## CONTENTS OF VOLUME III

<table>
<thead>
<tr>
<th>Number</th>
<th>Title</th>
<th>Plates</th>
<th>Pages</th>
</tr>
</thead>
<tbody>
<tr>
<td>13.</td>
<td>Notes on structure and phylogeny of Euryphthalmate cephalopods</td>
<td>1-3</td>
<td>1-56</td>
</tr>
<tr>
<td></td>
<td>By Rousseau H. Flower</td>
<td></td>
<td></td>
</tr>
<tr>
<td>14.</td>
<td>Two siphonophores from the Paleozoic</td>
<td>4-5</td>
<td>57-90</td>
</tr>
<tr>
<td></td>
<td>By Kenneth E. Caster</td>
<td></td>
<td></td>
</tr>
<tr>
<td>15.</td>
<td>Two abnormal Busycon shells</td>
<td>6</td>
<td>91-98</td>
</tr>
<tr>
<td></td>
<td>By Burnett Smith</td>
<td></td>
<td></td>
</tr>
<tr>
<td>16.</td>
<td>Fish remains from the middle Devonian bone beds of the Cincinnati Arch Region</td>
<td>7-11</td>
<td>99-160</td>
</tr>
<tr>
<td></td>
<td>By John W. Wells</td>
<td></td>
<td></td>
</tr>
<tr>
<td>17.</td>
<td>Two spine rows in a Florida Busycon contrarium</td>
<td>15</td>
<td>161-168</td>
</tr>
<tr>
<td></td>
<td>By Burnett Smith</td>
<td></td>
<td></td>
</tr>
<tr>
<td>18.</td>
<td>A new jellyfish (Kirklandia texana Caster) from the lower Cretaceous of Texas</td>
<td>16-20</td>
<td>169-220</td>
</tr>
<tr>
<td></td>
<td>By Kenneth E. Caster</td>
<td></td>
<td></td>
</tr>
<tr>
<td>19.</td>
<td>Observations on gastropod protoconchs. Parts I and II</td>
<td>21-23</td>
<td>221-268</td>
</tr>
<tr>
<td></td>
<td>By Burnett Smith</td>
<td></td>
<td></td>
</tr>
<tr>
<td>20.</td>
<td>Some species of Platystrophia from the Trenton of Ontario and Quebec</td>
<td>24</td>
<td>269-284</td>
</tr>
<tr>
<td></td>
<td>By G. Winston Sinclair</td>
<td></td>
<td></td>
</tr>
<tr>
<td>21.</td>
<td>Observations on gastropod protoconchs. Part III.</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Some protoconchs in Busycon, Fusinus, Heilprinia, Hesperisternia and Urosalpinx</td>
<td>25</td>
<td>285-302</td>
</tr>
<tr>
<td></td>
<td>By Burnett Smith</td>
<td></td>
<td></td>
</tr>
<tr>
<td>22.</td>
<td>Two marine Quaternary localities</td>
<td>26-28</td>
<td>303-318</td>
</tr>
<tr>
<td></td>
<td>By Burnett Smith</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Part I. A group of Pennsylvanian crinoids from the Ardmore Basin.</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Part II. Delocrinids of the Brownville formation of Oklahoma.</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Part III. Description of two new Cromyocrinids from the Pennsylvanian of Nebraska.</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Part IV. On new species of Alcimocrinus and Ulrichicrinus from the Fayetteville formation of Oklahoma</td>
<td>29-33</td>
<td>319-358</td>
</tr>
<tr>
<td></td>
<td>By Harrell L. Stimple</td>
<td></td>
<td></td>
</tr>
<tr>
<td>24.</td>
<td>Stereotoceras and the Brevicoceratidae</td>
<td>34-39</td>
<td>359-394</td>
</tr>
<tr>
<td></td>
<td>By Rousseau H. Flower</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>By Pedro Verástegui</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
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## Condensed Table of Contents of Bulletins of American Paleontology and Palæontographica Americana*

**BULLETINS OF AMERICAN PALEONTOLOGY**

<table>
<thead>
<tr>
<th>Volume</th>
<th>Notes</th>
<th>Pages</th>
<th>Plates</th>
<th>Price</th>
</tr>
</thead>
<tbody>
<tr>
<td>I.</td>
<td>(Nos. 1-5).</td>
<td>354 pp., 32 pls.</td>
<td></td>
<td>$8.00</td>
</tr>
<tr>
<td></td>
<td>Mainly Tertiary Mollusca.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>II.</td>
<td>(Nos. 6-10).</td>
<td>347 pp., 23 pls.</td>
<td></td>
<td>$10.00</td>
</tr>
<tr>
<td></td>
<td>Tertiary Mollusca and Foraminifera, Paleozoic faunas.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>III.</td>
<td>(Nos. 11-15).</td>
<td>402 pp., 29 pls.</td>
<td></td>
<td>$8.00</td>
</tr>
<tr>
<td></td>
<td>Mainly Tertiary Mollusca and Paleozoic sections and faunas.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>IV.</td>
<td>(Nos. 16-21).</td>
<td>161 pp., 26 pls.</td>
<td></td>
<td>$5.00</td>
</tr>
<tr>
<td></td>
<td>Mainly Tertiary Mollusca and sections of Paleozoic sections and faunas.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>V.</td>
<td>(Nos. 22-30).</td>
<td>417 pp., 68 pls.</td>
<td></td>
<td>$8.00</td>
</tr>
<tr>
<td></td>
<td>Tertiary fossils mainly Santo Domingan, Mesozoic and Paleozoic fossils.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>VI.</td>
<td>(No. 31).</td>
<td>288 pp., 21 pls.</td>
<td></td>
<td>$6.00</td>
</tr>
<tr>
<td></td>
<td>Claibornian Eocene pelecypods.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>VII.</td>
<td>(No. 32).</td>
<td>700 pp., 90 pls.</td>
<td></td>
<td>$12.00</td>
</tr>
<tr>
<td></td>
<td>Claibornian Eocene scaphopods, gastropods and cephalopods.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>VIII.</td>
<td>(Nos. 33-36).</td>
<td>337 pp., 15 pls.</td>
<td></td>
<td>$5.00</td>
</tr>
<tr>
<td></td>
<td>Mainly Tertiary Mollusca.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>IX.</td>
<td>(Nos. 37-39).</td>
<td>282 pp., 35 pls.</td>
<td></td>
<td>$7.00</td>
</tr>
<tr>
<td></td>
<td>Tertiary Mollusca mainly from Costa Rica.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>X.</td>
<td>(Nos. 40-42).</td>
<td>352 pp., 54 pls.</td>
<td></td>
<td>$8.00</td>
</tr>
<tr>
<td></td>
<td>Tertiary forams and mollusks mainly from Trinidad and Paleozoic fossils.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>XI.</td>
<td>(Nos. 43-46).</td>
<td>372 pp., 41 pls.</td>
<td></td>
<td>$5.00</td>
</tr>
<tr>
<td></td>
<td>Tertiary, Mesozoic and Paleozoic fossils mainly from Venezuela.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>XII.</td>
<td>(Nos. 47-48).</td>
<td>308 pp., 6 pls.</td>
<td></td>
<td>$6.00</td>
</tr>
<tr>
<td></td>
<td>Venezuela and Trinidad forams and Mesozoic invertebrate bibliography.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>XIII.</td>
<td>(Nos. 49-50).</td>
<td>264 pp., 47 pls.</td>
<td></td>
<td>$6.00</td>
</tr>
<tr>
<td></td>
<td>Venezuelan Tertiary Mollusca and Tertiary Mammalia.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>XIV.</td>
<td>(Nos. 51-54).</td>
<td>306 pp., 44 pls.</td>
<td></td>
<td>$6.50</td>
</tr>
<tr>
<td></td>
<td>Mexican Tertiary forams and Tertiary mollusks of Peru and Colombia.</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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NO. 13: NOTES ON STRUCTURE AND PHYLOGENY OF EURYSIPHONATE CEPHALOPODS

By

Rousseau H. Flower

November 19, 1941

Palaeontological Research Institution
Ithaca, New York, U. S. A.
## CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Introduction</td>
<td>5</td>
</tr>
<tr>
<td>Classifications</td>
<td>7</td>
</tr>
<tr>
<td>Phylogeny of the Eurysiphonata</td>
<td>10</td>
</tr>
<tr>
<td>Electronoceratida</td>
<td>13</td>
</tr>
<tr>
<td>Ellesmeroceratida</td>
<td>14</td>
</tr>
<tr>
<td>Tarphyceratida</td>
<td>15</td>
</tr>
<tr>
<td><strong>Endoceroid development</strong></td>
<td></td>
</tr>
<tr>
<td>Previous hypotheses</td>
<td>20</td>
</tr>
<tr>
<td>Phylogeny</td>
<td>21</td>
</tr>
<tr>
<td>Primitive Endoceroidea</td>
<td>25</td>
</tr>
<tr>
<td>Specialized ellipochoanitic Endoceroidea</td>
<td>27</td>
</tr>
<tr>
<td>Proterocameroceras brainerdi</td>
<td>28</td>
</tr>
<tr>
<td>Meniscoceras Flower, n. gen.</td>
<td>30</td>
</tr>
<tr>
<td>Meniscoceras, coronense Flower, n. sp.</td>
<td>30</td>
</tr>
<tr>
<td>Development of holochoanitic structure</td>
<td>31</td>
</tr>
<tr>
<td>Origin of the Actinoceroidea</td>
<td>37</td>
</tr>
<tr>
<td>Bathmoceras</td>
<td>38</td>
</tr>
<tr>
<td>Polydesmia</td>
<td>39</td>
</tr>
<tr>
<td>Origin of annulosiphonate deposits</td>
<td>42</td>
</tr>
<tr>
<td>Stratigraphy</td>
<td>45</td>
</tr>
<tr>
<td>Early stages</td>
<td>46</td>
</tr>
<tr>
<td>Summary</td>
<td>48</td>
</tr>
<tr>
<td>References</td>
<td>49</td>
</tr>
<tr>
<td>Explanation of plates</td>
<td>51</td>
</tr>
</tbody>
</table>
NOTES ON STRUCTURE AND PHYLOGENY OF EURYSIPHONATE CEPHALOPODS

By
Rousseau H. Flower

INTRODUCTION

Thin section investigation of siphuncle walls has brought to light hitherto unsuspected structures and shows that the generally accepted interpretation of many early Paleozoic cephalopods as holochoanitic is erroneous. On the basis of this new evidence, it becomes necessary to reexamine and revise the current concepts of the developmental trends among the more primitive cephalopods. The forms dealt with in the present work are those characterized by thick connecting rings, the tips of which are primitively differentiated into nonporous areas of fine-grained material, here termed the eyelets. The greater number of the genera which constitute this group are those included in the Actinoceroidea, and those formerly embraced in the too inclusive Endoceroidea. As Teichert (1933) has proposed the term Eurysiphonata to embrace these superfamilies, I have ventured to apply his name, although it has been necessary to include some other forms not previously considered in connection with either the actinoceroids or the endoceroids.

The first of the true Eurysiphonata are the Ellesmeroceratidae, which, aside from their complex connecting rings, are quite generalized. These forms are regarded as the ancestors of four distinct lines, each with its own specializations. The connecting rings of the Tarphyceratidae, as here restricted, are almost identical with those of the simpler endoceroids, and a much closer relationship between these two groups than has hitherto been considered seems inescapable. Thin section investigation of endoceroids has yielded many surprises. Not only are the older genera apparently dominantly, and perhaps universally, ellipochoanitic; but the earlier holochoanitic forms, of Chazyan age, retain connecting rings, clearly a heritage from their ellipochoanitic ancestors. Not until Middle Ordovician time are endoceroids found which lack rings.

It has been necessary to remove the Baltoceratidae from the Endoceridae, where they have commonly been placed in the past. Their thick connecting rings show their eurysiphonate affinities, and this and their ellipochoanitic structure make it necessary to revise Kobayashi's hypothesis of their relationship to some extent.
The Actinocerioidea are connected by Polydesmnia and Bathmoceras to the ancestral Ellesmeroceras. Not all of the problems of the development of the various morphological features are solved, but it is believed that the present knowledge is adequate to establish this relationship.

So different have our morphological deductions been from the currently accepted interpretations of the structures, and the phyletic implications have been of such exceptional interest in view of their bearing upon the theories of relationship recently proposed by Teichert and Kobayashi, that it is felt progress will be best served by the publication of our observations at the present time. These results are far from complete. Adequate material for the study of many of the crucial genera by means of thin sections has been lacking. Doubtless the present findings give only a faint indication of the rich mine of morphological information which awaits a more comprehensive study along similar lines. Particularly important is the investigation of the endoceroids by this method, for it has been found that in many cases opaque sections fail to give any indication of the true structures.

In erecting the phyletic scheme proposed here it has been necessary to draw extensively upon the works of others. No material of the ancient Plectronoceratidae was available. The family is thus far reported only from Manchuria, and, insofar as the writer is aware, is not represented by specimens in any collection in America. It has therefore been necessary to present a brief summary of the group, important as the oldest true cephalopods and the ancestors of the Eury-siphonata, based upon Kobayashi's descriptions and figures. Unfortunately the preservation of even the best of his figured specimens is none too good, and the strongly retouched photographs leave some doubt as to whether Kobayashi's morphological conclusions are altogether correct, particularly in reference to the pseudodiaphragms. Material of Ellesmeroceras consists of specimens from the Seward Peninsula of Alaska described in detail in another paper. For opportunity to study this interesting material, I am indebted to Dr. Josiah Bridge of the U. S. Geological Survey. For information concerning Bathmoceras, it has been necessary to draw very largely upon Holli's remarkably fine study of the genus. Bohemian material in the collection of the University of Cincinnati was examined, but the preservation was found to be inadequate for a similar study. Examination of specimens of Polydesmnia in the U. S. National Museum has supplemented Kobayashi's figures and descriptions. It has been necessary to reject his views both as to the holochanitic nature of the siphuncle and the phyletic interpretation concerning some other structures observed.

Most of the material which furnished the thin sections of the Tarphyceratidae and the endoceroids is from the collection of the writer. To this is added

some very significant material collected by Professor G. D. Harris from the Beekmantown limestones of the Champlain Valley, and endoceroid material brought together at the New York State Museum by Dr. Rudolph Ruedemann.

In the preparation of sections I have had the expert assistance of Miss Helen Duncan of the University of Cincinnati. The cost of photographic supplies and the expense of publication of the plates have been met by the Faber Publication Fund for Paleontology of the University of Cincinnati Museum.

CLASSIFICATIONS

There is no uniformity of opinion at the present time as to the proper classification of the cephalopods. Hyatt's (1900) scheme is the only one thus far proposed which attempts to place all of the genera. Subsequently Foerste, and many other investigators as well, described many new genera of Nautiloidea without assigning them to family or higher groups. Meanwhile investigation was showing that, while the long established subclasses Tetrabranchiata and Dibranchiata and the order Nautiloidea and Ammonoidea of the Tetrabranchiata were convenient, the major divisions proposed for the Nautiloidea were far from adequate. The studies of Kobayashi, and also of Ulrich and Foerste, showed that holochoanitic structure was far from universal among the older cephalopods and was not by any means as uniform among conchs of endoceroid and piloceroid aspect as had generally been assumed. Other investigations showed that the Cyrtocoanites were a polyphyletic group and indicated that the major divisions of the Nautiloidea were in need of drastic revision.

Teichert (1933) was the first to make any constructive suggestions of a revisionary nature. In connection with his classic study of the Actinoceroidea, he proposed two major divisions of the Cephalopoda: the Eurysiphonata, to include the Actinoceroidea and the Endoceroidea, and the Stenosiphonata, to include all other cephalopods including the Dibranchiata and the Ammonoidea. The supplanting of the long familiar subclasses and orders of the cephalopods may seem a radical step, but the proposal certainly deserves more serious attention than it has received from the hands of other investigators. In view of the widespread usage of the older subclasses and orders, Teichert's terms are employed here as suborders of the Nautiloidea. The question of the rank which is to be given to these divisions is, however, a matter of secondary importance. The essential problem involved is whether there was an early split in the cephalopod line, one branch producing the actinoceroids and the endoceroids, the other producing all other nautiloids and later giving rise to the Ammonoidea and Dibranchiata. Unfortunately Teichert's exposition of his proposed classification has been rather
brief and has not been given a very prominent position in his papers. One might wish that his reasons for proposing the groups had been set forth in greater detail. The evidence presented in the following pages seems to support his contention in the main, in that it establishes the connection between the actinoceroids and the endoceroids, though it does not succeed in demonstrating that other forms may not be related to this line.

Schindewolf (1935) objected to the supplanting of the old subclasses and orders and opposed Teichert's main thesis of a close relationship between the actinoceroid and the endoceroid. He held that the actinoceroid was very similar to stenosiphonate orthochoanitic and cyrtocoonitic cephalopods in its early stages and very different from the endoceroid. Unfortunately the specimen upon which he relied for the early stages of the actinoceroid, Carbacrinoceras torleyi Schindewolf, failed to show either the tip of the shell, the true tip of the siphuncle, or even the true apical chamber (Flower, 1940, p. 430). Schindewolf proposed a classification which differed from Hyatt's only in the suborders of the Nautiloida. He recognizes the Nautiloida as comprising the Endoceracea, Actinoceracea, Cyrtoceracea and Nautilacea, with the doubtful addition of the Gomphoceracea.

Kobayashi (1932) also discussed the phylogeny of the nautiloids and based his conclusions upon the early stages of the shell. He made known for the first time the condition of the apical end of the actinoceroid. Curiously, he failed to detect Schindewolf's error and, like him, concluded that the actinoceroids were related to other ellipochoanitic cephalopods. He considered the position of the siphuncle in the early stages the crucial feature and proposed to divide the nautiloids into the Centrosiphonata, which included all ellipochoanitic cephalopods, and the Ventrosiphonata, which included the endoceroids in the broad sense. He regarded the Actinoceroida and the Steroplasmoceratidae as divergent cyrtoschoanitic offshoots of the Orthochoanites. In an earlier study, he proposed the derivation of the Orthochoanites from the endoceroid line.

The use of early stages in classification is hampered because they are known for only a relatively small number of genera and species. Thus, it is uncertain whether the Electrorietoceratidae and the Ellesmeroceratidae would possess ventral or central siphuncles. Further, it is possible to see other features in the known apical ends which may be of equal or even greater significance. The writer has proposed that the presence or absence of an apical caecum might serve as a better criterion (Flower, 1940), and, on this basis, the Euryosphonata seem to lack the caecum uniformly while the Stenosiphonata possess a well-developed caecum. But even here there are not enough data assembled to permit any very wide use of such features.

