella quinqueloba (38), Xenacanthus tridentatus (2).

MORGAN COUNTY

Malta Township


MUSKINGUM COUNTY

Blue Rock Township

MUbr-6. Exposure along road, SE1/4 sec. 16, RURALVALE. Skelley. Peripristis semicircularis (1).

Falls Township


Hopewell Township

**MUho-14.** Exposure on north side of Interstate 70 at milepost 146.35, 0.65 miles south-southwest of Mt. Sterling (Hopewell P.O.) and 0.75 miles east of underpass of road leading south from Hopewell, SE1/4 oversized sec. 3, GRATIOT. OGS 16001. Columbiana. Cooleyella peculiaris (3), *Xenacanthus tridentatus* (1).

**Jefferson Township**

**MUje-1.** Exposure on west side of Ohio Rte. 90, 0.1 miles south of Dresden corporation boundary, NE1/4, NE1/4 oversized sec. 3, DRESDEN. OGS 16640. Lower Mercer. *Stethacanthus altonensis* (1).

**Muskingum Township**

**MUmu-3.** Exposures in valley of Blunt Run beginning at end of Frame Rd., 0.7 miles east of Stringtown and 0.4 miles west of the Muskingum River, DRESDEN. OGS 719, 722. Lower Mercer. Cooleyella peculiaris (1), Cooperella striatula (1), *Kirkella typicallis* (1), *Ohioella merrillii* (1), uncertain petalodont (1).

**MUmu-4.** Exposure along Muskingum Co. Rd. 2 or 416, Dresden Rd., opposite Twin Hills farm buildings, approximately 0.5 miles south of crossing with Conrail (abandoned) and N&W RR, DRESDEN. Putnam Hill. Cooperella typicallis (1), dermal dent. "E" (1), dermal dent. "F" (1), Moreyella typicallis (5), symmoriid muc. mem. dent. (4), *Williamsella striata* (1).

**Springfield Township**

**MUsp-1.** Exposure at dugway along Muskingum Ave. at Putnam Hill, on west side of the Muskingum River, in the city of Zanesville, NE1/4 sec. 1 (type locality for Putnam Hill limestone), ZANESVILLE WEST. OGS 788. Putnam Hill. Cooleyella peculiaris (2), *Sturmeonella quinqueloba* (1).

**MUsp-4.** Exposure on township road 422, north of road junction at elev. no. 779, NE1/4 sec. 16, ZANESVILLE W-ST. Lower Mercer. *Stethacanthus altonensis* (1).

**Union Township**

**MUu-5.** Exposure on either side of Interstate 70 at milepost 167.1, 0.1 miles east of overpass and 0.25 miles southeast of Sundale, SE1/4, NW1/4, NE1/4 sec. 14, NORWICH. OGS 16580. Ames. *Petalodus ohioensis* (1).
NOBLE COUNTY

Buffalo Township

Nbu-1. Pit of Ava Brick Co. (inactive), north of Ava on east side of Ohio Rte. 821, SE1/4, NW1/4 sec. 21 (type locality of the Noble limestone), CALDWELL NORTH. OGS 15894. Noble. Cooleyella peculiaris (16), Cooperella striatula (2), Cooperella typicus (1), dermal dent. "C" (6), Kirkella typicus (4), Lissodus duffini (4), Maiseyodus johnsoni (8), Moreyella typicus (3), Sturgeonella quinqueloba (14), symmoriid muc. mem. dent. (24), Twayella zideki (4).


Nbu-4. Exposure on north side of Ohio Rte. 821 at sharp "U" bend in road, 0.4 miles northwest of Ava Brick Plant, N1/2, SW1/4, SW1/4 sec. 30, CALDWELL NORTH. Ames. Cooleyella peculiaris (3), Maiseyodus johnsoni (8), Moreyella typicus (2), Nebraskella ossiani (1), Ohioella merrilli (7), symmoriid muc. mem. dent. (12), Twayella zideki (2), Zangerlodus williamsi (5).

Noble Township

Nn-3. Roadcuts on east and west sides of Interstate 77, 0.5 miles south of Ohio Rte. 821 exit at Belle Valley, SW1/4, SE1/4 sec. 20, CALDWELL NORTH. Ames. Cochliodont indeterminate (1), Cooleyella peculiaris (5), Maiseyodus johnsoni (11), Sturgeonella quinqueloba (6), symmoriid muc. mem. dent. (6), Zangerlodus williamsi (4).

Nn-13. Exposure on east side of Ohio Rte. 821, 1.1 miles north of Coal Ridge and 0.7 miles south of Ava, NW1/4, NE1/4, NW1/4 sec. 7, CALDWELL NORTH. OGS 15056. Cambridge. Cooleyella peculiaris (8), Cooperella striatula (1), Cooperella typica (1), Denaea saltsmanii (1), Maiseyodus johnsoni (12), Moreyella typica (4), Sturgeonella quinqueloba (6), symmoriid muc. mem. dent. (17), Twayella zideki (2).

PERRY COUNTY

Bearfield Township

Pb-1. Abandoned Wabash RR tunnel cut (railroad never built), N1/2, SW1/4 sec. 24 (type locality for Portersville), DEAVERTOWN. OGS 10375. Portersville. Cobelodus aculeatus (7), Stethacanthus altonensis (1).