A few other papers, while not proposing new classifications, are relevant either as revisions of restricted groups within the nautiloids or for suggestions con-
cerning the phylogeny. Teichert's studies of the Actinoceroidea have already been mentioned. He concluded that they were not related to other cyrtochoanitic or annulosiphonate cephalopods, and instead grouped them with the endoceroids. The present work supports this view in establishing the precise connection. He further presented a phylogeny of the actinoceroids in which the Actinoceratidae is regarded as the primitive radicle. The writer (1940) has suggested that the development of the group may be more complex if the ontogenetic stages noted in Actinoceras are recapitulatory in their significance. The sequence observed there, Polydesmia, Nybyoceras, Armenceras and Actinoceras, runs across families, but is in fairly close accordance with the stratigraphic appearance of the genera. Doubtless Polydesmia should be segregated into a distinct family. Kobayashi (1940) has already done this, though his basis for doing so is very questionable.

While the Actinoceroidea constitute one cyrtochoanitic group which is totally independent of the main body of the Cyrtoceranites, the Pseudorthoceratidae constitute another (Flower, 1939), this time a Silurian development from orthochoanitic orthoceracoids. The large group of Paleozoic stenosiphonate cephalopods remain for the most part without any comprehensive classification. Teichert has proposed a clear and logical classification of the Actinosiphonata, but this group contains only a relatively small number of the genera. Ulrich and Foerste reported (1933) that the Orthochoanites and Cyrtoceranites were not differentiated before the Ordovician. The writer has outlined (1941) what appear to be natural morphological divisions among the Lower Ordovician stenosiphonate nautiloids, recognizing five groups as follows:

1. Orthochoanitic forms with cylindrical siphuncles.
2. Suborthochanitic cephalopods.
3. Cyrtophanitic forms of suborthochanitic origin.
4. Stereoplasmoceratidae.
5. Primitive cyrtophanitic forms, the Discosoroidea.

The origin of the suborder Mixochoanites of Hyatt (1900) is to be found in the suborthochanitic cephalopods; indeed, Chazyan Mixochoanites are in themselves suborthochanitic and only later depart from the pattern. Certain difficulties presented by this classification are eliminated if the groups are restricted to cephalopods with thin and simple connecting rings, such as are here regarded as the Stenosiphonata. The Tarphyceratidae are eliminated from the orthochoanitic cephalopods, and the Actinoceratidae from the primitive cyrtophanitic cephalopods. Other difficulties, however, remain, such as the origin of the Discosoroidea and the problem of the relationship between the Tarphyceratidae and Ordovician coiled cephalopods with cylindrical thin-walled siphuncles.
PHYLOGENY OF THE EURYSIPHONATA

The Eurysiphonata were originally supposed to be characterized by septal necks longer than those of the Stenosiphonata. This feature does not hold throughout, but exceptions are clearly recognizable as specializations. The Sactoceratida of the Actinoceroidea have septal necks which approach the condition found in many Stenosiphonata. Even more remarkable reduction of the necks is found in *Eurystomites* and again in *Proterocameroceras*, where an aneuchoanitic condition is attained.

A somewhat better feature is found in the relatively thick connecting ring. This is absent in the primitive Plectronoceratidae, which are regarded as ancestral to the Eurysiphonata without belonging to it. The question of a precise boundary between the Stenosiphonata and the Eurysiphonata is not important, as it must inevitably be arbitrary if the groups are descended from a common ancestor. Such a common ancestor is believed to be represented by *Plectronoceras*. The thick rings are retained in the Tarphyceratidae, as here restricted. They are retained in the endoceroids, except where the neck is completely lost, a relatively late development and clearly a specialization. The ring is thick in the older Actinoceroidea, as shown by *Polydesmia*, where it is so thick that Kobayashi mistook it for a continuation of the septal neck. But in later forms, particularly in the Sactoceratidae, the ring becomes as thin as in any stenosiphonate cephalopod.

Persistent within the thick connecting rings of the Eurysiphonata is a dense area of calcite near the tip, which is here termed the eyelet. Though persistent and widespread enough that it must be primitive, it is not universal. It is lost under specialized conditions, notably in conjunction with the reduction of the neck to an aneuchoanitic condition. Reason is shown for regarding the eyelet as the origin of the annulosiphonate deposits of the Actinoceroidea.

The phyletic scheme presented here is of necessity built upon several premises which cannot be regarded as proved. It is assumed that the Plectronoceratidae are the ancestors of all other cephalopods. Without wishing to become involved in the question of the position of *Volborthella* and *Volborthella*, it is safe to say that there is no wide agreement as to whether they are even cephalopods. Certainly they fail to show any close relationship to any forms discussed in the present paper. The Plectronoceratidae therefore contain the oldest organisms which can be indisputably assigned to the Cephalopoda and do not differ radically from other older cephalopod groups in structure. They give rise on one hand to the first of the Eurysiphonata, the Ellesmeroceratidae, by the development of thick connecting rings, but with no other important modifications. Likewise, it is believed that the family must also have been the source of an ancient stenosiphonate line retaining thin connecting rings. I have had no material of Ozarkian or Canadian age which has yielded such forms with empty siphuncles, though it would
appear from the brief published summary (1933) of Ulrich and Foerste that such forms existed prior to the Ordovician. There also may belong the ellipchoanitic and sometimes anechoanitic Diphragmida, in which I do not include the piloceroid genus *Clarkioceras* in which diaphragms are secondary to endocones. Certainly enough is not known at present to trace this line in pre-Ordovician time. The diversity of structure in Chazyan stenosiphonate cephalopods is, however, ample evidence of a very considerable period of pre-Ordovician development.

The thickened connecting ring marks the initiation of the Euryisphonata and appears in the Ellesmeroceratidae. From the Ellesmeroceratidae, are derived three divergent lines, and possibly a fourth, all equipped with similar siphuncle walls. The Tarphyceratidae are specialized by coiling, but the siphuncle is small and remains empty. There is some specialization in wall structure, but this plainly occurs within the group rather than at its point of origin. The Endoceroida proper remain dominantly straight, but the siphuncle tends to enlarge and is differentiated mainly by the appearance of endocones. The earliest endoceroids are ellipchoanitic, contrary to the general prevalent opinion. Holochoanitic siphuncles develop relatively late, and there is as yet no good proof that they appeared before Ordovician time. The earlier holochoanitic cephalopods retain connecting rings. Such endoceroids persist until Trenton time. More specialized forms, of Middle and Upper Ordovician age, lose the connecting rings. It is apparently on the basis of such forms that Hyatt established the suborder Holoceratites.

Within the third group, the eyelet became inflated, producing heavy deposits within the siphuncle. This is seen in *Bathmoceras*. Subsequently cyrtchoanitic structure appeared in *Polydesmia*, and later modification of the deposit produced the typical annulosiphonate condition of the Actinoceroida.

This is, in brief, the conclusion which has been drawn from the evidence recorded in the following pages. The evidence is still far from complete, due largely to the lack of suitable material. The most serious lack has been material to investigate the role of the eyelet in the actinoceroid line, and my conclusions are based upon inference. The retention of the eyelet in the divergent endoceroids and Tarphyceratidae imply its presence in the ancestral Ellesmeroceratidae. The difference in fine structure between annulosiphonate deposits and the generalized part of the connecting ring in higher actinoceroids requires this explanation.

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2 The only suggestion of a Canadian holochoanitic condition is found in *Cassioderoceras explanator*. However, as it has not been possible to study the species in thin section, the evidence is hardly conclusive. The discovery of ellipchoanitic structure in *Protocamrroceras*, which appears holochoanitic in opaque sections as well as in other Canadian genera, makes this seem even more dubious.
While the relationships within the Eurysiphonata seem to be fairly well established by the present work, there is a possibility still to be considered that within the group there may be the origin of one or more groups now placed with the Stenosiphonata. The remarkable resemblance between the Tarphyceratidæ as restricted and coiled Ordovician genera with thin connecting rings is very striking. Plainly, there is either a relationship between the two, or else there is here one of the most remarkable cases of isomorphism within the Nautiloidea. In connecting the annulosiphonate deposits of the actinoceroid with the eyelet of the Eurysiphonata a grave possibility is opened that the same may hold true for the annulosiphonate deposits of supposedly stenosiphonate cephalopods, and may even have to be extended to include actinosiphonata cephalopods.

The present work is regarded as only preliminary and serves the purpose of pointing out relationships. Much further investigation is needed before a classification, even of the Eurysiphonata, can be proposed which can hope for any permanence. For this reason the taxonomic nomenclature employed is extremely conservative. Names for divisions of family or higher rank are those previously proposed. It is felt that an attempt to re-evaluate the rank of these categories at the present time would be premature, and they are frequently referred to non-committally as “groups.” Most of the groups are redefined, a procedure which has been necessary for clarity, because they have not infrequently been applied very differently in the past, and sometimes rather loosely. As a result the phylogeny is composed of very unequal divisions. The family Ellesmeroceratidæ gives rise, apparently through the genus Ellesmerocras rather than more specialized genera, to the family Tarphyceratidæ as here restricted, to the superfamily Endoceroidæ, probably to the family Baltoceratidæ, and to a last group composed of the superfamily Actinoceroidæ and the genus Bathmocras, formerly placed in the suborder Schistochoanites.

In view of the investigations of Ulrich and Foerste, now happily being completed by Miller, undescribed forms of Canadian and Ozarkian age have been drawn upon only when absolutely necessary, though the material examined for this study contained a good number of such species. To illustrate a primitive endoceroid it has been necessary to describe and figure an undescribed Canadian species. For reasons given below, this species has been arbitrarily placed in Cameroceras, a term which has served of late more as a wastebasket than a genus. The true generic position cannot be ascertained until genera now described have been subjected to closer examination of the siphuncle wall. The one new species and genus described here, Meniscoeras coronense, is drawn from my long delayed Chazyan study now nearing completion.

3 It should be noted that Bathmocras, as the best known genus of the Schistochoanites, apparently played a major part in the erection of that suborder. It is also the type and only genus of Holm's family Bathmocrasidæ.
PLECTRONOCERATIDÆ

The family Plectronoceratidæ is of particular significance, for not only does it contain in the genus Plectronoceras, the oldest form which can be assigned to the cephalopods with certainty, but it exhibits a plasticity of structure which is a common feature in primitive members of any group. The family is composed of cyrtoconic or rarely straight cephalopods with marginal siphuncles composed of short septal necks and thin fragile connecting rings which are more frequently destroyed than preserved. The necks vary in form and in length, passing from orthochoanitic to cyrtochoanitic in a single individual, and in some forms approaching, though not attaining a holchoanitic condition.

Plectronoceras Ulrich and Foerste, based upon Cystoceras cambria Walcott, was originally reported to be devoid of connecting rings (Ulrich and Foerste, 1933, p. 288). Kobayashi (1935) has since observed the connecting ring within the genus. He reports the septa as bent rectangularly in the early stage, i.e., orthochoanitic, but cyrtochoanitic in the later stages. His illustration (1935, pl. 4, fig. 3) is retouched to show the course of the septa, evidently originally very thin and poorly differentiated in color from the matrix, and one connecting ring near the adoral end of the specimen. This ring is as strongly cyrtochoanitic as that of an Actinoceras.

Other genera are known from the younger Wanwanian strata of Manchuria.4 Wanwanoceras Kobayashi (1933, p. 302, pl. 4, fig. 8) was originally described as a breviconic ellesmeroceroid. Actually, the structure of the siphuncle wall is typical of the Plectronoceratidæ and differs materially from that of Elllesmeroceras, as is shown below. Here again the siphuncle is ellipochoanitic, with the connecting rings thin and either poorly preserved or absent. The ontogenetic progression of Plectronoceras is here reversed, the early septal necks being cyrtochoanitic, the later ones orthochoanitic. Kobayashi reports the connecting ring to be cyrtochoanitic throughout. His illustrations fail to show it at all.

Sinoeremoceras Kobayashi (1933, p. 274, pl. 3, figs. 2, 5) is reported as possessing orthochoanitic early siphuncular segments which later are modified to cyrtochoanitic ones. This is shown clearly in his illustrations. Further, in the adapical portion of the shell where the segments are cyrtochoanitic, Kobayashi observed dissepiments within the siphuncle. Preservation as usual is not clear, and the validity of these dissepiments might be questioned. However, it is possible that Sinoeremoceras marks the beginning of the development which produces the Diphragmidæ of Ulrich and Foerste (1933) where the siphuncle is predominately ellipochoanitic, and, in some instances, the necks are so short that the authors introduced the new term anchochoanitic to describe them.

4 The Wanwanian of Manchuria, by the predominance of Elllesmeroceras, is to be correlated with the Ozarkian, though possibly only the Upper Ozarkian, as recognized in America. Kobayashi's overlying "Lower Ordovician" is Casadian, and apparently his "Middle Ordovician" includes the Lower Ordovician Chazyan of America.
Kobayashi's illustrations of this genus are considerably retouched; evidently preservation here again is of a type unfavorable for photographic reproduction. The connecting rings are known apparently only in the adapical part of the specimen. In the adoral portion they are not shown. Here the septal necks become long and approach a holochooanitic condition, though failing to attain it.

*Multicameroceras* Kobayashi (1933, pp. 273, 293, pl. 3, figs. 1, 3) is very similar to *Sinocremoceras* in the outline of the siphuncle being strongly cyrtocoanitic adapically and faintly reminiscent of *Polycosmia* in the outline of the siphuncular segments. Adorally the segments of the siphuncle become orthocoanitic, but details of the wall structure are obscure, and the connecting rings are not clearly shown. Kobayashi reports the presence of an irregular lining within the siphuncle which gives rise to irregular dissepiments. His unretouched photograph of the interior of the siphuncle resembles strongly the appearance of similar structures observed by the writer in Chazyan cephalopods, where they are known to be inorganic. Certainly the organic nature of the structures here also may be seriously questioned.

Evidently the *Ectenoceratidae* constitute a highly plastic group insofar as internal structure is concerned. Without much change in internal structure it could have given rise to the ellipchoanitic cyrtocerasaces with simple siphuncles of the Ozarkian and Canadian. Probably these forms in turn gave rise to the Stenosiphonata as known from the Ordovician onward. Certainly the stenosiphonate cephalopods of the Chazyan show a diversity of structure which indicates that the group was one which had already been developing for a considerable period, and it will be strange indeed if their ancestors are not found in these earlier strata.

Modifications of the connecting ring in this line are required, however, to produce the forms here included in the Eurysiphonata.

**ELLESMEROCERATIDÆ**

This family was defined as follows by Kobayashi (1934, p. 376): "Longiconic orthocone or cyrtocercone, laterally compressed or subcircular in cross section; septa and camerae crowded; septal funnel invaginated; siphuncle marginal and narrow; endosheaths, if present, very poorly developed near apical end, surface smooth or striated.

"The family contains *Ellesmeroceras* Foerste, *Ectenoceras* Ulrich and Foerste, and *Robsonoceras* Ulrich and Foerste. *Ectenoceras* differs from *Ellesmeroceras* in being a cyrtocercone; *Robsonoceras* from *Ellesmeroceras* in its cross section, which is circular instead of elliptical. (Range:) Basal Ordovician to Middle Ordovician."

Ulrich and Foerste (1933, p. 266) considered *Ellesmeroceras* and the genera
Pachendoceras and Walcottoceras, which were described as differing from Ellesmeroceras in external rather than internal features, as Ozarkian endoceroids. All of these forms have generally been assumed in the past to be holochoanitic. Kobayashi (1935, p. 32, text fig. 2) represents the Ellesmeroceratidae as holochoanitic, with the septal necks overlapping after the manner of Vaginoceras according to Hyatt, and as possessing diaphragms. Evidence of diaphragms in the family rests upon very questionable evidence, and the holochoanitic condition is erroneous. The Alaskan representatives of the genus discussed in a forthcoming paper by the present writer, show excellent reason for regarding the genus Ellesmeroceras as an ellipochoanitic form with thickened connecting rings; indeed, the sections cannot be interpreted in any other way.

It is not necessary to review here the evidence already given for the structural interpretation of Ellesmeroceras, but only to emphasize the essential features of the genus. The siphuncle is still marginal as in the Plectronoceratidæ, and the segments are markedly oblique, sloping strongly oral on the side closest to the margin of the shell. The connecting ring is thickened. Thus far no differentiation of structure within the ring has been observed. It is suspected that this is due to poor preservation rather than to actual homogeneity of composition, for as is shown below, similar differentiation of structure is observed in such remotely related types as the earliest holochoanitic endoceroids and the Tarphyccras, of which Ellesmeroceras, is probably the common ancestor.

The demonstration of ellipochoanitic structure in Ellesmeroceras makes it seem highly probable that those genera which were described because they differed from Ellesmeroceras in relatively superficial features of form and ornament, and which were supposed to be similar in internal structure, may also be ellipochoanitic rather than holochoanitic. The features distinguishing the three genera included in the family by Kobayashi have been quoted above in his description of the family. Robsonoceras (Ulrich and Foerste, 1935, p. 285) which possesses diaphragms is probably not a member of the family but is best placed in the Diphragmidæ. Pachendoceras was described as differing from Ellesmeroceras in section and sutures, while Walcottoceras differs from Ellesmeroceras mainly in the annulated condition of the exterior. The holochoanitic condition of all of these forms is extremely dubious.

**TARPHYCCRATIDÆ**

The genera Eurystomites and Tarphyccras possess relatively thick-walled siphuncles which are often preserved even in parts of the shell where the septa are destroyed. Hyatt considered the family Tarphyccras as orthochoanitic.
Foerste subsequently expressed the opinion that it was holochoanitic. Neither is an adequate expression of the true condition. Orthochoanitic in a purely descriptive sense, the siphuncle walls are made up of thick connecting rings strongly reminiscent of those of *Ellesmeroceras*, also formerly considered holochoanitic, but show a diversity of structure within the ring which it has been possible to detect in the strongly recrystallized material from which we have been obliged to study the older genus.

The septal necks are variable in length but never extend the length of a siphuncular segment. They may be very short as in *Eurystonites*, or nearly half the length of the segment. Their tips may be simple or forked.

The connecting ring may consist of a single layer (fig. 1C) or of two layers, forming an outer and an inner zone. Differentiation between the zones may be very obscure (fig. 1B) or sharp (fig. 1A), a condition which is in part, at least, the result of replacement rather than original structure, as it may vary critically within parts of the same specimen. The tip of the connecting ring is commonly differentiated into a structure which I have here termed the *eyelet*. This occurs in the Tarphyceratid in the part of the ring which lies within the neck of the next adapical segment of the siphuncle. Conditions of preservation appear to determine whether the structure is clear cut, obscure and apparently without real boundaries, or absent altogether. The generalized part of the eyelet offers a sharp contrast in composition to the remainder of the connecting ring. In thin section the connecting ring is made up of coarse, clear, crystalline material, though generally somewhat finer grained than the calcite of the septal neck. The eyelet consists of dense fine-grained or amorphous, relatively opaque material, sometimes showing a resemblance to very fine clay, but probably representing a very fine-grained deposit of calcite or, more probably, aragonite. In addition, at the base of the eyelet, sometimes at its tip and rarely at both regions in the same segment, black lamellar material may be deposited which resembles very strongly the perispatial deposits of the Actinoceroidea, but is unlike any other structure observed in cephalopods (fig. 1C).