Pb-3. Exposure along road east of road junction at elev. no. 881, SE1/4, NE1/4 sec. 12, DEAVERTOWN. Brush Creek. Cooleyella peculiaris (1), Denaea saltsmanii (1), dermal dent. "A" (1), Maiseyodus johnsoni (4), Symmorium reniforme (1).


Monday Creek Township


Monroe Township


SCIOTO COUNTY

Vernon Township


SCve-3. Small exposure on top of hill east of Boggs Rd., near Howard Furnace, and 1.2 miles east of Lyra, ctr. NW1/4 sec. 12, PEDRO. Vanport. Deltodus angularis (1), Sturgeonella quinqueloba (1).

STARK COUNTY

Bethlehem Township

Sb-4. Exposure in first valley south of north section line of sec. 22, east side of Tuscarawas River, on Ben Willins farm (formerly J. Hair), NE1/4, NW1/4, NW1/4 sec. 22, BOLIVAR. Lower Mercer. Cooleyella peculiaris (3), Cooperella striatula (1), Cooperella typicalis (3), Maiseyodus johnsoni (2), Ohioella merrilli (2), Periprisis semicircularis (1), Sturgeonella quinqueloba (2).

Canton Township

Sc-6. Pit of Metro Brick Co. (abandoned), on west side of Interstate 77 at milepost 102.6, on south edge of Canton, NE1/4 sec. 20, CANTON WEST. OGS 5289, 5290. Putnam Hill. Sturgeonella quinqueloba (1).

Pike Township

Spk-1. Exposure on east side of Interstate 77 at milepost 95.2, and abandoned strip mines in N1/2 of sec. 30, north of Gracemont St., BOLIVAR. OGS 13503, 13504. Putnam Hill. Symmoriid muc. mem. dent. (2), Symmorium reniforme (1).

Sandy Township

Ss-4. D & M Coal Co. strip mine, SE1/4 sec. 10, MALVERN. Columbiana. Dentition tooth "A" (1).
TUSCARAWAS COUNTY

Dover Township


Fairfield Township

Tf-1. Exposure on west side of Ohio Rte. 800, opposite Dover Dam on the Tuscarawas River, NW1/4, SW1/4 sec. 6, DOVER. Putnam Hill. Cooperella typica (4).

Franklin Township

Tfr-1. Exposure on south side of Sugar Creek, just downstream from Beach City dam, w. ctr. sec. 1, NAVARRE. OGS 13327. Lowellville. Maisyodus johnsoni (1), Ohioella merrillii (1).

Goshen Township

Tg-1. Exposure on south side of U.S. Rte. 250, approximately 0.3 miles east of junction of Interstate 77 and U.S. Rte. 250, on south edge of New Philadelphia, NEW PHILADELPHIA. OGS 12216. Putnam Hill. Sturgeonella quinqueloba (4), Symmoriid reniforme (1).

Jefferson Township

Tj-2. Strip mine, 0.75 miles west of Interstate 77 and 0.5 miles north of Blackband, STONE CREEK. Washingtonville. Stethacanthus altonensis (1), Symmoriid reniforme (1).

Lawrence Township

Tl-1. Pit of Bolivar Clay Products Co. (abandoned), west side of N & W RR, on west edge of Bolivar, BOLIVAR. OGS 1914, 4996. Lower Mercer. Cooleyella peculiaris (1), Cooperella typica (1), Maisyodus johnsoni (1), symmoriid muc. mem. dent. (1), Xenacanthus tridentatus (1).
Tl-7. Exposure along Tuscarawas Co. Rd. 103 (Norris Orchard Rd.) just east of rd. junction at elev. no. 913, on east side of Tuscarawas River, and east-southeast of Bolivar. (This portion of the road now abandoned) BOLIVAR. Lower Mercer. Cooleyella peculiars (1), Denaea saltsmani (1), Maiseyodus johnsoni (1), Ohioella merrilli (1), Xenacanthus tridentatus (3).

Sandy Township


Warwick Township

Twa-1. Abandoned strip mines, southwest side of Fox Valley, and extending into Clay Tp., SW1/4 sec. 4, NEW PHILADELPHIA. Columbiana. Symmoriid muc. mem. dent. (1).

York Township

Ty-3. Abandoned borrow pit and strip mine of Zoar Mining Co., east side of Interstate 77 and Stone Creek, NW1/4 sec. 17, NEW PHILADELPHIA. Putnam Hill. Cochliodont indeterminate (1), Cooleyella peculiars (1), Lagarodus angustus (1), Petalodus ohioensis (1), Venustodus argutus (1).


VINTON COUNTY

Clinton Township

Vc-8. Exposure on Clinton Tp. Rd. 194, approximately 100 yards north of the junction of this road and Vinton Co. Rd. 40, at elev. no. 767, SW1/4, SW1/4 sec. 19, HAMDEN. "Lower Mercer". Cooperella typicalis (1), Maiseyodus johnsoni (1), symmoriid muc. mem. dent. (1), Williamsella typicalis (1).
Vc-9. J. Hall strip mine (Quality Coal Co.), on north side of Ohio Rte. 324, NW1/4 sec. 14, MCARTHUR. Vanport. Cooperella typicalis (2), Maiseyodus johnsoni (1), Sturgeonella quinqueloba (1), symmoriid muc. mem. dent. (5), Xenacanthus tridentatus (1)

Elk Township


VeI-7. Exposures at tipple (abandoned) of Vinton Coal Co., on north side of U.S. Rte. 50, SW1/4, NE1/4 sec. 18, ALLENSVILLE. "Lower Mercer". Cooleyella peculiars (2), Cooperella striatula (4), Cooperella typicalis (8), Kirkella typicalis (3), Moreyella typicalis (3), Sturgeonella quinqueloba (73), symmoriid muc. mem. dent. (5), Xenacanthus tridentatus (2).