The three species thus far examined in detail show a diversity of structure in which the above features are combined in different ways, which suggests that further investigations should be highly productive of new information.

*Eurystonites kellogi* Whitfield of the Fort Cassin beds of Valcour, New York, shows the simplest septal necks. Those on the venter (text fig. 1A; Pl. 1, fig. 1) are essentially unbent, the septum terminating without bending at all apical. On the dorsal side a bend occurs so that the septa slope there as much as they do upon approaching the siphuncle wall ventrally. Differentiation between the inner and outer zone of the connecting ring varies from segment to segment. The ones illustrated in my plates are believed to represent the least altered condition. The
segment shown in the middle of the figure shows no clear differentiation of two layers; instead a thin outer layer and a slightly thicker inner layer both of clear calcite are separated by a broader grayer band. Differentiation is not strong.

Fig. 1.—Structure of the siphuncle wall in the Tarphyceratidae. A. Siphuncle wall of *Eurytomites kellogi* (Whitfield). Necks are vestigial, scarcely bifurcated, the connecting rings are strongly differentiated into a thin inner zone and a thick outer zone. The figure also approximates the condition of *Proterocameroceras*. B. Siphuncle wall of *Tarphyceras seeleyi* (Whitfield). Necks are long and deeply forked. The outer zone is obscurely differentiated, the eyelet is well developed. C. Siphuncle wall of *Tarphyceras* sp. The outer zone is wanting, the eyelet is strongly differentiated, with deposits at base, at tip, or both, resembling perispatial deposits of actinoceroids.

At the dorsal end of the connecting ring there is present a darkened area. This represents the type of alteration which sometimes affects the entire outer zone. It is seen, also, in the next adapical segment, the base of which is shown at the bottom of my illustration. Here the trapezoidal grey area at the base of the connecting ring continues on farther apicad, but it is sharply set off from the inner zone by an irregular line resembling a styliolite, and indicating that the differentiation is inorganic. At the top of the picture the adapical end of the next adoral connecting ring shows a clear and a natural differentiation of an inner and outer zone, and a light boundary is apparent on the outer zone. An anomalous and probably an inorganic feature is the small heart-shaped mass of calcite at the tip of the septal neck near the base of the photograph. Irregular masses of calcite within the cavity of the siphuncle apparently have no organic significance. Certainly they represent no original calcareous deposit.

A second specimen, too fragmentary for positive identification, but either identical with or very close to *Tarphyceras seeleyi* Whitfield of the Beekmantown, shows very different septal necks. They are long, fully half the length of the siphuncular segment, and are forked at the tip. The illustration (Pl. 1,
fig. 6) shows one of the clearer of the septal necks in which forking is pronounced. The connecting ring is attached in part to the adapical concave surface of the neck produced by the forking and in part to the outside of the neck. The neck is thick, and is very obscurely divided into an inner and an outer zone, the division occurring at about the position which a very thin connecting ring would be expected to occupy on the basis of the position of the septal necks. The structure suggests that the connecting ring was originally thin when first deposited, and that it grew subsequently outward and inward. The outer zone is so thickened that its base lies on the outside of the connecting ring, not only outside of the fork but extending well oral along the outer surface more than halfway to the free part of the septum. The other end is slightly expanded terminally and is truncated by the free part of the preceding septum. The inner zone, generally faintly darker in color, extends apicad to the tip of the next adapical septal neck, and bears prominent eyelets, though their boundaries are obscure. The inner surface is marked by a band of clear calcite, not uniformly present, but more suggestive of the endosiphining of the endoceroids than any other organic structure. The basal part of the inner zone is composed of finer grained material than is the outer zone and the differentiation of the eyelet is not clear, though there the material becomes denser, and apparently amorphous even under high power. Two eyelets are shown on the left side of my photograph. The lower one, composed of dense dark material, is, in part, covered, particularly at the extreme tip by the broken endosiphining, and is, in part, exposed to the cavity of the siphuncle. The other eyelet, on the same side of the siphuncle, is less differentiated on the basis of color, and is retouched. A unique feature shown by this segment, not observed elsewhere, is some of the material at the base of the inner zone which seems very similar to that composing the eyelet. A generalized interpretation of the structure is shown in text figure 1B.

A third section, also from a Tarphyceras from the Beekmantown of Valcour, New York, (Pl. 1, fig. 2) shows somewhat different structures. The fork of the neck is not nearly so well developed here, though the septal necks are still relatively long. The outer zone is not developed at all. The inner zone shows only very clear differentiation of the eyelet at the tip. The generalized condition of this specimen is shown in text 1C. Differentiation between the septal necks and the connecting rings is not clear in the present condition of the specimen, though curiously enough, this could be seen quite clearly when the section was slightly thicker. Further grinding was necessary to study the structure of the eyelet, which here showed more clearly than in any other specimen the differentiation from the remainder of the connecting ring. The material is yellow, and finely granular in the eyelet proper, while the rest of the connecting ring is composed of much lighter and more coarsely crystalline material. At the base of the eyelet in one segment, at its tip in another, and again at both places in a third,
there appears a deposit which recalls the perispatial deposit of the actinoceroid. It is darker in color than any of the other deposits, and shows faint curved lamellar structure. Its form seems to be variable, and it cannot be made out in all segments of the siphuncle even in the one section.

The family Tarphyceratida was erected by Hyatt (1900) and placed with the Trocholitidae and Plectoceratida in the Tarphyceratida. Taxonomic criteria were supplied by coiling, the section, sutures, growth, and other gross features of the conch. The position of the siphuncle was given attention but its structure was assumed to be uniformly simple and orthochoanitic throughout the groups. However, among these coiled forms two types of siphuncles appear. The first, typified by *Eurystomites, Tarphyceras* and the species described elsewhere as "*Plectoceras* sewardense," is characterized by thick connecting rings in which the eyelet and the development of zoning are dominant, if not universal, features. The other group, typified by *Trocholites, Plectoceras, sensu stricto*, and Chazyan species which are typical in all gross features at least of the Canadian genera *Aphetoceras, Pycnoceras, Falcilituites*, as well as the Chazyan species described as *Tarphyceras multicameratum* Ruedemann (1900), have simple thin connecting rings and show no trace of the eyelet, though septal necks are well developed and surround the tip of the connecting ring. These forms seem to constitute a group of coiled cephalopods of the Stenoceropoda, while the few Canadian forms thus far studied in thin section show, by their thick connecting rings and the structures within them, not only affinities with the Eurysiphonata, but also a close relationship with the Endoceroida, as here defined. For the purpose of the present discussion, the family Tarphyceratida is confined to coiled cephalopods known to have this type of siphuncle wall, and which are regarded as derived from the Ellesmeroceratida. In the present state of our knowledge, *Tarphyceras* and *Eurystomites* are the only genera which can be included here, but doubtless others will be found when more of these cephalopods have been examined in thin section.

Although the Tarphyceratida seem to constitute two unrelated groups of cephalopods on the basis of the structure of the wall of the siphuncle, the problem requires much further investigation before such a possibility can be proved or rejected. The morphological evidence assembled to date is admittedly far too meagre. It is possible to point out the characteristics of the two types of siphuncle wall which occur in the Tarphyceratida. One is represented by *Tarphyceras* and *Eurystomites*, discussed above and illustrated. For contrast, a thin section of the siphuncle of an undescribed species of *Barraudoceras* from the Valcour limestone of Little Monty Bay, Chazy, New York, is figured (Pl. 2, fig. 14) which typifies the relatively simple structure of the Ordovician genera noted above. It remains to determine into which group still other genera should be placed. Of particular interest is the wall structure of such Canadian genera as *Aphetoceras* and *Pycnoceras*. Chazyan species which apparently belong in those genera belong to the group of Ordovician forms, but the condition of the Canadian genotypes is unknown. It may be that they also are simple; certainly it is not im-
probable that the coiled Chazyan forms had coiled ancestors in the Canadian which can be recognized. There is also the possibility that, instead of representing genera which pass from the Canadian to the Chazyan, these cephalopods exhibit remarkable cases of homeomorphy. Another possibility which must be considered is that of a transition from thick complex connecting rings to thin simple rings within a genus. The problem is of particular interest in view of the genera concerned, which played an important part in Hyatt's (1894) application of the biogenetic law to the Nautiloidea. Although his classification has been questioned and the underlying principles have been attacked, no detailed reinvestigation of these forms has yet been undertaken. When this has been done with regard to the ontogenetic stages observed by Hyatt and the structures of the siphuncle wall indicated in the present work, it will be possible to evaluate Hyatt's principles as applied to the nautiloids on a much better basis than has hitherto been accomplished.

ENDOCEROID DEVELOPMENT

PREVIOUS HYPOTHESES

The term endoceroid has been used very loosely in the past to denote a slender cephalopod which was holochoanitic or looked as though it ought to be. Apparently the term has been used at times for members of the Endoceratidae of Hyatt and again to embrace most, if not all, of the genera placed in the Holochoanites. The suborder Holochoanites of Hyatt (1900) was supposed to be characterized by a siphuncle wall consisting only of septal necks without the adjunct of connecting rings. The greater number of the species were contained in the longiconic Endoceratidae and the breviconic Piloceratidae. In general, the descriptive terms endoceroid and piloceroid have been used for cephalopods which were regarded as members of these families. It was generally assumed that holochoanitic structure was primitive, being relatively ancient and relatively simple in comparison with ellipchoanitic structure in which the septal necks are supplemented by connecting rings. However, it was never a feature which it was very easy to see, and many shells of endoceroid and piloceroid aspect, that is, shells with large siphuncles containing endocoones, were placed in the Holochoanites without a very close examination of the siphuncle wall. Indeed, the endocoones themselves have come to be regarded as a sufficient criterion of holochoanitic structure.

However, it was not long before it was found that ellipchoanitic structure occasionally appeared in both endoceroids and piloceroids. The first case reported was that of Piloceras newton-winchelli Clarke, for which Ruedemann (1905) erected the new genus Clarkioceras. It was believed that this genus represented a form close to the origin of the ellipchoanitic cephalopods from the
simpler holochoanitic forms. When seen in the light of this explanation, *Clarkeoceras* suggested the origin of the connecting rings from the endosiphonining of holochoanitic cephalopods. Other cases of ellipochoanitic structure were subsequently reported by Ulrich and Foerste, and also by Kobayashi. It was quite generally assumed that holochoanitic siphuncles were primitive structures, and that the ellipochoanitic genera represented only isolated modifications of the primitive pattern.

The number of genera attributed to the Holochoanites has grown greatly since Hyatt's day. Ruedemann (1906) found holochoanitic structure in supposedly ellipochoanitic genera of the Beekmantown. More significant perhaps were the morphological investigations of the endosiphuncle due largely to the researches of Holm in Sweden and Ruedemann in America. Unfortunately this method of approach to the problem of the endoceroids was not followed up until Kobayashi undertook the examination of the Cambro-Ordovician cephalopods of eastern Asia some thirty years later. His investigations, set forth in a series of highly valuable papers, have brought to light not only many new genera and species, but also hitherto unsuspected modifications of the endosiphuncle. The variation of structure within the endoceroids was so great that they could no longer be contained in the two families which Hyatt found adequate. The taxonomic confusion was happily cleared up by Kobayashi (1935) who presented a new classification of the endoceroids in the broadest sense together with a scheme of their phylogeny. He regarded *Plectronoceras*, the only known Cambrian cephalopod, as giving rise to *Ellesmeroceras*, in which holochoanitic structure was initiated. From this genus sprang other holochoanitic cephalopods. The details of the scheme need not be repeated here. Filoceroids were grouped apart from the slender endoceroids, but it was found necessary to recognize several families. In various isolated cases ellipochoanitic structure appeared. One such case is the family Chilicoceratidae. The ellipochoanitic Baltoceratidae and Troedssonellidae are regarded as derived from the endoceroid line, at the point of divergence of the Endoceratidae, Manchucoceratidae and Chilicoceratidae. A line independent of the main group of the endoceroids, springing from the Plectronoceratidae, produces the supposedly holochoanitic families Wolungoceratidae and Protyloceratidae, and later the orthochoanitic Orthoceratidae. The Orthoceratidae, in turn, yield the cyrochoanitic Actinoceratidae. In a subsequent elaboration of his views concerning the phylogeny of these forms, Kobayashi has proposed that the cyrochoanitic Stereoplasmoceratidae and Sactoceratidae represent related but divergent shoots of the Orthoceratidae. The remaining families of the Actinoceridea are regarded as derived from the Sactoceratidae.

**PHYLOGENY**

The present investigation has yielded evidence which not only opposes nearly all of the views which underlie Kobayashi's phyllogenetic scheme, but also requires the adoption of an entirely new concept of endoceroid development. Previous interpretations of the siphuncle wall have been based upon opaque sec-
tions. Thin sections have been found to yield structures which were entirely unsuspected, and of which opaque sections often gave no indication whatsoever. Indeed, so startling has been the difference between the apparent structure as seen in opaque section and the results obtained from thin sections that further thin section examination is imperative before the position of any genus can be determined and anything approaching a correct revision of the endoceroids can be attempted. The present results are based upon a small but heterogenous selection of genera, dictated largely by what suitable material was available for sectioning. While this gives probably only a faint indication of the morphological results which await a more comprehensive study, it is sufficient to indicate the directions taken by certain of the lines of specialization within the endoceroids and to show the primitive condition.

The Canadian cephalopods thus far examined have failed to yield more than a single rather doubtful case of holochoanitic structure. The earliest forms which can be regarded as holochoanitic with certainty are Chazyan in age, and these retain connecting rings, clearly a heritage from ellipchoanitic Canadian ancestors. Not until middle Ordovician time is a holochoanitic genus encountered which lacks connecting rings. Evidently the endocones are a much older and a more universal structure than the holochoanitic neck. Further, it is necessary to conclude that holochoanitic structure is a relatively late development in endoceroids, possibly not occurring before the beginning of Ordovician time, and one confined to a relatively small portion of the Endoceroidea. In the light of this new information it is necessary to redefine the endoceroids for the purposes of the present discussion. The Endoceroidea are here defined as cephalopods with relatively large siphuncles containing endocones. The connecting ring, when present, is thick and of the euryisiphonate pattern noted in the Tarphyceratidae, under the term endoceroid, and likewise the Baltoceratid, as the siphuncles of this definition excludes the Ellesmeroceratid, which have been often included both families lack endocones, but includes the piloceroids which cannot be separated clearly from the slender endoceroids.

The development has already been traced from the Plectronoceratid to the Ellesmeroceratid. This is the progression proposed by Kobayashi, though Ellesmeroceras does not mark the initiation of holochoanitic structure as he supposed. The genus is apparently the origin of the Tarphyceratid, the Endoceroidea, the Baltoceratid, and the actinoceroid complex as divergent lines.

The first true endoceroid developed merely by the addition of endocones and an endosiphonule to the general pattern of an Ellesmeroceras. This condition is found in the species described below as "Cameroceras" annuliferum. The appearance of the eyelet in this genus is not to be regarded as a specialization and supplies a difference probably more apparent than real. The material of Ellesmeroceras which has been studied was too recrystallized to preserve the eyelet.
However, it is not conceivable that a structure present in such divergent lines as the Tarphyceratidi and the endoceroids could have been developed independently in each. Plainly it must have been present in Ellesmeroceras as the common ancestor.

Protococconicroceras and the new genus Meniscocceras show progressive specialization of the endosiphuncular structures of the endoceroids. The wall of the siphuncle shows specializations closely paralleling those previously noted in Eurystomites. In both groups, the aneuchoanitic neck, the loss of the eyelet, and the clear development of a thick outer zone seem to be intimately bound up with one another. Apparently the eyelet as a dense and perhaps impervious region of the connecting ring, could develop only where a metabolic connection was not maintained through the connecting ring between the camera and the siphuncle. Consequently it is confined at its origin to that portion of the ring through which no connection of that sort could have existed, because it was insulated by the surrounding impervious septal neck of true shell material. In view of this explanation, the connection between the aneuchoanitic neck and the loss of the eyelet becomes significant. The structural meaning of the outer zone is, however, not yet understood.

The oldest holochoanitic endoceroids which have been encountered in this investigation are Chazyan in age. Except for prolongation of both the neck and the ring, the structure is very similar to that noted in Tarphycereras. Endoceras proteiforme of the Trenton limestone, though studied only from opaque sections, appears to be identical in wall structure. The endoceroids which lack connecting rings are apparently more specialized. They are known to appear in the Black River limestone of Ottawa and are dominant, and perhaps universal, among the endoceroids of the Upper Ordovician of the Cincinnati region.

No material has been available for study of the siphuncle wall in piloceroids by means of thin sections. An opaque section of Cassinoceras explanator reveals connecting rings with well-defined eyelets. The condition of the septal necks is obscure, but appears to be holochoanitic as in Vaginoceras opulentm of the Chazyan. Evidently the siphuncle wall is not uniform among piloceroids, as Clarkeoceras and Manchuroceras are already known to exhibit ellipchoanitic necks. There is likewise great diversity in the structure of the endosiphuncle. The cones may be circular in section and simple, or may be specialized in several ways. Dissepiments are absent in Cassinoceras, but are present within the endosiphunculum of some other genera. In Clarkeoceras, they are few in number and widely spaced; in Manchuroceras, they are numerous and closely spaced. The endosiphonblades are capable of various modifications, those of Kotoceras and Manchuroceras being highly specialized and resembling the condition reported here in Meniscocceras. The blades of Cassinoceras, however, are numerous and irregular. When variations of the ectsosiphuncle and endosiphuncle are taken into consideration it becomes evident that the genera of breviconic piloceroids are
more closely related to individual longiconic genera than they are to each other. Kobayashi, in order to group like forms together as piloceroids, has included a number of quite slender forms in the group.

The family Baltoceratidae contains ellipchoanitic cephalopods with small siphuncles and without endocones. Thin sections of an undescribed Baltoceras from the Fort Cassin beds of the Champlain Valley show thick connecting rings and traces of the eyelet. Material of Protocydoceras from the same locality yields short septal necks, thick connecting rings, and well-preserved eyelets. According to Kobayashi, the Baltoceratidae constitute an ellipchoanitic family which originated from the endoceroids, while the Protocycloceratidae are holochonitic, are related to the Wolungoceratidae and are close to the origin of the Orthoceratidae.

Actually, the only difference now apparent between the families is the position of the siphuncle, and this is more apparent than real. Baltoceras possesses a marginal siphuncle. The siphuncle of Protocydoceras is not nearly so central as Kobayashi seems to believe and is markedly ventral of the center, especially in the early stages of the shell. Orygoceras, which is equipped with a submarginal siphuncle, serves to close the gap between the two even more completely. Such a gradational difference is not adequate as a basis for the separation of families, and therefore until more important differences are found, the family Protocydoceratidae is not recognized.