VeI-31. Exposure in abandoned strip mines on south side of east–west trending Elk Tp. Rd. 20, approximately 0.5 miles west of bend in road at elev. no. 936, NE1/4 sec. 30, HAMDEN. Vanport. Sturgeonella quinqueloba (1).

VeI-34. Exposure on south side of U.S. Rte. 50, NE1/4, NE1/4 sec. 27, MCARTHUR. "Lower Mercer". Cooperella typicalis (3), Kirkella typicalis (1), Maiseyodus johnsoni (11), Ohioella merrilli (8), symmoriid muc. mem. dent. (7), Venustodus argutus (1).

Richland Township

WASHINGTON COUNTY

Newport Township

Wn-1. Exposure on north side of Ohio Rte. 7, on north side of Ohio River, 1.1 miles west of Newport and 1.0 miles east of Newell Run, N1/2, NW1/4 sec. 33, BELMONT, RAVEN ROCK. OGS 15327. Ames. Cooleyella peculiaris (1), Symmorium reniforme (4).

OTHER STATES

COLORADO

CO-1. Exposures near McCoy, Eagle County, NW1/4, NE1/4, NW1/4 sec. 1, T.2S, R.84W, BLUE HILL. Robinson Member of Minturn Formation. Lagarodus angustus (14).  


KENTUCKY

KY-1. Roadcut at milepost 51, north of and adjacent to the Rockcastle River bridge on Interstate 75, Rockcastle County, BERNSTADT. Pennington (Chesterian). Xenacanthus tridentatus (1).  

KY-2. Exposure in abandoned borrow pit along old U.S. Rte. 23, north from Savage Branch Rd., Boyd County, BURNAUGH. OGS 16669. Lower Brush Creek. Denaea saltmanii (3).

MONTANA

MT-1. Exposure in SE1/4, sec. 34, T.8S, R.11W, Beaverhead County, ELI SPRINGS. Heath Formation (Chesterian) or Alaska Bench Formation (Morrowan). Xenacanthus tridentatus (1).
OKLAHOMA

OK-1. Exposure in gully, approximately 2 miles east and 2 miles south of Homer, S1/2, NW1/4, SW1/4 sec. 4, T.3N, R.7E, Pontotoc County, FRANCIS. Locality originally known as Lovelady School (Mapes, 1979, p. 10, loc. P-8). Wewoka Formation. Phoebodus heslerorum (1), Xenacanthus tridentatus (5).


OK-3. Exposure on north side of Delaware Creek, 300 feet east of bridge on Oklahoma Rte. 48, approximately 2 miles north of Wapanucka, Johnston County, SW1/4, SW1/4, NW1/4 sec. 1, T.2S, R.8E, WAPANUCKA NORTH. Atoka Formation. Ohioella merrilli (18).

PENNNSYLVANIA

PA-1. Rip-rap blocks (now removed) on east side of Pennsylvania Rte. 286, 2.05 miles south of overpass of Pennsylvania Rte. 380, Allegheny County, MURRAYSVILLE. Ames. Maiserodus johnsoni (10), Phoebodus heslerorum (1).

PA-2. Roadcut on north side of U.S. Rte. 22, 2.3 miles west of Murrysville and 0.9 east of the Pittsburgh exit of the Pennsylvania Turnpike, Allegheny County, MURRAYSVILLE. Ames. Cooleyella peculiaris (3), Maiserodus johnsoni (1).

PA-3. Roadcut on north side of Pennsylvania Rte. 130 (Broadway Ave.), 1.2 miles west of Pennsylvania Rte. 130 and Pennsylvania Rte. 48 junction at Pitcairn, Allegheny County, MURRAYSVILLE. Ames. Cooleyella peculiaris (2), Cooperella striatula (3), Cooperella typicalis (2), Lissodus zideki (4), Maiserodus johnsoni (8), Morevella typicalis (4), Ohioella merrilli (13), Sturgeonella quinqueloba (17), symmoriid muc. mem. dent. (4), Williamsella striata (19).
PA-4. Exposure at building excavation on north side of Old William Penn Highway, next of Meier's Hardware store, 0.4 miles from junction of U.S. Rte. 22 and William Penn Highway, just west of Export, Westmoreland County, MURRAYSVILLE. Ames. Cooleyella peculiaris (13), Cooperella striatula (3), Cooperella typicallis (2), Denaea saltsmani (29), Kirkella typicallis (1), Lissodus zideki (1), Maiseyodus johnsoni (17), Sturgeonella quinqueloba (2), Twavella zideki (3).


PA-9. Pit of Carbon Limestone Co. (abandoned), 1.25 miles northeast of Bessemer, Lawrence County, BESSEMER. Vanport. Lagarodus angustus (1).

A-2.-LOCALITIES THAT YIELDED NO MICROSCOPIC
CHONDRICHTHYAN REMAINS

OHIO

ATHENS COUNTY

Ames Township

Aam-10. Exposure in creek bed, along road and uphill, NE1/4, SW1/4 and SE1/4, NW1/4 sec. 25, JACKSONVILLE. Skelley. OGS 8975.

Athens Township

Aa-1. Exposure near hilltop, northeast side of Ohio Rte. 13, approximately 0.1 mile northwest of junction of Ohio Rte. 13 and U.S. Rte. 33 at elev. no. 659, NW1/4, SE1/4 sec. 18, ATHENS. Lower Brush Creek. OGS 11484.

Dover Township

Ad-49. Steep road cut north of junction of U.S. Rte. 33 and Ohio Rte. 682 at southeast edge of Beaumont, NELSONVILLE. Upper Brush Creek. OGS 15062.

Trimble Township

At-3. Exposures along road from east of 711 road intersection towards Bishopville, CORNING. Brush Creek. OGS 6675.

At-45B. See list A-1 for description. Cambridge.

At-51. See list A-1 for description. Cambridge.

Waterloo Township

Aw-57. Exposure just northwest of spillway on northwest side of Fox Lake Dam, THE PLAINS. Brush Creek.

York Township

Ay-56. Exposure on northeast side of U.S. Rte. 33, approximately 0.25 miles east of Athens-Hocking County line, UNION FURNACE. Putnam Hill. OGS 14301.
COLUMBIANA COUNTY

Center Township

Cc-4. Exposures in vicinity of Excelsior Clay Products Co. and along Ohio Rte. 164, LISBON. Washingtonville. OGS 5263.

Madison Township

Cma-11. Exposure along secondary road just south of junction with Hammond School Road, 0.8 miles east of Ohio Rte. 45, WEST POINT. Cambridge.

COSHOCTON COUNTY

Jackson Township

CSj-3. Exposure on north side of east-west road, just east of 864 road junction, on east side of Simmons Run, RANDLE. Lower Mercer, Upper Mercer. OGS 6242.

Oxford Township

CSo-2. See list A-1 for description. Upper Mercer, Putnam Hill.

GALLIA COUNTY

Addison Township

GAA-1. Exposure on east side of Bulaville-Porter Road, on south bank of east-flowing tributary of Little Chickamauga Creek and 1.1 miles north of U.S. Rte. 35, NW1/4, NE1/4, NE1/4 sec. 31, GALLIPOLIS. Ames.

Gallipolis Township

GAg-1. Exposure on northeast side of Ohio Rte. 160, 0.1 miles south of U.S. Rte. 35 and 0.4 miles northeast of Hanersville, SW1/4, SE1/4, NW1/4 sec. 36, GALLIPOLIS. Ames.

Perry Township

GAp-2. Exposure on south side of Ohio Rte. 141, 0.7 miles southwest of Gage, SE1/4, SW1/4, NE1/4 sec. 28, PATRIOT. Cambridge. OGS 12202.
Walnut Township

GAw-1. Exposure on east side of Hannan kTrace Road, 0.85 miles southeast of Patriot and Ohio Rte. 775, NWE1/4, NW1/4, NE1/4 sec. 2, RODNEY. Cambridge.

GUERNSEY COUNTY

Jackson Township

Gja-2. Exposure on west side of Interstate 77 at milepost 40, 1.8 miles south of Byesville (Ohio Rte. 209) exit, just north of rest area on east (northbound) side, w. ctr. sec. 3, BYESVILLE. Brush Creek. OGS 15936.

Oxford Township

Go-1. See list A-1 for description. Noble.

Westland Township

Gwe-4. Exposure near top of hill on southwest side of Interstate 70 at milepost 173.2, 0.3 miles east of overpass and 0.4 miles southwest of weigh station, NW1/4 oversized sec. 1, NEW CONCORD. Cambridge. OGS 16528.

HOLMES COUNTY

Berlin Township

HOb-2. Strip mine of Holmes Limestone Company, east of U.S. Rte. 62 and 0.6 miles northeast of Bunker Hill, SW1/4, NW1/4, NE1/4 sec. 7, BERLIN. Columbiana.

JACKSON COUNTY

Lick Township

Jli-1. Exposure on south side of exit ramp from westbound Ohio Rte. 124 onto northbound U.S. KRte. 35, 0.7 miles southeast of Jackson, SW1/4, SE1/4, NE1/4 sec. 28, WELLSTON. "Lower Mercer".
MAHONING COUNTY

Poland Township

Mp-4. Exposure in bed of Yellow Creek, south of bridge and just east of Ohio Rte. 616, 0.4 miles south of Lake Hamilton, at the north edge of Poland (Merrill loc. 27), CAMPBELL. Lower Mercer. OGS 5027.

MORGAN COUNTY

Deerfield Township

MOd-3. Exposure along road on ridge south of Island Run, s. ctr. sec. 4, ROKEBY LOCK. Ames.

York Township

MOy-7. Exposure along Ohio Rte. 669, northeast of Tropic Station, NW1/4, NE1/4 sec. 34, DEAVERTOWN. Brush Creek. OGS 8058.

MUSKINGUM COUNTY

Blue Rock Township

MUbr-1. Exposure in Coal Hollow, SW1/4, NW1/4 sec. 29, PHILO. Gaysport.

Falls Township

MUf-5. Exposure on north side of Interstate 70 at milepost 151.4, just east of overpass, SW1/4, SE1/4 oversized sec. 3, ZANESVILLE WEST. Putnam Hill. OGS 15989.

Hopewell Township

MUho-1. Exposure in south-southeast trending valley on west side of road, sec. 18, GRATIOT. Lower Mercer.