Neither is there much justification for the derivation of the Baltoceratidae as proposed by Kobayashi. According to his scheme, the Baltoceratidae are derived from the endoceroid line close to the origin of the Endoceratidae, Manchuceratidae, Chiliceratidae and Troedssoniellidae. This implies, that in the development of the Baltoceratidae, the siphuncle becomes small, ellipchoanitic structure appears, and the endocones are lost. There is nothing in the Baltoceratidae to indicate that it was derived from a true endoceroid, that is, a form possessing endocones. Further, there is no necessity of attempting to derive the family from a holochonitic ancestor, inasmuch as true holochonitic structure is an extremely specialized condition, appearing late in endoceroid development. Equally unjustified is the connection traced by Kobayashi between the endoceroid family Wolungoceratidae and the Protocydoceratidae.

The connecting rings of the Baltoceratidae are clearly eury siphotomate in structure. It seems best to regard the family as representing a line of specialization derived from the Ellesmeroceratidae quite independent of the Tarphyceratidae, Endoceroidea and the actinoceroid complex. The conch is relatively small and remains straight. The siphuncle is empty throughout most of the family at least, and never develops endocones. The main specialization has to do with the reduction of the diameter of the siphuncle in proportion to that of the conch. The possibility of an affinity between this group and cyrtococic Canadian cephalopods with thick connecting rings, such as are found in Onychoceras Ulrich and Foerste remains to be investigated.
PRIMITIVE ENDOCEROIDEA
(See Plate 1, figures 9, 10)

What is believed to represent the most primitive condition observed among endoceroids exists in a single specimen which combines the ectosiphuncular features of an *Ellesmeroceras* with the general endosiphuncular plan of an endoceroid. This specimen, collected by Professor G. D. Harris from the Beekmantown of the vicinity of Ticonderoga, New York, superficially resembles the common Fort Cassin species, *Proterocameroceras brainardi* (Whitfield), but thin sections show that it is neither conspecific nor congeneric with that form. It clearly represents an undescribed species, and no genus has been described possessing its features. However, Ulrich and Foerste (1933) have described a number of Canadian and Ozarkian genera which are erected upon the form of the shell, the condition of the section and sutures, and the position of the siphuncle; but little attention is given to the details of the structure of either the ectosiphuncle or endosiphuncle. As the gross features of this specimen are not well displayed, a comparison with the rather brief generic description published is not possible. Doubtless this will be remedied when the researches of Ulrich and Foerste, now happily being completed by Miller, have been published. Meanwhile, I find it necessary to have a name by which to refer to this species. The name "*Cameroceras* annuliferum" Flower, n. sp, is proposed, because of the annulated endosiphinctube. The reference to *Cameroceras* is doubtless incorrect, but that genus has served as an endoceroid wastebasket for so long that it might as well continue in this function at least until other investigations supply a more accurate basis than now exists for comparison of this with described genera of Canadian endoceroids.

The type does not clearly display the gross features of the conch, being imbedded in limestone. The shell is straight, slender, and very faintly depressed in section. The sutures are not exposed, but from the course of the septa in a natural weathered oblique section, there is only a very slight development of lobation if any. The camere are very closely spaced. The siphuncle is subcircular, marginal, with no septal structures between it and the ventral wall of the shell. No other species described is known to combine the *Ellesmeroceras*-like ectosiphuncle with endoceroid of circular section and a central annulated endosiphinctube. The two endoceroids generally identified in the Beekmantown of New York are *Proterocameroceras brainardi*, here shown to have very different structure, and "*Endoceras* champlainense" Ruedemann, which differs from this form by the lateral annihilations of the siphuncle wall and has much more strongly curved septa.

The connecting ring is equal to the septal neck in thickness, and in opaque sections it is usually impossible to distinguish the two structures. Thin sections, however, show that the septal neck is short and orthochoanitic, being bent so as to lie parallel to the axis of the conch. The tip of the neck is simple. The connecting ring is equal to the neck in thickness at its point of origin and may retain
this thickness throughout; but it is normally slightly inflated at the middle of the segment, being lens-shaped in section like the ring of *Ellesmeroceras*. The tip of the ring is enclosed within the neck of the next adapical segment. The outer surface is generalized and uniform with the rest of the ring in section. The inner surface is marked by an area of dense fine-grained yellowish calcite which is clearly identical with the eyelet observed in other groups. The position of the eyelet on the inner surface of the ring is particularly significant in this generalized endoceroid, as such a feature must have been present in the ancestors of *Bathmoceras* and the actinoceroids in order to produce the processes projecting into the cavity of the siphuncle which are finally differentiated into annulosiphonate deposits.

The siphuncle walls of this form and of *Ellesmeroceras* are so similar in other respects as to suggest that they were actually identical in fine structure, and that *Ellesmeroceras* possessed an eyelet which has not yet been observed owing to unfavorable conditions of preservation. This belief, as will be seen later, is also suggested by other evidence.

Combined with the simple siphuncle wall there is the typical endosiphuncular structure of a generalized endoceroid. The endocones are relatively short, circular in section, and terminate in a thin-walled tube which is annulated and expands within each segment of the siphuncle (Pl. 1, fig. 9). The spacing of the endocones and the number and position of the blades are not known.

The type of "*Cameroceras* annulariferum" is of particular interest in that it retains the apical end of the siphuncle. Moreover, it is probably the only endoceroid specimen in which it has been possible to make a thin sagittal section through the extreme apical portion, thereby permitting the study of structures in a detail not hitherto attempted. The apical portion of the shell in section is shown in Plate 1, figure 10. The central endosiphutube is not preserved in this portion. Careful observation of the specimen during grinding indicated that the endosiphutube was actually absent. It is not certain, however, whether its absence is original or is the result of replacement. The ventral side of this portion of the specimen is very incompletely preserved. Its loss is apparently due to solution subsequent to burial, as shown by stylolitike contact in many places between the extant portion of the shell and the matrix. On the dorsum, the wall of the siphuncle is preserved intact, though the septa and the shell wall have been destroyed at the apex. There is, therefore, some reason to doubt whether the siphuncle wall is preserved intact. The beginning of the siphuncle is a small bulbous process. No similar structure has been observed in any slender endoceroid, but an almost identical condition has been found in the apical ends of the piloceroid genera *Manchuroceras* and *Chilioceras*. I have observed traces of a similar apical swelling in the siphuncle of an undescribed Fort Cassin species which possesses well-defined dissepiments crossing the endosiphutube and is either a *Manchuroceras* or a related, but undescribed, genus. The apical swelling in "*Cameroceras* annulariferum" shows that the structure is not confined to forms of

5 The tip of the siphuncle is also reminiscent of the small protococonch postulated for *Proterocameroceras* by Eudesmann (1905).
piloceroid aspect, as Kobayashi (1937) believed, and brings to light a type of apical end hitherto unknown among longiconic endoceroids. Unfortunately the wall of the apical swelling is not preserved clearly enough to determine its structure with certainty. The wall is evidently thickened, but it cannot be stated with certainty whether this represents the wall of the shell, as seems likely on the basis of observations on other endoceroids, or whether it is a connecting ring producing an apical cæcum.

This genus serves to connect *Ellesmeroceras* with the true endoceroids and represents a stage following the development of endocones but preceding the specialization of the siphuncle wall.

*Holotype.*—Paleontological Research Institution, No. 5943.

*Occurrence.* From the Beekmantown dolomite of Ticonderoga, New York. The actual horizon is unknown; presumably it is slightly lower than the Fort Cassin horizon which has yielded most of the known cephalopods of the Beekmantown formation.

**Specialized Euficochoanitic Endoceroidea**

Under this heading I include two genera which show in the ectosiphuncle specializations very similar to those previously noted in *Eury stomites* of the Tarphyceratidae, already mentioned above. These consist of three modifications which seem to be associated with one another in both groups:

1. Reduction of the septal neck to an aneuchomitic condition.
2. Loss of the eyelet.
3. Strong development of the outer zone of the connecting ring.

When these features were first noted, it was not certain whether they represented generalized or specialized conditions. It is evident that these variations of wall structure of the connecting ring could have no deep phyletic significance. The grouping of *Tarphyceras* and other endoceroids on one hand against *Eury stomites* and *Proterocameroceras* on another is opposed by so many other morphological features that it cannot be considered seriously. It remained to determine which set of conditions was the more generalized. The aneuchomitic necks which characterize *Eury stomites* and *Proterocameroceras* are not features which are known in the ancestral Electromeroceratid or Ellesmeroceratid and therefore are probably features developed independently in the Tarphyceratid and Endoceroida. The outer zone of the connecting ring, likewise absent in the ancestral families, is clearly specialized in the Tarphyceratid, where all phases of thickness and clarity of differentiation have been noted. Likewise it is probably a specialization in the Endoceroidea as well. The eyelet, as a feature prominent in apparently generalized members of both families, and one which was probably

*Subsequent collecting in the Beekmantown of the vicinity of Smith's Basin, on the Fort Anne Quadrangle, of eastern New York (Sept. 1941), and also in the Bald Mountain limestone south of Middle Falls, New York, has brought to light additional material of this species in association with other cephalopods, notably *Clitendoeceras*, sp., aff. *C. seeleyi* Ulrich and Foerste. This material suggests even more strongly the resemblance of this species with *Ellesmeroceras* in the wall of the siphuncle and further suggests that *Clitendoeceras* and other associated genera may be similarly constructed.*
present in the ancestral Ellesmeroceratidae, appears to be generalized. Certainly it seems improbable that such a marked specialization in the tip of the connecting ring could have been developed several times independently. It involves a real difference in composition of the ring, while the outer zone apparently is concerned only with varying differences in texture, but not, apparently, in chemical or crystalline composition. As already noted, it is suspected that as Ellesmeroceras bridgei Flower$^6$ differs from Cameroceras annuliferum Flower, n. sp. in no other feature of the siphuncle wall than the absence of the eyelet, and, since our material was so recrystallized that preservation of the eyelet could not be expected, the difference may be more apparent than real. Further, while form alone is sufficient to explain the modification of the deposits of the Actinoceridae from the siphuncle wall of Ellesmeroceras, the difference in composition noted between the deposits and the generalized connecting ring requires origin of the deposit from the eyelet, and again suggests the presence of the eyelet in Ellesmeroceras.

Then, too, both Eurystomites and Proterocameroceras show other features than those of the siphuncle wall which indicate that they are highly specialized genera. This is shown by the strongly modified section of Eurystomites, the migration of the siphuncle at an early stage from a subcentral to a ventral position, the relatively rapid expansion of the conch, as well as minor modifications of section and sutures. Proterocameroceras, while generalized in form, is clearly an example of very remarkable specialization of the endosiphuncle, as shown by Ruedemann’s (1905) study.

Proterocameroceras brainerdi (Whitfield)

Plate 1, figures 3-5.

Proterocameroceras brainerdi (Whitfield), the genotype of Proterocameroceras Ruedemann (1905), was selected as a representative of Canadian endoceroids, partly because of the availability of material, and in a large part because the structure of the interior of the siphuncle is already far better known than is that of any other American endoceroid, due chiefly to the classic investigations of Ruedemann (1905). However, study of the siphuncle wall by means of thin sections showed that it was quite as specialized in its own way as was the endosiphuncle. The septal necks are very short, essentially aneuchoanitic, as they do not extend apically along the siphuncle, but only come into contact with the primitive inner zone of the connecting ring. While the outer zone of the connecting ring forms a considerable area of contact with the septum at the adapical end of a segment of the siphuncle, this is more in the nature of an area of adnation, faintly analogous to that found commonly in the Actinoceridae.

The best preserved specimens are from bed A3 of Ruedemann’s (1905, p. 307) section of the Beekmantown at Valcour, New York. The septal necks are replaced by white calcite. They terminate where they attain the thin inner zone

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$^7$ This species, temporarily a *nomen nudum*, is described in “Early Paleozoic cephalopods from the Seward Peninsula of Alaska”, to appear in the Bulletins of American Paleontology.
of the connecting ring and are faintly, and sometimes obscurely, bifurcated at their tips. The inner zone of the connecting ring is preserved as very dark material and is always clearly set off from the outer zone, which is composed of light calcite. The inner zone is relatively thin, uniform in width throughout, and forms faintly concavosiphonate segments. There is no trace of the eyelet. The outer zone is relatively thin adorally, but thickens rapidly at the adapical end of each segment, and is broadly truncated adapically by the septum. It shows under favorable conditions of preservation faint lamellae parallel to the axis of the conch.

Another specimen collected by the writer from slightly lower beds of the same region, (A2 of Ruedemann, 1905) occurs in iron-grey dolomites and presents a very different aspect of the same structure under different conditions of replacement. The necks are preserved as before, but the entire connecting ring cannot be made out. Light patches of calcite indicate the position of the outer zone, but the zone is not preserved in its entirety, and the outline is very irregular. No trace of the inner zone is visible, and the thin adoral portion of the outer zone is generally destroyed. The specimen from which this section was taken represents the adoral end of the phragmocone of a moderately large-sized individual. When found, a good natural section of the conch was exhibited which showed the usual holochaoanitic aspect of the siphuncle, an illusion which was not dispelled by thick-polished sections, but only by thin section investigation.

The structures within the endosiphuncle have been carefully studied by Ruedemann and need only be summarized here. The essential features consist in the presence of an endosipholinining, generally appearing as a lining of coarsely crystalline black calcite against the very white calcite which, for the most part, has replaced the endocones. The cones are depressed in section, being flattened on the venter and rounded on the dorsum. The endosiphoblades are specialized, two being lateral and a third, dorsal. The cone terminates in a flattened endosiphocoleon, which adapically is filled laterally by supplementary material forming the wall of a rounded endosiphutube. The apical end of this cephalopod is reported as consisting of the siphuncle alone within the wall of the shell. Ruedemann notes only a very faint expansion of the siphuncle in the apical end of the shell, a conclusion which I have been able to confirm both from his own and other material. The most remarkable and perplexing feature of the genus is the reported rotation of the endosiphocoleon of the siphuncle. This is shown well by his own material, but I have been unable to find it in supplementary specimens. It is possible that the specimen exhibiting this feature is abnormal, and that the rotation is rather a waving of the soft parts previous to calcification. This may be in some ways comparable to the habit, exhibited by many coiled cephalopods, of the siphuncle to depart sufficiently from the plane of symmetry that it will not be entirely exposed in flat sections.
Genus MENISCOCERAS Flower, n. g.

Genotype—Meniscoceras coronense Flower, n. sp.

This new genus and species of the Chazyian is known only from siphuncles. No complete shells have been obtained from the beds which yielded the two types. The conch is straight and slender. The siphuncle is very faintly incised at the septal foramina. The siphuncle wall is very poorly preserved, and is known only from a single specimen. The necks are ellipochoanitic, very short, and are supplemented by thin, well-defined, connecting rings, probably homologous to the inner zone of Proterocameroceras. No trace of the outer zone has been found.

The endosiphocone becomes invaginated on its dorsal side forming a broad groove, and later gradually becomes semicircular in section; the venter rounded, the dorsum first flattened and then becoming concave as the apex of the cone is approached. At this stage the two lateral endosiphoblades can be seen passing from the lateral angles of the cone dorsad, convex laterad, blending with the endosiphollining of the dorsal wall of the siphuncle. The extreme tip of the endocone, where it blends with the endosiphocleon, becomes a depressed oval, with both dorsum and venter faintly convex. The endosiphotube is seen only near the apical end of the siphuncle and is rounded in form. Apparently it is formed as in Proterocameroceras by a filling of the endosiphocleon.

Discussion.—This genus is included here because it is regarded as a further specialization of Proterocameroceras which developed in Chazyian time, and is the only ellipochoanitic Ordovician endoceroid so far recognized. The position of the endosiphoblades corresponds to that of Proterocameroceras. However, in that genus the ventral side of the endosiphocone is flattened and the dorsal side is rounded. Orientation is based here both upon the prevalent flattening of the side of the siphuncle close to the shell wall and the wall of the conch, which in some sections can be seen in contact with the siphuncle.

The aspect of the siphuncle of Meniscoceras in cross section is very strikingly similar to that of Kotoceras Kobayashi and also of Corcanoeceras. However, the orientation in both genera is directly the opposite of that found in Meniscoceras, and further differences are supplied in the small supplementary ventral invagination of the cones in those genera, which are completely lacking here. Nevertheless, so similar are the blades in Meniscoceras to those of the Asiatic genera, that only the conclusive evidence of the orientation of the shell, as supplied by the marginal position of the ventral siphuncles in both cases, can be accepted as evidence of a complete absence of relationship, and leads, rather, to the conclusion that remarkably deceptive isomorphism is involved.

Meniscoceras coronense Flower n. sp.

Plate 2, figures 1-11

The essential features of this species have already been given in the generic description. It is known from two siphuncles. The holotype expands from 16 mm. and 17 mm. to 20 mm. and 23 mm. in 120 mm. in the basal portion, and
increases to a width of 28 mm. in the next 110 mm. The siphuncle extends 150 mm. farther oral, showing the adoral portion of the last endocone which is about 120 mm. in length. The dorso-lateral surface, polished from a natural section at the same position, is oblique so that the left side as shown in our figure is more dorsal than the right side. This section shows a peculiar hump in the deposit on one side which has not been encountered elsewhere in this specimen or in the paratype and is therefore believed to be abnormal. Certainly it is unlike any structure previously noted in endoceroids. The paratype lacks this projection, although the internal mold of the endosiphoncone is well exposed, and shows at its adoral end the flattening which is not so well shown on the holotype. The paratype expands from 10.5 mm. and 18 mm. to 22 mm. and 26 mm. in a length of 170 mm. This specimen shows clearly the depth of the cameræ in the adoral portion, a siphuncular segment there being 15 mm. in length, where the width of the siphuncle is 20 mm. The specimen seems to be very slightly flattened, but preservation of internal structure is excellent, and there is no evidence of distortion. This specimen shows the median endosiphoblade, not well displayed on the holotype. There the area dorsal of the endosiphocoleon is recrystallized, presenting much the aspect of a cross section of a Kotoceras.

Types.—University of Cincinnati, holotype, No. 22862; paratype, No. 22863.

Occurrence.—From the Middle Chazy limestone of Crown Point, New York. The holotype is from limestones at the base of the small sailboat light on the point, not far from the Champlain bridge. The paratype is from the grounds of the English fort ruins, collected by Mr. Herrick Smith.

DEVELOPMENT OF HOLOCHOANITIC STRUCTURE

In placing the Holochoanites at the beginning of the Nautiloidea, Hyatt assumed that they were both ancient and simple. Upon casual examination, it would appear that the holocoanitic siphuncle wall is simple and therefore potentially primitive in consisting only of septal necks. The ellipochoanitic siphuncle is more complex, consisting of necks supplemented by connecting rings. The implication is that the connecting ring arose by a differentiation of a part of the septal neck. The writer (Flower, 1939, p. 41) has shown reason to believe that while the septal neck is a true shell structure and is laid down by mantle epithelium, the connecting ring is secreted within tissues and is almost certainly mesodermal in origin. Obviously, if this is correct, the connecting ring could never have arisen from the septal neck.

The antiquity of the Holocoanites is now open to grave question. Hyatt assumed that they were the oldest of the nautiloids. Foerste at one time regarded all pre-Ordovician cephalopods as holocoanitic, but abandoned the view as the result of further study. The family Plectronoceratidae, the only group of cephalopods thus far known in the Cambrian, is clearly ellipochoanitic. The Ozarkian forms include, in addition to the Plectronoceratidae, the Diaphiragmidae, (largely, if not entirely, ellipochoanitic or aneuchoanitic) and the Ellesmeroceratidae. The Ellesmeroceratidae were formerly regarded as the holocoanitic cephalopods of the Ozarkian. However, the siphuncle of Ellesmeroceras is ellipochoanitic, as discussed above, leaving the holocoanitic structure of related genera a matter to
be regarded with serious doubt. In the Canadian, holochoanitic structure has been reported, and such structure has generally been assumed to occur in the majority of endoceroids and piloceroids. However, Kobayashi has already found ellipochoanitic structure in the Chiliceratids, though he regards most other forms as holochoanitic. The present investigation reveals that *Proterocamero ceras*, which is holochoanitic in appearance in opaque section, is actually a very specialized ellipochoanitic form. This suggests that similar conditions may obtain in other Canadian forms now considered to be holochoanitic, and extensive examinations of siphuncle walls will have to be made in order to establish the true nature of the structure. My material has been very limited, and observations of a greater variety of forms are needed; but at the present time the earliest form which is demonstrably holochoanitic is Chazyan in age.

If the Holochoanites are neither particularly ancient, as shown by stratigraphic evidence, nor particularly simple, it is to be expected that somewhere in the group there would be evidence of the connecting ring, which is found in the oldest nautiloids and can be safely regarded as a structure which appeared very early in the development of the cephalopod. Such evidence is supplied in the Chazyan cephalopods described as *Vaginoceras appletum* Ruedemann and *Nanno noreboracum* Ruedemann (1906). (Pl. 3, figs. 8-11; Pl. 2, figs. 12-13). Except that the connecting ring is complex in structure, the development is very similar to that of *Altaria* of the Tertiary (Miller and Thompson, 1937).

The general nature of the siphuncle wall is shown in text figure 2A. The

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7a This opinion has been considerably strengthened by further thin section investigations of Canadian cephalopods of endoceroid aspect.
septal necks are prolonged, extending for the length of one siphuncular segment. At the tip, the neck is simple, pointed, and is curved slightly centrad. From its adapical surface, the connecting ring arises. This extends for the length of another segment. The tip is more or less inflated, and consists of the dense, fine-grained structure of the eyelet, though I have never found the eyelet structure as well delimited as in the clearest of the Tarphyceras sections (fig. 1C). The eyelet is variable in extent and clarity, and the three segments of the connecting ring shown in the accompanying figure (fig. 2A; see also Pl. 3, fig. 10) have been modified to show some of the different aspects presented by various sections. The upper segment shows the eyelet poorly set off from the remainder of the ring and indicated only by finer grained material. The second shows the generalized condition observed in the large-sectioned specimen illustrated on Plate 3, figs. 8-9. The third represents a condition in which bands of clear calcite separate the main part of the ring from the interior of the siphuncle on one side and from the septal neck on the other. This was observed only in one considerably distorted specimen and is believed to represent an artificial condition attendant upon recrystallization following distortion.

The base of the connecting ring extends between the tip of one septal neck and the bent portion of the next adjacent one. Very rarely, it may extend a considerable distance within the camera and may develop a structure along the outside of the neck simulating cameral deposits and resembling the outer zone as developed in some of the Tarphyceratidae. This, however, has been observed only in a few cases, is not uniform in any considerable series of camera, and is suspected of being adventitious, the result of poor differentiation between the calcite replacing the connecting ring and that representing an originally inorganic deposit within the camera.

The structure of the siphuncle wall of *Vaginoceras opulentum* Ruedemann is certainly identical with that which Hyatt (1900, text fig. 1105, also Ruedemann, 1906, fig. 3) figured for *Endoceras*. Here a structure similar to a connecting ring is represented as arising from the tip of a septal neck, extending apical, and surrounding a space regarded as a vacant ring around the siphuncle. Hyatt's vacant ring is our eyelet, which, because of its dark color and fine texture, often does resemble a space filled by matrix. There is, however, abundant evidence of the organic nature of the eyelet filling in my thin sections. Not only does it differ in appearance from the matrix under such conditions, but it is often found in parts of the specimen where matrix could not have penetrated, as it is bounded on one side by camera which were closed to the exterior and filled with infiltrated calcite, and on the other by the solid endoskeleton which filled the siphuncle. Fortunately a specimen of *Endoceras proteiforme* in the collection of the New York State Museum is clearly enough preserved, even in opaque section, to confirm this interpretation of Hyatt's figure, presumably based upon the same species.
This specimen shows wall structure which does not differ from that of *Vaginoceras oppletum*; even the eyelets are well preserved, an unusual feature in opaque sections.

Ruedemann (1906, pl. 4, fogs. 2-3) has illustrated the wall structure in *Vaginoceras oppletum*, but his drawings show the dark connecting ring only as a terminal darker portion of the septal neck. Opaque sections often give this impression; indeed, thin sections were necessary to demonstrate that the true condition was actually quite different. His drawing shows the tip of the ring to be hooklike and to enclose a light-colored space. This, as shown by examination of the type from which the drawing was made, is the eyelet occupied by fine-grained, light-colored calcite.

The wall structure of *Nauno noreboracum* Ruedemann (1906, p. 427, pl. 7, fogs. 6-7) differs in no way from that of *Vaginoceras oppletum* Ruedemann, and the two are obviously congeneric and possibly conspecific. I retain both names here as it is not intended to enter at this time upon a discussion of the specific and generic problems in holochoninitic endoceroids. Quite possibly the two forms represent an as yet undescribed genus. This cannot be determined until careful studies have been made of the siphuncle wall of the types of the genera already established.

The lucky find of several specimens identical with the holotype of *Nauno noreboracum* permitted a further study of the condition of the apical end of cephalopods which are holochoninitic but retain connecting rings. Unfortunately the material was somewhat friable, and the tendency for siphuncles to separate from the camera along the septal necks has obscured some vital features. The most complete specimen (Pl. 3, fig. 5) consists of a part of the paragmacone containing the adoral end of the apical bulb of the siphuncle, and continues to an immature living chamber, which bears fine transverse striae and lirae and also shows a peculiar and irregular constriction, at first thought to represent a geronic condition. Other specimens, however, lack such features, which in the above are probably the result of distortion. Another form indicates very clearly the relationship between the type of structure of typical *Vaginoceras oppletum* and *Nauno noreboracum*. This specimen, when sectioned horizontally, so as to expose the ventral side of the siphuncle, showed the apical bulb very clearly, followed by annular segments similar to those of *Cameroceras* in appearance. The structure of the wall, however, was that of *Vaginoceras oppletum*. A further structure made in the same specimen parallel to the previous section, but taken at the middle of the siphuncle, showed the siphuncle to be straight-sided and failed to show any trace of the apical bulb (Pl. 3, fig. 6).

A vertical section wasground through one of the specimens and the surface was examined at intervals to determine the condition of the internal de-

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8 The limestone tends to break across the fossils rather than around them. Usually it was not possible to recognize this rare species until it was broken. As breaks commonly occur along the siphuncle wall, most of the specimens were unsatisfactory for the features which it was most necessary to observe.
posits. This section, as photographed (Pl. 1, fig. 8) passes slightly beyond the center of the siphuncle. The endocones are developed adapically and also against the contracting sides of the anterior end of the bulb. Careful examination failed to show the endosiphontube penetrating any nearer to the apex than is indicated in my figure. Further, the specimen was adequate to show that the wall of the apical end of the shell is complete with no sign either of a perforation or of a protoconch such as was postulated for Proterocameroceras by Ruedemann (1905).

Two segments of the siphuncle wall are preserved in my sectioned specimen, though only on the dorsal side (Pl. 1, fig. 8; text fig. 2B). The adoral septal neck is thin, curved inward at its tip, and within it lies a connecting ring, such as is typical of Palaeoceras oppletm, preserved in dark-grey calcite. The tip of this septal neck gives rise to a band of white calcite which apparently represents its connecting ring. This extends along the outside of the first septal neck to the wall of the conch. There is no trace of an eyelet in this connecting ring, and its tip cannot be determined. It appears to merge into the wall of the shell, here represented by white calcite, as shown in the text figure (2B), and an apparent line of contact of the ring and the shell wall can be seen. This is probably false, however, as it can be traced all the way around the apex of the shell and onto the ventral side. In this course it moves to a position halfway between the inner and the outer walls, and becomes a band of grey calcite, clearly an inorganic phenomenon of replacement. No trace of the connecting ring can be seen on the apical septal neck. The apparent absence of the connecting ring here may have considerable significance. It was also found to be absent from the apical septal neck of Actinoceras; further, the growth of annulosiphonate deposits over the adapical surface of the first septum shows clearly that there could have been no ring present there at the time when that material was deposited. The evidence supplied by Nammo nevoboracum indicates that here also the apical septum bears no connecting ring. The resemblance between the two groups in this respect may have considerable systemic value. At present the structural significance of the missing apical connecting ring is not known.

Although connecting rings are present in holochoanitic endoceroids from the Chazyian through the Trenton, they are not universal. Another and apparently a more specialized group of endoceroids has lost the connecting ring completely. Such forms are known to encompass a range from Black River through Richmond time. A thin section of an endoceroid from the Black River limestone of La Petite Chaudière, Ottawa, is illustrated on Plate 1, figure 7, which shows the septal necks so closely appressed as to indicate that the connecting rings were originally absent and not lost through destruction and conditions of poor preservation. Fine examples of holochoanitic necks without connecting rings occur in the Upper Ordovician of the Cincinnati region. Insofar as is known, none of
the endoceroids with connecting rings persist into the Upper Ordovician. The
generic position of such endoceroids is at present uncertain.

Probably no group of cephalopods is in worse need of revision than the
Ordovician endoceroids. They are common enough to serve as potentially valu-
able horizon markers and faunal indices; but so much confusion surrounds both
specific and generic determination at the present time that they are really useless
in this respect. Species have been based, by necessity, upon fragmentary material.
However, there is little justification for basing not only determinations, but
also descriptions, upon poorly preserved material, as has often been done. For
many of the described species nothing is known except the general aspect of the
types. Descriptions have relied upon gross features of the shell, too often variable
within endoceroids, and no attention has been given to the more reliable and
valuable structures of the siphuncle. A large number of species probably still
await description. Probably, also, two-thirds of the specimens which have been
identified as *Endoceras proteiforme* are too incomplete or too poorly preserved
to justify generic or specific identification. Certainly the great range attributed
to the species, from Trenton to Richmond, over eastern and arctic North Ameri-
ca, presents such a sharp contrast with the extremely restricted range of most
other cephalopod species that one is led to regard it with grave suspicion.

Generic characters have not been much better. Some genera were separated
on the basis of relatively superficial features, such as the annulated exterior of
*Cyclendoceras*, or the annulated siphuncle of *Cameroceras*. Some are of little
practical value because they deal with parts of the conch rare, encountered, as
*Nanno* and *Succoceras* which were based upon apical ends of the shells. Still
others are founded upon observations of doubtful accuracy. It is suspected,
for example, that the septal necks extending for the length of two siphuncular
segments, on the basis of which *Vaginoceras* was recognized, are instead necks
supplemented by connecting rings as in *Vaginoceras oppletum* and *Endoceras
proteiforme*. My own rather desultory observations indicate that both in the wall
of the siphuncle and the structures of the endosiphuncle, there is a wealth of val-
uable morphological data potentially of great value in the reorganization of the
Endoceroida.

At the present time I have not attempted any reorganization of the holo-
choanitic endoceroid genera, having failed up to the present to obtain suitable
material for determining the structures of the ecto- and endosiphuncles in the
types of the genera now described. Both must be known before a reevaluation of
the generic boundaries can be attempted. The most serious weakness of Ko-
hayashi’s classification is an assumption of knowledge, without data, concerning
the siphuncles of such genera as *Endoceras*, *Cameroceras*, and *Vaginoceras*. The
siphuncle wall itself of *Endoceras proteiforme* is made known here. The wall
structure is unknown in the types of the other genera for the most part. En-
**Doceras proteiforme** appears to have endocones of slightly depressed section, but the endosiphuncle is still not adequately known. The endosiphuncle of *Vaginoceras longissimum* and *V. multitubulatum*, which are possibly different phases of preservation of a single species, is characterized by compressed cones terminating in a compressed tube or coleon, broad and rounded at the top, and pointed ventrally, and supported by two vertical blades. Yet the wall of the siphuncle is still unknown. *Vaginoceras applectum*, of the Chazyan, is the largest and most abundant cephalopod of the Valcour limestone of the Champlain Valley. All specimens examined show the same sort of wall structure, but exhibit some variation in the condition of the endosiphuncle which suggests that either there is considerable variability within the species, or, more probably, that at present more than one species is retained under the name. Typical specimens exhibit a compressed endocone as in the genotype of *Vaginoceras*, which is pointed ventrally (Pl. 2, fig. 12). Sometimes this is supported by a dorsal and ventral blade. This is not constant, however, and one specimen was observed showing five blades arranged in a starlike pattern (Pl. 2, fig. 13). Whether this species should be placed in *Endoceras* on the basis of the siphuncle wall, or in *Vaginoceras* on the basis of the endocones, or whether it represents an undescribed genus must await more thorough knowledge of the types of these genera. Moreover, fuller use of the endosiphuncular features requires a more complete knowledge of the significance of the structures involved.

**ORIGIN OF THE ACTINOCEROIDEA**

Although Teichert (1933) came to the conclusion that the actinoceroids were more closely related to the endoceroids than to any other cephalopods, no attempt seems to have been made previously to establish the point of union of the two lines. Kobayashi (1935, p. 750) has presented a highly constructive diagram of the phylogeny of the older cephalopods, but regards the actinoceroids as derived from orthochoanitic cephalopods. This view is rejected here, since a connection between the actinoceroid and the endoceroid has been found. Further, Kobayashi's subsequent proposal of a division of cephalopods into Centrosiphonata and Ventrosiphonata is based upon facts which can be given quite a different interpretation.

The two main lines already traced, those leading to the Tarphyceratidae and to the Endoceridae, deal with only secondary modifications of the connecting ring within each group. Primitively, the ring is thick, and its tip is occupied by the eyelet; but no connection between the ring and endosiphuncular structures seems to exist even in the endoceroids where such structures exhibit a variety of forms. In the line leading to the actinoceroids, however, the connecting ring is modified to form deposits within the siphuncle which have generally been considered as structures quite apart from the siphuncle wall.

The ring of *Ellesmeroceras* is a simple structure, lens-shaped in section (fig. 3A). Disregarding growth lines within the ring, inasmuch as they are unknown in *Ellesmeroceras* and *Bathmoceras*, it is possible to trace these directly to the
annulospinonate deposits exhibited by *Polydesminia*, the oldest, and therefore probably the most primitive, of the true actinoceroid cephalopods. *Bathmoceras* (fig. 3B) represents the first step in the development of processes from the inner surface of the ring which project oral and central into the cavity of the siphuncle. Holm's photographs and drawings show that the processes of *Bathmoceras* vary considerably in mass and thickness and sometimes approach very closely in form the more massive deposits developed in *Polydesminia*. Indeed, the similarity between the deposits of the two genera is so marked as to suggest strongly a close relationship, which, rather strangely, has not previously been considered (fig. 3C).

Fig. 3. Siphuncle wall and deposits of *Ellesmeroceras*, *Bathmoceras* and *Polydesminia*, showing progressive growth and modification of a lobe of the connecting ring which eventually develops into annulospinonate deposits. Growth lines are not known for *Ellesmeroceras* or *Bathmoceras*. Their course in *Polydesminia* is indicated by the middle segment only. The dense black body at the base of the segment indicates the original form of the deposit, essentially a repetition of the primitive eyelet in a curved connecting ring. A. *Ellesmeroceras*, based upon *E. bridgei* Flower from the Seward Peninsula of Alaska. B. *Bathmoceras*, after Holm. C. *Polydesminia*, considerably modified from Kobayashi.

These data are, however, insufficient, as in dealing with actinoceroids many more structures than the deposits of the siphuncle exist and must be considered; such as the vascular system, the perispatial deposits, and especially the composition of the generalized connecting ring and the annulospinonate deposits.

**BATHMOCERAS**

Holm's (1896) study of *Bathmoceras* contains all that is known of the internal structure of this singular genus. An attempt to supplement his observations by sections of the Bohemian *Bathmoceras propostorium* was unsuccessful, for the material, consisting of silicious internal molds, had apparently not only been subjected to considerable weathering and solution after burial, but had also been partly dissolved previous to, or during, the processes of fossilization. It proved unsatisfactory for thin section investigation and, indeed, only preserved the thickened connecting rings very poorly and incompletely, though permitting verification of some of the gross features of the siphuncle.

The septal necks of *Bathmoceras* are somewhat variable in length and generally straight. In general, too, they are somewhat longer than in the figure repro-
duced here. Further, in Bathmoceras limarassoni Angelin, the species which Holm studied, and also in B. preposterae Barrande, the curvature of the necks tends to vary somewhat, and in many of Holm's figures there can be detected more than a faint suggestion of the beginning of a cyrtochonanic development which is brought to a fuller expression in the actinoceroids proper (Holm, 1890, pl. 7, fig. 4). Holm has made careful sections and has established the form of the deposits, which vary in form and position somewhat from dorsum to venter. This feature does not seem significant in connection with the actinoceroids, but is strangely and probably significantly reminiscent of the dorso-ventral variations found in the wall of the siphuncle of the older and presumably ancestral genus Ellesmeroceras (fig. 3B).

Although Holm's study of Bathmoceras stands quite alone among cephalopod studies of its period by virtue of its precise and detailed nature, it unfortunately leaves unsolved several problems which are of particular importance to the present investigation. The deposits are illustrated as growths from the connecting ring. No differentiation is shown within them. As it is suspected that the deposits are derived from eyelet, growing oral and central and covering the generalized part of the ring, apparently very thin here, since it escaped observation, the genus must be reexamined, preferably by means of thin sections, with these possibilities in mind. Further, no trace of vascular structures has been found within the deposits. Areas of light calcite, generally located in a segment near the tip of the septal neck, show structures of uncertain affinities. These may be secondary deposits showing lamellae of growth, vestiges of vascular structure, or inorganic phenomena. Obscure traces of a possible central canal are shown.