Jackson Township

MUj-1. Exposure along Mt. Zion Rd (Co. Rd. 313) near road elev. no. 1078 in northeast corner of the township, TRINWAY. Putnam Hill.
Madison Township

MUMa-3. Exposures along Symmes Creek at Stoner Cemetery, at bridge elev. no 729 (Symmes Ford), 0.6 miles northeast of the Muskingum River, ADAMSVILLE. Lower Mercer, Upper Mercer, Putnam Hill. OGS 513, 520.

MUMa-4. Exposure on east side of Ohio Rte. 666 and the Muskingum River, 0.5 miles northeast of Rock Cut and just south of elev. no. 709 at the mouth of Symmes Creek, ADAMSVILLE. Lower Mercer, Upper Mercer. OGS 516.

Newton Township

MUN-3. Abandoned quarry on west side of former Ohio Rte. 93 (not bypass), 0.3 miles north of the Muskingum-Perry County line and approximately 1 mile north of Roseville, NE1/4, SE1/4 sec. 33, TOPO. Putnam Hill.

Noble County

Noble Township

NN-1. Exposure on west side of stream bank behind Belle Valley Jr. High School, in town of Belle Valley, SW1/4, NE1/4 sec. 20, CALDWELL NORTH. Portersville. OGS 12896.


Perry County

Harrison Township

PHA-4. Exposure along west side of Ohio Rte. 93 near boundary between secs. 20 and 21, CROOKSVILLE. Putnam Hill.

Monroe Township

Reading Township

Pr-3. Exposures in B&O RR cut at Somerset, NW1/4 sec. 10, SOMERSET. Lower Mercer.

PORTAGE COUNTY

Atwater Township

POa-1. Strip mines in vicinity of junction of Ohio Rtes. 224 and 225, approximately 2.3 miles west of Deerfield and 2.2 miles south of Yale, DEERFIELD. Lower Mercer.

STARK COUNTY

Bethlehem Township


Paris Township

Sp-1. Kefer and Rose strip mine, west side of U.S. Rte. 30, approximately 1.5 miles west of Minerva, SW1/4, NE1/4 sec. 34, MALVERN. Washingtonville.

Pike Township


TUSCARAWAS COUNTY

Lawrence Township


Sandy Township

Ts-9. Strip mines of Zoar Mining Co., SW1/4, NW1/4 sec. 6, BOLIVAR. Columbiana. OGS 16224.

Salem Township

Tsa-6. Exposure on east side of Interstate 77 at milepost 68.2, across from Hardings Antiques store, ctr. irregular sec. 13, NEWCOMERS TOWN. Putnam Hill. OGS 12230.
VINSON COUNTY

Elk Township


Vel-20. Abandoned strip mines, E. ctr. and NE1/4 sec. 15, ZALESKI. "Lower Mercer"?

Vel-23. Abandoned strip mine, SW1/4 sec. 23 and NW1/4 sec. 26, MCArTHUR. Vanport. OGS 78, 79.

Richland Township

Vr-1. Exposure on north side of road, SE1/4 sec. 13, HAMDEN. "Lower Mercer".

WAYNE COUNTY

Baughman Township

WAb-1. Exposure on west side of Deerfield Ave. on Wayne-Stark County line, 0.2 miles north of Pennsylvania RR and Newman Creek, DALTON. Lower Mercer. OGS 11422.

Salt Creek Township

WAsa-1. Exposure in small valley on east side of Ohio Rte. 94, 0.4 miles south of Maysville Church (Smyth loc. 89), E. ctr. sec. 4, FREDERICKSBURG. Upper Mercer.
A-3. Localities from Which Samples Did Not Disaggregate

Ohio

Athens County

Ames Township


Trimble Township

At-62. Exposure along Ohio Rte. 13 between Jacksonville and Trimble, NE1/4, SE1/4 sec. 8, JACKSONVILLE. Lower Brush Creek. OGS 11494.

Guernsey County

Cambridge Township

Gca-3. Exposure on southeast side of exit ramp from Interstate 77 (northbound) onto Interstate 70 (eastbound), S. ctr. sec. 4, CAMBRIDGE. Cambridge. OGS 12211.

Morgan County

Deerfield Township

Kod-1. Exposure along road southeast of road junction at elev. no. 787, south of Island Run, NE1/4, NE1/4, NW1/4 sec. 2, ROKEBY LOCK. Brush Creek. OGS 7837.

York Township

MoY-6. Exposure along road east-southeast of Deavertown, W. ctr. sec. 31, DEAVERTOWN. Brush Creek. OGS 8063.

Muskingum County

Hopewell Township

Muho-3. Exposure at abandoned G. L. Porter mine, at junction of Hopewell Tp. rd. 415 and Interstate 70, approximately 0.5 miles south of Hopewell, NW1/4 sec. 3, GRATIOT. Putnam Hill.
MUho-15. Exposure on south side of Interstate 70, along eastbound approach from county road, at milepost 139.9, sec. 6, GRATIOT. OGS 14989. Lower Mercer.

MUho-13. Exposure in roadcut on north side of east-west road, 3.0 miles west of Dillon Falls, ZANESVILLE WEST. Columbiana.

MUho-15. Abandoned strip mine on east side of Black Road, NE1/4, NW1/4 sec. 11, GRATIOT. Vanport.