**Polydesmia**

Kobayashi's (1940) recent study of Polydesmia has supplied excellent descriptions and figures of the genus, but failed to consider sufficiently the relationship of the deposits here with those of nonactinoceroid cephalopods. Further, his own illustrations, as well as specimens of Polydesmia in the U.S. National Museum, indicate that the siphuncle wall is not holochonanic as he states, but ellipchoananic. Teichert (1937) was able not only to determine the tip of the ellipchoananic neck, but to measure it in the genotype. A number of Kobayashi’s illustrations show a definite break in the wall of the siphuncle at the point at which the septal neck may reasonably be expected to terminate. This is shown in Polydesmia canaliculata (Kobayashi, 1940, pl. 4, fig. 17; also pl. 5, fig. 20) and Polydesmia watanabei (pl. 5, fig. 23). The siphuncle wall of Polydesmia is very deceptive in possessing a connecting ring which is essentially the same in thickness as the septal neck, though it is much easier to detect the point of contact here than in the endoceroid genera which exhibit a similar uniformity. The connecting ring is thinner in the younger actinoceroids. That of Actinoceras rudemannii Foerste and Teichert, while thinner than the septal necks, is still relatively thick, and approaches the condition of Polydesmia quite closely (Pl. 3, fig. 1).
The outline of the siphuncular segments has been adequately discussed by Kobayashi. The segments are very broadly expanded, similar in general to those of *Actinoceras*, and differing in some, but not all, species in the interruption of the area of adnation to form an interseptal cavity⁹ (text fig. 3C; Kobayashi, 1930, text fig. 1).

The deposits within the siphuncle are annulosiphonate, built up of concentric lamelae which Kobayashi correctly recognizes as original and as representing lines of growth of the deposit. These lamelae are probably common to all actinoceroids, but are often, in fact generally, absent as a result of alteration.

The deposits are attached to the connecting ring at its adapical end, at the point where the eyelet has been found in other euryphosphonate cephalopods, within the part of the ring enclosed by the neck of the next adapical siphuncular segment. This is consistent throughout the Actinoceroida. No data exist for a comparison with *Bathmoceras*.

Kobayashi has discerned and named three stages of growth for the annulosiphonate deposit of *Polydesmia*. The first, the pro-*Actinoceras* stage, persists until the deposit attains the middle part of the constriction. The very earliest stage of deposition has not been noted in *Polydesmia*, as the point of attachment of the ring is usually too crystallized. However, it is doubtless similar to that of other actinoceroids and essentially linear, though curved in accordance with the bend of the connecting ring. This is indicated in black in one segment of figure 3C. In its form it suggests the eyelet as developed in the Tarphyceratidae Endoceroida and is perhaps an ontogenetic retention of this ancestral condition.

The *Actinoceras* stage of the deposit, as named by Kobayashi, is reached when two adjacent segments of the deposit are nearly in contact. Growth is essentially annulosiphonate, the surfaces of the deposit being fairly equidistant from the point of origin. The ring is rounded in section and strongly inflated. Its recapitulatory significance can be questioned, however, in view of the fact that the stage it is supposed to reproduce is characteristic of *Actinoceras*, a genus considerably younger than *Polydesmia*. The third stage, the *Polydesmia* stage, is concerned with the growth of the forward projecting processes of the deposit, which Kobayashi regards as a specialization peculiar to this genus. Except that the mature deposit is more massive at the base, it is not greatly different from that of *Bathmoceras*, once the "*Actinoceras* stage" is past. Whether these stages have any real phylogenetic significance is extremely dubious.

A more significant feature of the ontogeny of the deposits of *Polydesmia* is the direction of growth along the connecting ring. Originating at the adapical tip of the ring, the deposits grow forward, but are never increased apicad. Thus each deposit grows only along the surface of the ring from which it springs. This is consistent with the general trend of growth found in *Bathmoceras*, as can be clearly seen even without the guidance of growth lines. It is, however, a feature

⁹ The term is an unfortunate one, inasmuch as the cavity lies against the true septum on one side but on the other is bounded by the thick connecting ring rather than another septum as Kobayashi supposed.
lost in younger actinoceroids, in which growth of the deposit may proceed as rapidly and as far apicad as oral from the center of deposition, and may encroach upon the generalized part of the next adapical connecting ring, as well as upon the surface of the ring from which it originates.

Narrow spaces separate the adjacent annulosiphonate deposits in *Polydesmia*. These are contact lines and are sometimes vestigial. They are not, as Kobayashi suggests, the radial canals. Instead, the radial canal system is embedded within the annulosiphonate deposits. It consists of fine, complexly branched tubules which Kobayashi has illustrated but considered as a part of the structure of the annulosiphonate deposit. In possessing such a system of numerous, fine irregular tubes, *Polydesmia* is clearly primitive in relationship to all other actinoceroids. The generalized siphuncle contains numerous fine blood tubes. In the Actinoceridae these are gradually specialized by reduction and simplification to a series of fewer and larger tubes; first into the system of double arcs characteristic of *Nybyoceras* and many of the Armenoceratidae, then into the system of single arcs found in *Actinoceras* and its allies, and finally into the system of simple horizontal tubes radiating from the central canal which characterize the Sactoceratidae. The acme of specialization is perhaps found in *Metarmenoceras* Flower, where even these simple canals are reduced in number and have come to form a bilaterally symmetrical pattern in their arrangement. *Polydesmia* clearly lies near the beginning of this development. Even the walls of the central canal are not precisely marked, suggesting that it also was composed of numerous fine tubes. In higher forms the central canal can be recognized as containing a small number of large tubes, sometimes as few as two, in which case one is apparently arterial and the other venous. The perispatium is not definitely marked in *Polydesmia*, nor has its peculiar dark deposit been observed. Quite probably the perispatium was not of great functional importance here, as there was necessity in *Polydesmia* for only minor division of the numerous radial canals to tubes fine enough to penetrate the connecting ring (Flower, 1939, p. 60).

It is questionable whether any structures representing the vascular tubes are present in any related or ancestral types. Information on the detailed structure of the connecting ring is lacking for the crucial genera *Ellesmeroceras* and *Bathmoceras*. Possibly the blades figured by Ruedemann (1905) for *Cassinoceras explanator* (Whitfield) might have served such a function. They appear to be discrete tubes rather than continuous dissepiments. The endosiphoblades of endoceroids, however, could hardly have served such a function. They are continuous longitudinally and do not connect any specific part of the siphuncle wall with the central canal. Instead, they apparently terminate in the endosiphonining. While the nature and function of the blades are not well understood, it is clear that they served as a point of weakness in the endosiphuncle. A remarkable specimen of a *Vaginoceras* from the Black River limestone of Watertown in the collection of the New York State Museum shows that the siphuncle was capable of breaking along the blades. This specimen was broken in this way prior to burial. One half of the specimen represents half of the endosiphuncle, split vertically. The other half is missing, and the opposing surface (Pl. 3, fig. 7) shows
only the impression of the broken surface on a slab of limestone. Without the other half, this would never be recognized as a cephalopod. The broken surface shows the endosiphuncule clearly. On either side of the tube are transverse wrinkles of a natural surface along which the split occurred. Except that all outlines are relatively smooth, this is suggestive of split guards of Mesozoic belemnites, which are composed of long columns of aragonite crystals perpendicular to a central axis. How far the similarity can be carried safely is extremely dubious. Nevertheless this specimen suggests strongly that rather than blood tubes the blades were, as Kudenmann originally proposed, supporting membranes which persisted after calcification of the endosiphuncle.

ORIGIN OF ANNULOSIPHONATE DEPOSITS

The hypothesis outlined above requires that the annulosiphonate deposits of the Actinoceroida be derived from the connecting ring of ancestral forms. This is opposed to the hypothesis previously presented by the writer (1939, pp. 51-55) that the annulosiphonate deposits were laid down by a siphonal mantle. Further, it is consistent with Teichert’s earlier proposal that the annulosiphonate deposits were laid down within the tissues within the siphuncle. Several other bits of evidence suggest that annulosiphonate deposits are very different from cameral deposits and other true shell structures, and that they are intimately bound up with the connecting ring.

It is common to find that annulosiphonate deposits differ in appearance from the cameral deposits. This is particularly well shown in material from the Silurian (Etage E) of Bohemia. Where most shell structures are replaced by white calcite, the annulosiphonate deposits are filled with very fine-grained dark-colored calcite with a waxy luster. A very similar appearance was noted in the holotype of Geisonoceras teichertii Flower (1939, p. 164, pl. 7, fig. 8; pl. 9, fig. 10). Similar differences in texture were noted in Devonian Pseudorthoceratidae from the limestone layer at the top of the Pompey member of the Hamilton in central New York, and are found again in some of the better preserved specimens from the Laurel limestone of the Silurian of Indiana. The reexamination of my original material leads me to conclude that the markings normal to the lines of growth of the annulosiphonate deposits in *Pseudorthoceras*, which were regarded as representing rows of aragonitic prisms and indicative of true shell structure, were adventitious in the siphonal deposits, though real in the case of the cameral deposits. Numerous other examples could be cited of difference in composition, or texture, or both in cameral and siphonal deposits. The evidence overwhelmingly suggests that cameral and siphonal deposits are so different in their present preservation as to demonstrate that they were originally very different in texture and probably also in composition, the result of which was different behavior during fossilization and replacement. As the connecting ring is markedly different in composition and structure from other shell parts in *Nautilus*, a connection between annulosiphonate deposits and the connecting ring seems likely.

The intimate connection between the annulosiphonate deposits and the connecting ring is further shown by the remarkable genus *Leurocyloceras* (Foerste,
extend, Flower, 1911). This genus is peculiar in possessing very well-developed cameral deposits and no connecting rings or siphonal deposits. Here connecting rings are absent, and the annulosiphonate deposits, which must spring from the connecting ring, consequently are not developed, although cameral deposits may invade the cavity of the siphuncle and may even line the septal foramen.

In the Actinoceridae, the annulosiphonate deposit always springs, not from the septal neck, but from the tip of the connecting ring lying within the neck. This is demonstrable in Actinoceras (Pl. 3, fig. 1) by means of thin sections and can be seen in many specimens in opaque polished sections. In the Pseudorthoceratidae, however, the connecting ring is so very thin that it is hardly possible to determine where its tip is located, and in that family I have encountered no specimens, even among thin section material, which show the connecting ring extending along the inside of the adapical septal neck nearly to the tip of the brim.

An apparent objection to this explanation of the origin of annulosiphonate deposits of the Actinoceridae is found in the fact that the deposits are strikingly different in their mode of preservation from the connecting ring, even at the point of their original seat of attachment. This may be due to the origin of annulosiphonate deposits from the eyelet. Though direct evidence of this is lacking at the present time, such an interpretation is strongly suggested by various lines of evidence. The eyelet has not been demonstrated in the ancestors of the Actinoceridae, Ellesmeroceras and Bathmoceras, but the possibility remains that it was probably present in both genera. The material which furnished the basis for the investigation of the siphuncle of Ellesmeroceras was so extensively recrystallized that it was exceedingly difficult to make out the boundary between the septal neck and the connecting ring, and under such circumstances the preservation of the eyelet could not be expected. All that is known of the structure of Bathmoceras is due to the investigations of Holm, and while his study gives very careful attention to the larger features of the siphuncle and its deposits, thin sections were not used, and neither growth lines within the deposit nor the eyelet, which are important to the present investigation, were then suspected. To test the present hypothesis, it is necessary that both genera be reexamined in thin section on the basis of well-preserved material.

Indirect evidence, however, suggests that the eyelet was present in the ancestral Ellesmeroceras, and was therefore in all probability retained in Bathmoceras and Polydesmia, where it became increasingly expanded until it formed the annulosiphonate deposit which is apparently distinct from the connecting ring. The eyelet has been observed as a persistent structure in two very different groups, the Tarphyceratidae which are specialized by coiling, and the endoceroids which are straight but are specialized by the structures developed in the interior of the siphuncle. The logical common ancestor of these forms is one which combines their simpler features, the empty siphuncle of the Tarphyceratidae with the uncoiled condition of the endoceroid. Ellesmeroceras fulfills these requirements. The presence of other features common to the two lines of descent, but as yet unknown in Ellesmeroceras, owing to unsuitable conditions of preservation, may be safely
inferred if it can be demonstrated that they are generalized rather than specialized. As has already been shown above, in connection with the discussion of the endoceroids, there is adequate basis for regarding the eyelet formed within septal necks as primitive and the condition noted in *Eurystomites* and *Proterocamrococeras* as highly specialized. The presence of the eyelet in *Ellesmeroceras* is likewise suggested by "Camrococeras" annuliferum, as the apparent absence of the eyelet is the only feature in which the siphuncle wall of *Ellesmeroceras* shows any difference from that species. Further, by assuming the presence of the eyelet in *Ellesmeroceras*, and its preservation in the actinoceroid line, this obstacle to the present hypothesis is removed. In order to form the deposits of *Bathyoceras*, the eyelet must grow by the addition of material largely in an adoral direction. The strong adoral projection of the deposits is adequate evidence of this, even without growth lines. There is no reason, at least, to assume that the direction of growth was not uniform throughout its period of development. In *Polycystina*, the tendency toward anterior growth is somewhat reduced, but it still dominates, particularly in the final stages. Reassertion of a modified primitive condition in late stages of growth is no new phenomenon in animal development. Subsequently even this vestige is lost, and finally the "typical" annulosiphonate deposit is formed. Theoretical as this explanation appears, it is consistent with the known facts and serves to account for the widespread difference in replacement phenomena of the connecting ring proper, the annulosiphonate deposits, and true shell structures, not only in the Actinoceroidea, but also elsewhere.

There is one further implication of this hypothesis to be considered. What is true of the structure of the annulosiphonate deposits of the Actinoceroidea appears to apply as well to the annulosiphonate, and probably also actinosiphonate, deposits as developed in supposedly stenosiphonate cephalopods. This implies that as in the Actinoceroidea, these deposits must have been developed similarly from the eyelet of the connecting ring. From this it must follow that these annulosiphonate cephalopods sprang from the eury-siphonate line, that the eyelet is actually far more ancient in the development of cephalopods than the present evidence will permit us to believe, or that the structure was developed more than once.\(^{38}\)

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\(^{38}\) Strand, T.: The upper Ordovician cephalopods of the Oslo Area, Norsk Geol. Forh., Bd. 14, 1934, pp. 1-118, pls. 1-13. Strand remarks upon the relationship of actinosiphonate deposits and the annulosiphonate deposits which he terms bullettes with the connecting ring, (pp. 3-7) but regards the bullettes, which include annulosiphonate deposits of the Actinoceroidea and the "Orthocerasidae" as distinct in origin. The present investigation supports Strand's conclusions concerning bullettes, but fails to show that the bullettes are fundamentally different in structure or origin.
STRATIGRAPHY

It should be noted that the evolutionary scheme proposed above is quite consistent with the stratigraphic range of the various groups involved. The Plectroceratidae are in this respect admirably fitted as candidates for the position of ancestors of other cephalopods, as the genus *Plectroceras* is the only true Cambrian fossil which can be attributed without doubt to the cephalopods. The Ellesmericeratidae, the first of the true Eurysiphonata, are Ozarkian\(^\text{10}\), or perhaps more accurately, Wanwanian in range. By Middle Canadian time, the descendant radicles of the Ellesmericeratidae were distinct. Some probably extend farther back. In Canadian time the Tarphyceratidae reached their apex. The Endoceroidea were not only well established, but frequently highly specialized. The Bactoceratidae attained their optimum development. *Bathmoceras* also belongs here in the stratigraphic column. The Maurayama limestone, which yields most, if not all, of the species of *Polydesmia*, intervenes between the Lower and Middle Ordovician of Kobayashi’s Manchurian section. His Lower Ordovician, or Wolungian, as shown by the development of piloceroids, is Canadian, while his Middle Ordovician, or Toufangian, as shown by the presence of a considerable number of genera present in America only in the Chazyan, among them certain of the Stereoplasmoceratidae, *Sactorthoceras*, *Centroönoceras*, and *Xybyoceras*, embraces also the Lower Ordovician as recognized in America. Kobayashi has regarded the presence of *Polydesmia* as an actinoceroid, apparently sufficient for grouping the Maurayama beds with his Toufangian or Ordovician, which he terms the “age of actinoceroids,” while his Wolungian, or Canadian, is termed the “age of piloceroids.” Whether the Maurayama bed can be correlated with anything in America is doubtful. As pre-Chazyan and post-Middle Canadian, in which the piloceroids attain their great development, its position appears to be probably best placed tentatively as Upper Canadian. In tracing the actinoceroids further, the correspondence holds somewhat less exactly, though precise correlation becomes more uncertain as well. Certainly the Lower Ordovician *Xybyoceras* precedes most other actinoceroid types. While *Amenoceras* in the ontogeny precedes *Actinoceras*, it is not certain that it is the older genus, as both appear at about the same point at the beginning of the true Middle Ordovician. The Sactoceratidae, which appear in the Upper Chazyan, offer perhaps the gravest discrepancy, though not a fatal one.

Of the other lines, except for the doubtful continuance of the Tarphyceratidae, only the endoceroids remain. A few of the ellipsoceraniform endoceroids probably persist into the Lower Ordovician. One such survival is *Meniscoceras* described above. Holochoanitic forms dominate, however, and until Trenton time these retain connecting rings. More specialized forms which have lost the connecting rings appear in the Middle Ordovician and persist to the close of the Upper Ordovician.

\(^{10}\) It is needless, and indeed futile, to enter here upon the still debated points of the merits and demerits of the Ozarkian as a system. From the point of view of the present work, the term is a convenient one. Therefore I have employed it. The Wanwanian of Manchuria appears to be Upper Ozarkian.
EARLY STAGES

As already noted in the introductory portion of this discussion, a serious handicap in the basing of phylogeny or classification on the early stages of nautiloids is a lack of enough information to permit a careful comparison with other features which appear to be of equal, if not greater, value. A serious weakness in the proposed Ventrosiphonata and Centrosiphonata of Kobayashi is that on the basis of known facts only a very small number of cephalopod genera can be referred to either group. This does not imply that early stages do not furnish valuable clues to relationship, but it is not always easy to select the significant features and to weed out accidental resemblances. It is nevertheless pertinent to review briefly the known phenomena of the early stages of the cephalopods here considered as constituting the Eurysiphonata and to note consistencies and inconsistencies with the phylogenetic scheme proposed above.

No early stages are known as yet for either the ancestral Electrionoceratidae or the first of the Eurysiphonata, the Elesmosmeroceratidae. The siphuncles are consistently ventral and marginal or submarginal, and it seems probable that this condition may have been present also in the first stages of the shell. This, however, is supposition for which there is actually no real evidence.

The early stages of the Tarphyceratididae, as restricted, are not known clearly. Hyatt (1894) has shown that the siphuncles of coiled Ordovician genera terminate in a closed apical cecum, and that the first septum is perforated at, or ventrad of, the center. However, Hyatt’s observations are confined to the Trochollitidae, and it is not certain whether these forms are even closely related to the Tarphyceratidae. The siphuncles of *Eurystomites* and *Tarphyces* lie ventral of the center in the earliest stages and are reputedly not marginal, but it has not yet been ascertained whether an apical cecum is developed. Not only the cecum, but also a false siphuncle connecting the cecum to the apex of the shell is suggested by one of my sections of *Tarphyces* sceleyi; but these may be adventitious. Certainly such an interpretation does not seem consistent with the apical cicatrix noted by Ruedemann (1906, p. 301, pl. 18, figs. 6-7.) for *Eurystomites amplexans*. The correct interpretation of the apical ends of the Tarphyceratidae involves problems still unsolved, in particular whether there was originally a fragile protoconch, which has been destroyed in all specimens so far observed, and if so, whether the siphuncle penetrated to it.11

The early stages of the endoceroids are so variable in form that it is difficult to separate the primitive from the specialized. Though the siphuncle immediately beyond the apical portion is apparently uniformly ventral, the siphuncle generally occupies the entire apical chamber and cannot be said to be ventral rather than dorsal. It is believed that the large inflated apical portions of siphuncles, such as are contained in *Nanno* and *Succoceras*, are specialized rather than prim-

11 Subsequent sections of *Tarphyces* sceleyi show unsuspected features in the early stages. The siphuncle is ventral in the first whorl and opens to the apparent apex of the shell. This suggests a relationship with the Eurysiphonata on the basis of the absence of an apical cecum. Also, by the position of the siphuncle it should fall with the endoceroids in the Ventro-siphonata of Kobayashi’s proposed classification.
It is true; for although they sometimes continue the domination of the siphuncular cavity over the cavity of the chamber for a considerable distance within the conch, they are not particularly early features. *Succoceras* is Canadian but *Nanno* is Ordovician. Similar inflated apical ends of siphuncles are unknown in the Ozarkian. Possibly "*Cameroceras* annuliferum", which appears to be primitive in so many other respects, retains the primitive condition in the small inflated apical end of the siphuncle. If so, the piloceroids, though specialized in many other respects, are also primitive in this feature.

The apical ends of the Actinoceroida, insofar as they are known, show more uniformity. The first siphuncular segment seems to be open into the apical chamber, and the first septum seems to have no connecting rings. Apparently *Nanno* exhibits a similar condition, though in that genus the first septum has well-developed necks, which appear to be absent in *Actinoceras*. Following the first segment, there occur a series of siphuncular segments which are relatively large in proportion to the rest of the shell and tend to decrease in size oral. Sometimes the decrease is gradational and merges gradually into the adult condition of the siphuncle. Again it may be abrupt, as in *Actinoceras* itself, and marked by a pronounced expansion of the siphuncle at the beginning of the ephebic portion. Since observing the condition in *Actinoceras* (Flower, 1940), I have had the opportunity to examine a number of the types of various species of *Kochoceras*, which tend to confirm the opinion presented on the basis of Foerste's published figures that these also represent apical ends of siphuncles, though with the true apical chamber destroyed. This has been further shown in some beautifully silicified material of *Actinoceras* to be described shortly from the Black River limestone of the Parquette Rapids of the Ottawa River. These lack the apical chamber, but the outline of the exterior of the shell suggests strongly that such a chamber was present to complete the smooth outline of the apical end of the conch.

Aside from the absence of the apical ceccum, one other feature of the early stages of the actinoceroid suggests a relationship with the endoceroids. The central canal describes a peculiar course, being central in the first segment, swinging toward the venter, and then resuming a nearly central position again in the ephebic portion. This peculiar modification seems to be without any explanation insofar as the actinoceroid is concerned, but suggests a striking resemblance to the course of the central canal in *Nanno*, where it is the result of modifications of the form of the siphuncle in the early stages. However, in view of the probable specialized condition of *Nanno*, it was probably not in the direct line leading to the actinoceroid, and the resemblance may be adventitious. It is equally possible however that such a course might mark the central canal in older and more primitive endoceroids, where it has not as yet been studied closely. Indeed, even in such primitive endoceroids as "*Cameroceras* annuliferum", the siphuncle may be seen as occupying a faintly sinuous course analogous to that noted in *Nanno*, though not nearly so pronounced. The beginning of the siphuncle is essentially central in that it occupies the whole of the apical chamber. It then becomes
ventral by the building of expanded camera on the dorsal and lateral surfaces. In the later stages of growth it is common to find that the siphuncle is at length entirely surrounded by camerae and thus removed slightly from the venter, completing the S-shaped curve. This condition is even found in the later stages of some species of Ellesmeroceras and is therefore probably primitive.

As can readily be seen from the present summary, many of the crucial features of early siphuncular stages are too little known to more than suggest relationships. It is felt that these features are to be trusted only when corroborated by other characters and other lines of evidence. Kobayashi’s emphasis on the value of the position of the siphuncle does not seem to be warranted by the present available evidence. Certainly there is not enough proof to justify the acceptance of the Centrosiphonata and Ventrosiphonata on such slender evidence as has so far been offered. The previous suggestion of the writer (Flower, 1930) as to the greater value of the apical caecum in taxonomy likewise requires much fuller investigation. At present it appears that the apical ends are at least not inconsistent with the present proposed relationship of the actinoceroid and the endoceroid. Adequate criteria are lacking as to the relation of the evidence supplied by the siphuncle wall and that supplied by early stages of the Tarphyceratidae and can be ascertained only by further investigations. Certainly much more must be known concerning the early stages of these cephalopods before their use in taxonomy can be justified by more than a general acceptance of Haeckel’s biogenetic law.

SUMMARY

The Electronicsceratidae are here accepted as the most primitive of the true cephalopods and are considered as primitive in the thin septal neck and in the plasticity of the siphuncular outline. They are regarded as giving rise to two divergent lines. One is characterized by thin connecting rings and constitutes the Stenosiphonata. In the other, thick connecting rings develop, which characterize the Eurybiosiphonata better than the relatively long septal necks.

The Ellesmerocerotidae are regarded as the most primitive of the Eurybiosiphonata, characterized by short necks and thick rings, lens-shaped in section. Reason is shown for believing the eyelet, an area of dense fine-grained material in the tip of the ring, to be present in this family, though it has not been observed. The eyelet, and a tendency for a development of an outer zone of the connecting ring, link the Tarphyceratidae, as here restricted, and the Endoceridae. Probably the Bulloceratidae constitute another distinct line. The known Tarphyceratidae show specialization in coiling, but the siphuncle remains generalized in structure, though showing considerable variation and specialization within the family.

The Endoceridae are characterized by the development of endocones. Elipoceranitic structure is dominant and perhaps universal among the older genera, though many other specializations develop, as exemplified by the brevicephalic form of the piloceroids, and many modifications of the eutesiphuncle. The siphuncle wall itself is capable of specializations, closely paralleling those noted in the Tarphyceratidae.

The Actinoceroida are traced through Polidesmia and Bathinoceras to an
origin in *Ellesmeroceras*. Though in form the annulosiphonate deposits are clearly derived from the connecting ring, they differ from the generalized part of the connecting ring sufficiently to necessitate the hypothesis that they are produced by growth of the eyelet. Additional evidence leads to the belief that all annulosiphonate deposits are thus derived from the connecting ring, and that they were not true mantle secretions.

Relationships within the Euryphosphonata are indicated, but the limits of the group have not yet been ascertained. The possibility of a relationship between the Tarphyceratidae and coiled Ordovician genera with thin-walled connecting rings remains to be examined. If the strong resemblance between these two groups is not a mark of relationship, there is here one of the most remarkable cases of isomorphism among the Nautiloidea.

The discovery that most of the supposed Holochonolites are ellipsochrome and that holochonolitic structure is confined to a small part of the Endocaroidae, possibly to a specialized group which did not appear before the beginning of the Ordovician as now restricted, shows clearly that the suborder must be rejected. Likewise, investigation of endoceroids has necessitated radical revision of current concepts of their developmental trends, based largely upon the primitive nature of ellipsochrome structure and the specialized nature of the holochonolitic siphuncle.

The clearly ascertained facts concerning the early stages are not inconsistent with this scheme of phylogeny, but such stages are too little known as yet to serve as valuable criteria.

Perhaps the most valuable contribution of the present work is the demonstration of some of the morphological data which can be obtained from the study of thin sections, not hitherto widely employed in the Nautiloidea. It is hoped that the present findings will stimulate other investigations along similar lines.

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Ulrich, E. O. and Fuerste, A. F.

EXPLANATION OF PLATE 1 (1)

Figure

1. *Eurystomites kelleyi* (Whitfield) ........................................ 16
   Siphuncle wall in thin section, X7, showing zones of connecting ring and the vestigial condition of the necks. Fort Cassin beds, Valcour, New York.

2. *Tarphyceras, sp. aff. scleyi* (Whitfield) .................................. 18
   Siphuncle walls in thin section. Outer zone absent, eyelets well developed, set off from generalized portion by dark deposits. Fort Cassin beds, Valcour, N. Y.

3-5. *Proterocamococeras brainerdi* (Whitfield) .............................. 28
   Sections of the siphuncle wall. (3) Wall, X7, showing dark inner and light outer zone of connecting ring. (4) Enlargement of a part of the same section, showing the tip of the neck. (5) Another part of the same specimen with an unusually thick outer zone developed. Fort Cassin beds, Valcour, New York.

6. *Tarphyceras scleyi* (Whitfield) .............................................. 17
   Thin section of siphuncle showing long forked necks, connecting rings with obscure zoning and the eyelet obscurely differentiated. The eyelet, seen only on the left side of the siphuncle as oriented here, is dense black in the lower part of the photograph, grey near the tip. Fort Cassin beds, Valcour, New York; X7.

7. *"Endoceras", sp.* ......................................................... 35
   Thin section of the wall of an endoceroid from La Petite Cambriére, Ottawa, Canada, in the Black River limestone. The connecting rings are missing, and the necks are intact; X7.

8. *Nanno noreborahacum* Ruedemann .......................................... 35
   Opaque section, about X22, with venter on right. Valcour limestone, Little Monty Bay, Chazy, New York.

9-10. *"Canieroceras" annuliferum* Flower, n. sp. ............................ 25
   Adoral portion of siphuncle (9) and apical portion (10) of siphuncle. Canadian of Ticonderoga, New York.
PLATE II (VOL. PL. 2)
EXPLANATION OF PLATE II  (2)

Figure  Page

1-11. *Meniscoceras coronense* Flower, n. sp. .................................. 50

(1) Adoral portion of holotype, about X2/3; a polished section parallel to weathered surface, oblique, extending further ventrad on the right. (2-9) a series of transverse sections approaches the apical end, about X5. (2-5) Endosiphoncone shown with the blades represented only laterally by remnants of the outer cones. In fig. 5 the first traces of the endosiphoncone, better shown in 6, are seen. (7-9) Adapical sections showing the clear lateral blades and the dorsal blade developed in 8 and 9. Fig. 10 is an enlargement of the column of the same section as figure 6. Fig. 11 is the weathered adoral end of the paratype showing the flattening of the adoral end of the endosiphoncone and faint grooving. Holotype and paratype, Univ. of Cincinnati, Nos. 22862, 22863, Crown Point, New York, from the Middle Chazy. 32, 37


Two transverse sections through the siphuncle of *Vaginoceras cf. appletum*. The typical condition in fig. 12 shows compressed cones with a dorsal and a ventral blade. Fig. 13 is unique in the starlike arrangement of the blades. Valecour limestone, Little Monty Bay, Chazy, New York.

14. *Barrandeoceras*, sp. .............................................. 19

Thin section, X7, of the siphuncle of a *Barrandeoceras*, one of several undescribed species from the Valecour limestone of Little Monty Bay, showing the thin connecting rings and their simple structure.
PLATE III (VOL. PL. 3)
EXPLANATION OF PLATE III (3)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td><em>Actinoceras ruedemanni</em> Foerste and Teichert</td>
<td>39</td>
</tr>
<tr>
<td></td>
<td>Section of siphuncle wall at foramen showing continuity of apical end of connecting ring within the neck. Perispatial deposits are seen apicul of the tip of the neck. The white calcite in the siphuncle represents the annulus-siphonate deposits. Watertown limestone, Black River, Watertown, New York.</td>
<td></td>
</tr>
<tr>
<td>2-6</td>
<td><em>Nanno novboracum</em> Ruedemann</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td>(2) Dorso-lateral aspect of siphuncle containing upper part of apical bulb, (3) Adoral part of siphuncle showing annulated ventral side, simulating the condition of <em>Cameroceras</em>. (4) Section at base of living chamber and (5) Dorso-lateral aspect, of a nearly complete immature individual. (6) Transverse longitudinal section through center of siphuncle, where the apical bulb is not evident. A more ventral section in the same individual shows the bulb clearly, also the annulated condition of the siphuncle which is here lost. Valcourt limestone, Little Monty Bay, Chazy, New York.</td>
<td></td>
</tr>
<tr>
<td>7.</td>
<td><em>Vaginoceras</em> cf. <em>longissimum</em> (Hall)</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td>Impression of surface of a siphuncle split along the vertical blades, Black River limestone, Watertown, New York. New York State Museum specimen.</td>
<td></td>
</tr>
<tr>
<td>8-11</td>
<td><em>Vaginoceras</em> <em>oppleatum</em> Ruedemann</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>(8) Sagittal section, XI. (9) Enlargement of siphuncle from opposite side of same specimen, adoral end only. (10) Thin sections of several segments of the siphuncle from another specimen showing structural details. (11) Cross section through siphuncle cutting endosiphonite.</td>
<td></td>
</tr>
</tbody>
</table>
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<thead>
<tr>
<th>Volume</th>
<th>No's</th>
<th>Pages</th>
<th>Plts</th>
<th>Price</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>1-5</td>
<td>519</td>
<td>75</td>
<td>$12.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Monographs of arcs, Lutetia, rudistids and venerids.</td>
</tr>
<tr>
<td>II</td>
<td>6-12</td>
<td></td>
<td></td>
<td>$12.00</td>
</tr>
<tr>
<td>III</td>
<td></td>
<td></td>
<td></td>
<td>Number 13</td>
</tr>
</tbody>
</table>
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Frontispiece. Restoration of Plectodiscus eothumensis, n. sp., a Devonian "by-the-wind-sailor" (discocladate siphonophore). Based largely on the holotype pneumatophore. The fleshy details have been inferred from preserved specimens of Velella velella (mutica), common "sailor" of the Gulf Stream. Drawing by Anneliese S. Caster.
NO. 14: TWO SIPHONOPHORES FROM THE PALEOZOIC

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## Contents

### Text

<table>
<thead>
<tr>
<th>Abstract</th>
<th>5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Introduction</td>
<td>5</td>
</tr>
<tr>
<td>Descriptions</td>
<td>6</td>
</tr>
<tr>
<td>Genus Plectodiscus Ruedemann, 1916</td>
<td>7</td>
</tr>
<tr>
<td>Plectodiscus cortlandensis Caster, n. sp.</td>
<td>9</td>
</tr>
<tr>
<td>Occurrence</td>
<td>12</td>
</tr>
<tr>
<td>Speculative Biology</td>
<td>13</td>
</tr>
<tr>
<td>Comparison with the Siphonophora</td>
<td>15</td>
</tr>
<tr>
<td>Genus Paleosia Caster, n. gen.</td>
<td>26</td>
</tr>
<tr>
<td>Paleosia floweri Caster, n. sp.</td>
<td>26</td>
</tr>
<tr>
<td>Occurrence</td>
<td>26</td>
</tr>
<tr>
<td>Discussion</td>
<td>27</td>
</tr>
<tr>
<td>Bibliography</td>
<td>29</td>
</tr>
<tr>
<td>Plates</td>
<td>31</td>
</tr>
</tbody>
</table>

### Illustrations

Frontispiece. Restoration of life appearance of *Plectodiscus cortlandensis* Caster.

### Text Figures

Text Figure 1. General plan and finding-diagram of the features shown on the natural mold and cast of *Plectodiscus cortlandensis* Caster

Text Figure 2. Generalized morphology of a submature corn of *Velella*

Text Figure 3. Ontogenetic and specific modifications in the outline and symmetry of the immature velellid pneumatophore

Text Figure 4. Four stages in the development of *Velella velella* (spirans)

Text Figure 5. Ratoria cristata Haeckel, early *Velella* stage (LeLoup's nomenclature) in larval growth of a cormidium the mature aspect of which has not been identified

Text Figure 6. An interpretation of the trapezoidal area of *Plectodiscus cortlandensis* Caster, as an archaic pneumatocyst crest and keel of a velellid siphonophore

### Plates

| Plate 1. Plectodiscus cortlandensis Caster, n. sp. | 32 |
| Plate 2. Paleosia floweri Caster, n. gen., n. sp. | 34 |
TWO SIPHONOPHORES FROM THE PALEOZOIC

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ABSTRACT

Two discoidal Problematica from the Devonian and Ordovician respectively appear to be new discometate Siphonophora. *Plectodiscus cortlandensis* Caster, n. sp., is described from the Ithaca beds of the Upper Devonian, near Cortland, New York. Fortuitous preservation of the material reveals characters which seem to solve the long-standing problem of the biologic nature of the form-genus. It appears to be a siphonophore and to establish for the first time the Paleozoic existence of the "by-the-wind-sailors" (Velellidae). *Paheoscia florae* Caster, n. gen., n. sp., is a radially symmetrical umbrella having the general attributes of the porpital siphonophores. Coming from the Corryville formation, Marysville division of the Cincinnati series (Upper Ordovician) of southwestern Ohio, it apparently establishes the first record of the Siphonophora in strata of the Cincinnati-Nashville Uplift.

INTRODUCTION

Two lots of so-called "jellyfish" fossils in the University of Cincinnati Museum collections are the basis for this discussion. The first is from the Upper Devonian of Central New York State; the other from the Ordovician of the Cincinnati region. Both appear to be Siphonophora and new to science. Each would appear to be an important milestone in organic distribution.

Although long scrutiny of problematical objects has been known to engender hallucination, the manifest similarities between the Devonian specimens and the pneumatophores of Recent Velella appear to be bona fide and homologous. Comparisons have been made with formalin preparations of *Velella* and other siphonophores in the University of Cincinnati collections, and with new materials obtained from the General Biological Supply House of Chicago. All of the pertinent morphologic data in the three great monographs on the oceanic hydromedusae by Huxley (1859), A. Agassiz (1883) and Haeckel (1888A), as well as in many more recent writings (acknowledged in the text and listed in the bibliography), have been painstakingly collated, and are in general accord with the features of the Devonian fossils. The close similarities between these fossils and the larval stages of *Velella* shown by LeLoup (1929) and Haeckel (1888A) impress the writer as extremely important biogenetic checks on conclusions first reached solely from ephippial similarities. The Devonian fossils apparently give us the first paleontologic clue to the significance of the interesting metamorphosis undergone by modern "little sail" siphonophores in their astontogeny.