Muskingum Township


PERRY COUNTY

Hopewell Township

Pho-3. Highwall and spoil banks of pit of Central Silica Co. (abandoned), on southwest side of Sand Rock Rd. (Perry Co. Rd. 36), 0.55 miles south of Goodhope Church, SE1/4 sec. 4, SW1/4 sec. 3, NE1/4 sec. 9, NW1/4 sec. 10, GLENFORD. Boggs. OGS 14898.

Monday Creek Township

Pmc-1. Exposure in ravine on southeast side of northeast-southwest road, ctr. sec. 9, JUNCTION CITY. Lower Mercer.

Reading Township

Pr-2. Exposure along road, 0.5 miles south of St. Joseph's Priory, north of center branch of Rush Creek, ctr. sec. 23, SOMERSET. Lower Mercer. OGS 8350.

Pr-8. Exposure along Ohio Rte. 668, 0.8 miles south of Somerset, NW1/4, NW1/4 sec. 15, SOMERSET. Lower Mercer.

Salt Lick Township

Ps1-1. Exposure in ravine, SE1/4, SE1/4 sec. 5, NEW LEXINGTON. Putnam Hill. OGS 8297.

TUSCARAWAS COUNTY

Dover Township

Goshen Township

Tg-1. See list A-1 for description. Vanport.

VINTON COUNTY

Elk Township

Vel-12. Strip mine (abandoned) of Vinton Coal Co., on northeast side of road, 1.1 miles north-northwest of road junction at elev. no 799, ctr. sec. 20 and NW1/4 sec. 17, ALLENSVILLE and ZALESKI. Putnam Hill. OGS 238.
PLATES

All images are scanning electron micrographs
Xenacanthus tridentatus

Figures 1-3.- OSU 35354, Upper Mercer, Mp-3. 1, labial; 2, oral; 3, lateral.

Figure 4.- OSU 35358, Boggs, Hwa-1. Oral view.

Figures 5, 6.- OSU 35367, Heath Formation?, MT-1. 5, labial; 6, oral.

Figure 7.- OSU 35376, Lower Mercer, Tl-1. Oral view.

Figure 8.- OSU 35370, Lower Mercer, Tl-7. Oral view

Figure 9.- OSU 35357, Lower Mercer, Tl-7. Aboral view.

Figure 10.- OSU 35355, Upper Mercer, Mp-3. Oral view.


Bar scales represent 0.5 mm.
PLATE II

Zangerlodus williamsi n. g., n. sp.

Figure 1.- OSU 35361a, Ames, Nn-3. Oral view.

Figure 2.- OSU 35360, Upper Mercer, Mp-3. Lingual view.

Figures 3-6, OSU 35361b, Ames, Nn-3. 3, oral; 4, lingual; 5, lateral; 6, labial.

Figures 7-9.- OSU 38628, Noble, Nbu-1, symphyseal? tooth. 7, labial; 8, oral; 9, lingual.

Figure 10.- OSU 35369, Cambridge, Nn-13. Aboral view.

Figures 11-14.- OSU 35368, holotype, Cambridge, Nn-13. 11, oral; 12, lingual; 13, lateral; 14, labial.

Figures 15-17.- OSU 38641, Ames, Gwi-3. 15, aboral; 16, labial; 17, lingual.

Bar scales represent 0.5 mm.
PLATE III

HYBODONE

Figures 1, 2.- *Lissodus duffini* n. sp. OSU 35445, Noble, Nbu-1. 1, oral; 2, labial.

Figures 3-5.- *Lissodus duffini* n. sp., OSU 38630, holotype, Noble, Nbu-3. 9, labial; 10, lingual; 11, labiolingual; 12, oral.

Figures 6-8.- *Maiseyodus johnsoni* n. g. n. sp., OSU 35416, Ames, PA-4, symphyseal? tooth. 6, labial; 7, lingual; 8, oral-labial.

Figures 9-12.- *Maiseyodus johnsoni*, OSU 35383, "Lower Mercer", Vel-34, holotype. 9, labial; 10, lingual; 11, labiolateral; 12, oral.

Figure 13.- *Maiseyodus johnsoni*, OSU 35363a, "Lower Mercer", Vel-34. Lingual.

Figure 14.- *Maiseyodus johnsoni*, OSU 35363b, "Lower Mercer", Vel-34. Labial.

Figure 15.- *Maiseyodus johnsoni*, OSU 35363a, "Lower Mercer", Vel-34. Labial.


Figure 18.- *Maiseyodus johnsoni*, OSU 35363d, "Lower Mercer", Vel-34. Oral.

Figure 19. *Maiseyodus johnsoni*, OSU 35363c, "Lower Mercer", Vel-34. Oral-lingual.


Figures 24-26.- *Lissodus zideki*, OSU 35362, "Portersville", GAgr-1. 24, oral; 25, labial; 26, lingual.

Bar scales represent 0.5 mm.
PLATE IV

SYMMORIIDS

Figure 1.- *Denaea saltsmanii* n. sp., OSU 38639, Lower Brush Creek, KY-2. Aboral.

Figures 2-5.- *Denaea saltsmanii* n. sp., OSU 38638, holotype, Lower Brush Creek, KY-2. 2, lateral; 3, labial; 4, oral; 5, lingual.

Figures 6-8.- *Denaea meccaensis*, OSU 35423a, Wewoka, OK-1, 6, labial; 7, lingual; 8, oral.

Figures 9-11.- *Denaea meccaensis*, OSU 35423b, Wewoka, OK-1. 9, labial; 10, aboral; 11, oral.

Figure 12.- *Cobelodus aculeatus*, OSU 35359a, Brush Creek, Aw-47, mandibular tooth. Labial. Bar scale represents 0.25 mm.

Figure 13.- *Cobelodus aculeatus*, OSU 35359b, Brush Creek, Aw-47, mandibular tooth. Lingual. Bar scale represents 0.25 mm.

Figure 14.- *Cobelodus aculeatus*, OSU 38666, Portersville, At-45B, palatoquadrate tooth. Anterolateral.

Figure 15.- *Cobelodus aculeatus*, OSU 38601, Ames, PA-3, palatoquadrate tooth. Lateral.

Figures 16-18.- *Stethacanthus altonensis*, OSU 35143, Portersville, Aal-11. 16, labial; 17, oral; 18, lateral.

Figure 19.- *Symmorium reniforme*, OSU 35433, Ames, Aa-63. Aboral.

Figure 20.- *Symmorium reniforme*, OSU 35432, Putnam Hill, Tg-1. Oral.

Bar scales represent 0.5 mm except where noted.
PLATE V

Cooleyella peculiaris

Figures 1, 2.- OSU 35394a, Portersville, At-45B, parasymphysial? tooth. 1, labial; 2, lingual.

Figures 3, 4.- OSU 38645, Noble, Nbu-1, parasymphysial? tooth. 3, oral; 4, lingual.

Figures 5, 6.- OSU 38642, Ames, Nbu-4. 5, labiolateral; 6, labial.

Figure 7.- CM 27243, Ames, CA1-3. Oral.

Figures 8, 9.- OSU 35386, Lower Mercer, MUmu-3. 8, labio-oral; 9, lateral.

Figure 10.- OSU 38643b, Portersville, At-45B. Aboral.

Figure 11.- OSU 38643c, Portersville, At-45B. Aboral.

Figure 12.- OSU 38637, Ames, PA-5. Aboral.


Figure 16.- OSU 38637, Ames, PA-5. Lateral.

Figure 17.- OSU 38643a, Portersville, At-45B. Labio-oral.

Figure 18.- OSU 35394b, Portersville, Aw-47. Labio-oral.

Bar scales represent 0.5 mm.
PLATE VI

HYBODONTS AND OTHER TEETH

Figures 1, 2.—Hybodont tooth "A", OSU 38361, Upper Mercer, Mp-1. 1, labial; 2, oral.

Figures 3, 4.—Hybodus? sp., OSU 38633, Ames, PA-3. 3, labial; 4, oral.

Figures 5, 6.—Tooth whorl of presumed hybobont, OSU 38634, Ames, PA-3. 5, lateral; 6, labial.

Figure 7.—Venustodus argutus, OSU 38622, Lower Mercer, MUsp-4. Incomplete tooth in oral view.

Figures 8, 9.—Venustodus argutus, OSU 35436, "Lower Mercer", Vel-34. 8, oral; 9, lingual.

Figure 10.—Dentition tooth "A", OSU 35167, Washingtonville, CAr-2. Oral-lateral view.

Figures 11, 12.—Dentition tooth "B", OSU 38615, Vanport, Lw-2. 11, labial; 12, lateral.

Figures 13, 14.—Phoebodus heslerorum, OSU 35438, Vanport, Ld-1. 13, labial; 14, lingual.

Figures 15, 16.—Lagarodus angustus, OSU 35352, Putnam Hill, Ty-3. 15, lateral; 16, lingual view of a portion of the specimen.

Bar scales represent 0.5 mm.
PLATE VII

DERMAL DENTICLES

Figures 1-3.- Cooperella striatula, OSU 38652, "Lower Mercer", Vel-7. 1, anterior; 2, lateral; 3, posterior. Bar scale represents 0.25 mm.

Figure 4.- Cooperella striatula, OSU 38667. Anterior view. Bar scale represents 0.25 mm.

Figures 5-8.- Cooperella typicallis, OSU 38653, Upper Mercer, Mp-3. 5, anterior; 6, lateral; 7, apico-anterior; 8, posterior. Bar scale represents 0.25 mm.

Figure 9.- Cooperella striatula, OSU 38649, "Lower Mercer", Vel-7. Anterior view. Bar scale represents 0.25 mm.

Figure 10.- Cooperella striatula, OSU 38650, "Lower Mercer", Vel-7. Anterior. Bar scale represents 0.25 mm.

Figure 11.- Nebraskella ossiani n. g., n. sp., OSU 35450a, Ames, Acn-31. Anterolateral view. Bar scale represents 0.5 mm.

Figures 12, 13.- Nebraskella ossiani n. g., n. sp., OSU 35449, Portersville, At-45B. 12, anterior; 13, lateral. Bar scale represents 0.5 mm.

Figures 14, 15.- Kirkella typicallis, OSU 38646, Vanport, Jmi-2. 14, apical; 15, lateral. Bar scale represents 0.5 mm.

Figure 16.- Kirkella typicallis, OSU 38651, Lower Mercer, MUmu-3. Apical. Bar scale represents 0.25 mm.

Figure 17.- Kirkella typicallis, OSU 38644, Ames, Cma-10. Apical view. Bar scale represents 0.25 mm.

Figure 18.- Kirkella typicallis, OSU 38648, Ames, PA-3. Lateral view. Bar scale represents 0.5 mm.

Figure 19.- Kirkella typicallis, OSU 38647, Portersville, At-45B. Lateral. Bar scale represents 0.25 mm.
PLATE VIII

Moreyella typicalis and Twayella zideki n. g., n. sp.

Figures 1, 2.- Moreyella typicalis, OSU 38654, "Lower Mercer", Vel-7. 1, anterior; 2, lateral.

Figures 3-5.- Moreyella typicalis, OSU 38657, Portersville, Aw-47. 3, anterior; 4, lateral; 5, posterior.

Figure 6.- Moreyella typicalis, OSU 38656, Portersville, Aw-47. Anterolateral view.

Figures 7, 8.- Moreyella typicalis, OSU 38620, Putnam Hill, CSo-2. 7, lateral; 8, anterior.

Figure 9.- Moreyella typicalis, OSU 38635a, Portersville, At-45B. Basal view.

Figures 10, 11.- Moreyella typicalis, OSU 38635b, Portersville, At-45B. 10, lateral; 11, anterior.

Figures 12, 13.- Moreyella typicalis, OSU 38635c, Portersville, At-45B. 12, anterior; 13, lateral.


Figure 17.- Twayella zideki n. g., n. sp., OSU 38653, Portersville, At-45B. Anterior.

Figures 18-20.- Twayella zideki n. g., n. sp., OSU 35448, holotype, Ames, Acn-31. 18, anterior; 19, posterior; 20, lateral.

Figures 21, 22.- Twayella zideki n. g., n. sp., OSU 38627, Portersville, Aw-47. 21, lateral; 22, anterior.

Bar scales represent 0.25 mm.
PLATE IX

Ohioella merrilli n. g., n. sp.

Figures 1-4.- OSU 35446, holotype, "Lower Mercer", Vel-34. 1, anterior; 2, antero-apical; 3, lateral; 4, posterior.

Figure 5.- OSU 35447a, "Lower Mercer", Vel-34. Anterior.

Figure 6.- OSU 35447b, "Lower Mercer", Vel-34. Basal.

Figures 7, 8.- OSU 38662, Ames, PA-3. 7, lateral; 8, anterior.

Figures 9, 10.- OSU 38661, Upper Mercer, Mp-3. 9, lateral; 10, apical.

Figure 11.- OSU 38659, Skelley, Nbu-3. Lateral.

Figures 12, 13.- OSU 38659b, Skelley, Nbu-3. 12, apical; 13, lateral.

Figures 14-17.- OSU 38660, Skelley, Nbu-3. 14, posterior; 15, apical; 16, posterior; 17, anterior.

Bar scales represent 0.5 mm.
PLATE X

Sturgeonella quinqueloba, Williamsella striata, and Williamsella typicalis

Figures 1, 2.- Sturgeonella quinqueloba, OSU 38663a, Portersville, At-45B. 1, apical; 2, anterior.

Figure 3.- Sturgeonella quinqueloba, OSU 38664a, "Lower Mercer", Vel-7. Anterolateral.

Figure 4.- Sturgeonella quinqueloba, OSU 38665a, Portersville, At-45B. Apical.

Figures 5, 6.- Sturgeonella quinqueloba, OSU 38665b, Portersville, At-45B. 5, posterior; 6, anterolateral.

Figures 7, 8.- Sturgeonella quinqueloba, OSU 38664b, "Lower Mercer", Vel-7. 7, anterior; 8, lateral.

Figure 9.- Sturgeonella quinqueloba, OSU 38664c, "Lower Mercer", Vel-7. Basal.

Figures 10-12.- Sturgeonella quinqueloba, OSU 38663b, Portersville, At-45B. 10, anterior; 11, lateral; 12, anterolateral.

Figure 13.- Sturgeonella quinqueloba, OSU 38619, Putnam Hill, CSo-2. Anterior.


Bar scales represent 0.25 mm.
PLATE XI

DERMAL DENTICLES AND MUCOUS MEMBRANE DENTICLES

Figures 1, 2.- Dermal denticle "B", OSU 38607, Portersville, Aw-47. 1, anterior; 2, lateral.

Figures 3, 4.- Dermal denticle "C", OSU 38607, Portersville, At-45B. 3, antero-apical; 4, lateral.

Figure 5.- Dermal denticle "E", OSU 38613, Putnam Hill, MUMu-4. Anterolateral.

Figure 6.- Dermal denticle "F", OSU 38614, Putnam Hill, MUMu-4. Anterolateral.

Figures 7, 8.- Dermal denticle "D", OSU 38611, Cambridge, Pmo-10. 7, apico-lateral; 8, apico-lateral.

Figure 9.- Dermal denticle "D", OSU 38612, Portersville, At-45B. Apico-lateral.

Figure 10.- Dermal denticle "A", OSU 35190a, "Cambridge", ALe-19. Anterior.

Figure 11.- Mucous membrane denticle "A", OSU 38613a, Skelley, Nbu-3. Anterolateral.

Figure 12.- Mucous membrane denticle "A", OSU 38618b, Skelley, Nbu-3. Anterolateral.

Figures 13, 14.- Symmorniid mucous membrane denticle, OSU 38602a, Brush Creek, Aw-47. 13, anterior; 14, anterolateral.

Figures 15, 16.- Symmorniid mucous membrane denticle, OSU 38602b, Brush Creek, Aw-47. 15, lateral; 16, antero-apical.

Bar scales represent 0.25 mm.