Not excepting Walcott's Middle Cambrian fossils from Burgess Pass, all objects thus far identified as fossil siphonophores are in reality Problematica, since they disagree in certain fundamentals from any of the known groups of hydromedusae, and probably will require special dispensation (separate families) for admission when they finally receive the study they deserve. Most of the so-
called fossil siphonophores of the Paleozoic and more recent ones have escaped my notice) recall the disconnectate (Chondrophore) types. Among the living ones of this sort, there is a basic cleavage between the drifters (Porpitas) and the sailors (Velellas), the latter being generally considered the more advanced type. Up to this time, no "by-the-wind-sailors" (Vellellidae) have ever been reported, or even considered, from the Paleozoic (or from any other geologic era for that matter), although Ruedemann's (1916) problematical form-genus Plectodiscus seems to be the proper receptacle for the new Devonian fossils. Should the present biologic interpretation of these fossils prove right, they would seem to offer paleontologic corroboration of the developmental evidence submitted by LeLoup (1929) that the Chondrophores are primitive hydrorhizose, probably closest of all siphonophores to the ancestral and stazoic hydrozoans. Although Agassiz (1883) appears to have held the same view, and most certainly Haeckel (1888, 1888A) did, the general zoological feeling has reverted in recent years (e.g., Hyman, 1920, p. 470) to an older tenet, antedating the great monographs, that these are secondarily simplified and highly derived siphonophores. The Ordovician medusoid bells appear to be without congener, but their affinities seem to be with Cambrian to Devonian-ranging Problematica which Ruedemann (1916, 1934) has rather convincingly compared with the Porpitas. Since there appear to be no previous records of siphonophores, or even of "fucoids" or Problematica that might be so interpreted, from the rocks of the Cincinnati Uplift, these new fossils are doubly interesting.

I am grateful to various members of the Paleontological Research Institution of Ithaca, New York, for assistance in searching for these and related Problematica in Central New York. To the Board of Directors of that Institution, I am also indebted for the privileges of publication. The first Devonian specimen was found in 1934 while on a spring vacation trip with a group of geology students at Cornell University. Dr. Rousseau H. Flower, Curator of the University of Cincinnati Museum, discovered the Ordovician specimens in the fall of 1941 and has kindly made them available for study. The Librarian and staff of the University of Cincinnati Library have been most cooperative in securing necessary literature not available in Cincinnati. The drawings were made by my wife, Anneliese S. Caster, Cost of the illustrations has been met by the Faber Fund for Paleontologic Research at the University of Cincinnati Museum.

DESCRIPTIONS

On the basis of similarities to be brought out below, the suprageneric taxonomy of the problematical fossils appears to be as follows:

1 Most of the Paleozoic siphonophoraceous Problematica have been illustrated by Ruedemann, 1934.
Paleozoic Siphonophores: Caster

Phylum CNIDARIA (Coelenterata)
Class HYDROZOA (Hydromedusae)
Subclass SIPHONOPHORA (Siphonophorae)
Superorder DISCONANTHA Haackel, 1888
Order Chondrophora Chamisso und Eysenhardt, 1821 (Discoeotae Haeckel, 1888)
Family Velellidae Brandt, 1835
Genus Plectodiscus Ruedemann, 1916


The genus and species were established by Ruedemann (1916) for a Problematicum from the Ithaca (Nunda) formation, near Ithaca, New York. The holotype mold is the sole example known. Ruedemann made no serious pretension of explaining the curious fossil. It was described more or less as an appendix to his reappraisal of Clarke's (1900) Paropsome nae cryptophya, to which he thought his new impression bore certain remote resemblance. He hoped that by giving the Ithaca fossil a name others might be inspired to search out new material from which relationships could be determined. The two specimens described below, from Cortland, New York, seem to be the first stage of wish-fulfillment, for they are the only other specimens of the genus yet known.

Doctor Ruedemann indirectly compared his specimen with porpitid siphonophores in suggesting, by way of a trial, that it might be another aspect of Paropsome nae. He also mentioned the possibility that the remains might be a soft coral.

Proposed as a subclass of the Class Siphonophorae by Haackel, who was convinced that on the basis of the ocellaridial and medusoidal larva (Discoeotae), the siphonophores with poly-thalamous floats are not only distinct from, but more primitive than all others of the pelagic poly-personal hydromedusae. The category usually listed as suborder Physophorilia or Physophorae (based almost solely on the possession of a float) seems not warranted by either ontogeny or paleontology. Although the Portuguese-men-of-war (Physalia) are low in cormidial organization, there is little proof that they are allied closely in the Discoeotae. Most surely there is only analogous comparison between the mantle float of Physalia and the many-chambered pneumatophore of the existing Chondrophora.

Although many modern zoologists consider the Velellidae and the Porpitidae as one family, the Velellidae, the elevation between the existing porpitids and Velellas appears to persist into the early embryonic and larval stages (e. g., LeLoup, 1929) and in the present paper is supposedly carried back into the Devonian. Considering the nature of the differentia involved, as well as mere time, it would seem that Brandt's (1835) proposal of families (followed by Agassiz, 1888, and Bigelow, 1911, and some others) has considerable merit.

Dr. R. H. Flower reports the discovery several years ago of a large slab of sandstone from the Ithaca beds in Full Creek gorge near Cornell University, which appeared to be covered with imprints of Plectodiscus. Unfortunately the specimen has been misplaced, but the discovery is significant as the second finding of the genus in the type area.
in accordance with a suggestion made to him (1916, p. 27) by Dr. Van Name, then State Zoologist of New York. Clarke had described his fossil as an aberrant echinoderm—a view which was not shared by any echinoderm specialists according to Ruedemann—but Fuchs (1905) speculated that it might be the float of a porpitid siphonophore. This was apparently the first time anyone had postulated the existence of fossil Siphonophora. Ruedemann (1916, 1934) was inclined to agree with Fuchs and actually made the comparisons Fuchs had suggested.

The characters of the form-genus, as demonstrated by the genotype, have been shown in as complete a manner as possible by the photograph of a plaster mold of the holotype impression in Ruedemann’s two papers. The illustrations (i.e., cast of the original) show an oval, compressedly coniform body which was apparently invested by a delicate, perhaps chitinous, membrane. The body is radially lobate in two nearly alternating series; there are perhaps 17, but more likely 16, knobs “knots” or lobes in the outer series and only 12 or 13 in the inner one. Between some of the lobes there appear to be narrow and deep natural sulci, which seem in some instances to have been lines along which deeper folding or breaking of the membrane occurred. Over the entire surface are closely spaced, undulatory concentric furrows; these lend a rugose appearance to the knobby and lobate cast.

From data to be brought out in ensuing discussion of the Cortland specimens, it seems that a diagonal crease from the NW-SF, the lengthwise axis being N-S, may represent a meager relict of a sail structure such as that known only in the velellid siphonophores.

In assigning the Cortland specimens to *Plectodiscus* and evaluating them as specifically distinct, the genotype features have been analyzed in the following manner. Generic, and probably familial, traits include: the elliptical outline and compressedly conical shape; chitinous, or chitinoid, external membrane (?); concentric sulci which give a corrugated appearance; large size (genotype is 125 mm. by 110 mm.); and (new observation) presence of a diagonal keel or sail. Specific criteria would appear to be such details as: deviation in outline, contour and elevation of the cone (and disk); size variations; variations in “ornamental” features, such as radial and concentric corrugations and knobs, “knots” and bosses; of particular value would seem to be deviations in direction of orientation, size or shape of any sail structure, as well as variations in proportion and plan of the component sail parts.

Obviously, with so very little known of these enigmatic fossils, it is impossible, statistically, to weigh their morphologic features. Throughout, we have admittedly been influenced by the conviction that we deal with siphonophores and have been freely guided by current zoological evaluation of taxonomic features among the living organisms.
Plectodiscus cortlandensis Caster, n. sp.

Plate 1, figs. 1-7; text fig. 1

The following description is based on four adequate, but incomplete, natural molds and casts of two individuals. They are ellipsoidal disks, measuring in the holotype 135 mm. by 104 mm. along the normal axes, and in the paratype about 100 mm. by 75 mm. All of the features are shown by the photographs and the finding-diagram of the holotype (text fig. 1). In the frontispiece, a restoration has

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Figure 1.—General plan and finding-diagram of the features shown on the natural mold and cast of *Plectodiscus cortlandensis* Caster. The orientation is that of the cast and original organism. The parenthetical comments which follow are based on similarities to the velellids (disconectae Siphonophora). The compass directions (NESW) are conventional designations of the radii of Porpitas and Velellas. A-A’ areuate, irregular furrow at base of the trapezoidal area; probably in the main due to slipping of the tepped cone from its original position at k-k’ to its present one at k-k; a reentrant apex of the tepped cone (either the position of the aboral pore of the first pneumatocyst, or a reflection in enwrapping subsequent pneumatocyst crests of the fundamental reluctance of the mantle to cross the zone of the aboral pore); a”, a””, a””- concentric lobation of the cone in a shallow sulcus on the wall of the cone which was probably continuous with the F sulcus of the disk (all presumably reflecting
been ventured of the life appearance of the organism possessing the structures about to be described.

The holotype (natural external mold and cast), as shown in text figure 1, give nearly a complete outline of the disk, which for convenience of description may be divided into the disk proper and the central trapezoidal area. The entire surface of the disk has a concentrically corrugated appearance due to shallow, subangular and concentric grooves only a fraction of a millimeter in depth. These are progressively more widely spaced toward the center of the ellipse. The peripheral spacing is more crowded on the N and S sides than on the E and W ones (text fig. 1 for these and subsequent symbols). On the N-S (t-f') axis the concentric sulci are 3 mm. apart at 17 mm. from the center; 2 mm. apart at 32 mm.; from this point to the periphery the spacing grows closer until they are nearly in contact. The grooves are asymmetrical, the steeper slope being consistently peripherad. Both the concentric course and the amount of depression of the sulci are variable, largely in accordance with a multiplicity of swell radial corrugations of the disk. The net result is a somewhat rugose appearance, (see Pl. 1, figs. 6, 7). In the several small areas of the disks, delicate, closely spaced, radial raised lines, possibly corrugations, cross the concentric corrugations.

As shown in text figure 1, several furrows and crumples traverse the holotype disk. Most prominent and unequivocally original is that marked F along the radius f'-f. It appears to follow a somewhat undulatory course to the periphery of the disk, but no sign of the groove is seen on the opposite side of the disk, where, however, two radii, G and H, appear to converge on the center and either of which might be the sinusoid continuation of the F furrow. Since the furrow marked X is without either an opposite or NE quadrant equivalent, and does not seem to be radial, it is judged to be an adventitious crumple of the disk. The crumpling marked as an arc, A-X', appears to be, in part, deformation of the disk caused by the toppling of the once erect structures now impressed in the trapezoidal area.

The central hiatus in the pneumaticyst ridge occupied in the Rotaria larval stage by the closed aboral pore; d:- deltoid sulci (possibly a vascular sinus at the crest of the pneumatic...ridge on either side of the keel (K), or merely the abrupt change from gossamer inflated chambers of the cone to bifidate chitinous keel); F: principal radial sulci of the disk (possibly the W half of the primary groove occupied by the main vascular vessel to cross the disk from the limb of the mantle); f-f': probable course of the F radius if it were completed; G, H: radial sulci of the disk (G may be the sinusoid continuation of the F furrow, or more likely the two are remnants of the original {Rotaria} radial sulcation of the larva); K: keel (sagittal chitinous crest above the pneumaticyst ridge; support for the sail mantle); k-k': probable original axial position of the k-k present axis of the trapezoidal area; L: naturally compressed, elongate cone (probably in the main the central-bellied, "liver", cone, but quite possibly occupied from the apex to the apex by inflated chambers of the pneumaticyst ridge); l-l': longitudinal axis; m-m': bilateral depression of the keel; n: crowing border (possibly shrunken free mantle, extending beyond the keel; more likely delicate wrinkled edge of the keel); o-o: three truncate apertures in the concentric rings (correspond in axial position and general morphology to the initial stigmata of Velida); o-o' projected NW-SE axis of the a pore; t-t' transverse axis of disk; v: anastomosing vascularlike marking of the keel; x: adventitious furrow. Based on University of Cincinnati specimen No. 24081A.B. Drawn by Ameliolle N. Coster.
The trapezoidal area (L and K) in the upper half of the disk has been painstakingly excavated under the microscope. The features of the K area are well shown on the cast and the details of the deltoid area L have been revealed on the mold (Pl. 1, figs. 1, 2, 4). They seem almost certainly to represent a recumbent, but onetime vertical, keeled and boatlike elevation along the general line of the transverse axis (N-S) of the disk. The median, over-all length (height) of the area (f' to arcuate crest) is about 34 mm. The base of the trapezoid is about 55 mm. Within the trapezoid, three subareas (L, K and n) are clearly outlined. In the mold L is a trigonal depression, 30 mm. high, deepest at the crumpled base (A'-f'-A) and becoming shallower toward the apex and the two legs. Along the midline (a-f') of the mold a broad swell occurs, on which three lobes, concentric with the reentrant (a) apex, are found. (See text fig. 6 for details of this area.) The basal cross-section (parallel to the plane of the disk) of this trigonal area in life must have been lenticular with shallow, subangular concavities where the maximum convexity of the lens would occur—presumably very similar to the condition seen in figure 5, D. In life, the L area was apparently a compressed cone, on each face of which was a furrow, probably corresponding to a continuation of the F sulcus of the disk. The presence of the furrow on the far (E) side of the cone, suggests that the G furrow of the eastern half of the disk is probably a continuation of the F furrow of the west. The compression of the cone had apparently progressed so far that the faces met acutely, but on this crestal carina there was apparently a crowning depression now represented by the barial furrow d which delimits the deltoid area from the K area. On the cast there are two faint lines converging from the reentrant apex of the cone to a point a little below the position of the first concentric lobe of the mold (the concentric lobes are not preserved on the cast).

Rising above the compressed cone as a sagittal crest is a broad, trilobate and shallow imprint (K). The outline of this area superimposed on the deltoid area of the cone, completes the central trapezoid. The sides of the keel are now sigmoidally arcuate; they appear to originate at the basal angles of the cone and rise more steeply than the legs of the deltoid area; at about the level of the top of the cone, the arcuate sides of the keel begin the reverse curve which forms the border of the upper expansion. The upper edge of the crest is broadly trilobate. At the level of the truncated cone, the keel area is 30 mm. wide and about 15 mm. high. From the reentrant apex, the outer angles of the keel measure about 25 mm. On either side of the vertical axis, in the broadest part of the keel, there is a shallow depression in the mold (m) which suggests the flexibility of the K area and perhaps a congestion of mantle substance here. The surface of the K area in both the mold and cast shows anastomosing furrows intimating vascular markings (V'). The entire periphery of the keel area in the cast is delimited by a shallow groove (w). This may represent a very thin flexible and peripheral border.

At the place marked o on the text figure 1. (Pl. 1, figs. 2, 5) the holotype carries three limbate pores or porelike apertures on the first three concentric rings outside the trapezoidal zone. The extension of this linear series makes
about a 45° angle with the N-S transverse (t-t') axis. If the pores series originally extended to the periphery of the disk and on the opposite radius, it will have to be determined by new material, for it so happens that the surface of the present specimens is destroyed in just those areas where extension might be expected.

The paratype (Pl. 1, fig. 3) appears to preserve the exterior aspect of the inferior surface of the disk. It is a smaller individual than the holotype, but is too badly warped and crushed to make present proportions very reliable. In the upper concave area of the fossil, a large Grammysia shell had come to rest and had all but destroyed the disk details. The area marked L on the photograph may represent half of the compressed cone shown on the holotype. If this is correct, the other half of this deltoid area was completely destroyed beneath the penebopod shell. The crushed zone at P on the photograph probably corresponds to the similarly marked sulcus on the holotype. The furrow shown as A would appear to be a lateral extension of the keel line. Unfortunately, the specimen is too poorly preserved to indicate how much, if any, inferior cavity correlated with the conic elevation above the disk. The surface details of the disk are better preserved on some areas of this specimen than on the holotype. The very fine, radial corrugations show especially well, and likewise the waveling nature of the concentric sulci (Pl. 1, fig. 6). The arrow indicates a sharp fold in the disk and seems to demonstrate that the original substance was both tough and flexible.

Occurrence.—The only occurrence of the species is that of the type, in an abandoned flagstone quarry on the east side of New York State Highway 13, about 1.5 mile northeast of South Cortland and about 1 mile southwest of the corporation limits of the city of Cortland (as of the topographic survey of 1913). The elevation of the specimens was approximately 1210 A. T. They came from the upper and more weathered quarry face. All original substance has been leached away, leaving only manganese stain between the molds and casts. The stratigraphic horizon lies in the upper part of the Ithaca formation which is here made up of olivaceous mudstones and micaceous flaggs. The facies is much the same as that of the Devonian section at Ithaca, New York.

Associated with the disks are many fossils, most common of which are: Camarotachia eximia, Palaeonello constricta, Feucestrellina, sp., Spirifer mesacostalis, orthoceroid cephalopod fragments, a very thin-shelled variant of Grammysia elliptica, and much very finely divided plant substance.

Paleontologic comparisons.—Although at first glance there is little similarity, except in general outline and type of ornamental detail, between Ruedemann's Plectodiscus molestus and the Cortland species, closer examination indicates that they are probably congenerous, although diverging widely on details judged to be only specific. Ruedemann's specimen is either compressedly cone-shaped or was distorted during fossilization. The great knots and lobes suggest more the warping of an already conical disk than of a much flattened one. The preservation is such that we cannot make comparisons between the sails (if the diagonal ridge in Ruedemann's specimen is a sail remnant) except for general orientation, in which they seem to agree, with this exception, that the N-S axis of P. molestus appears to be greater than the E-W. Of this fact we cannot be sure because of
the possibility of crushing in Ruedemann's specimen. The knobs and lobes of the specimen may be in part shrinkage, but certainly not wholly so; nor can they be completely accounted for as adjustment to underlying soft parts such as gonozooids and feeding polypites.

Only more material from Cortland or Ithaca showing intermediate forms or further details of differences can really settle the question of just what is the relation of the two species, and the real nature of the genus. It is highly improbable that Ruedemann's original site* will ever be available again but hundreds of equivalent exposures exist in the Ithaca region. That *molestus has never been found, before or since, despite more than a century of rather intensive geological study of the Ithaca region, attests to its rarity†.

Types.—The types of *Plectodiscus cortlandensis have been given to the University of Cincinnati Museum: holotype, No. 24081 A, B; paratype, No. 24080 A, B.

Speculative Biology

Let us now turn to the possible biological explanations of the structures preserved on *Plectodiscus cortlandensis. The generic discussion and figure 1 have already suggested some of the data from which it is urged that the organism was a hydromedusan of velellid aspect. This opinion, which was approached in the first stage by elimination, and later furnished its strongest support by accident, has been materially fortified by the results of much closer inspection and comparisons than at first was even dreamed would be profitable.

When first recovered, and before the details of the trapezoidal area had been worked out, the specimens seemed to show no features which would bar them from belonging equally well to any of a variety of organisms. As a possible bulwark against snap-judgments inimical to the present considered views, it seems worthwhile to review briefly some of the "leads" that have at one time and another since 1934 seemed promising.

Brachiopoda.—Because of certain gross resemblances, some of the large discoid brachiopods were seriously examined by the writer and urged upon him by others. *Uniostracella and *Ehrlebertella grow to large size in the Middle Devonian and might be expected in the so-called recurrent Middle Devonian fauna of the Central New York Upper Devonian. These shells do possess certain analogous characteristics (see, for example, Hall and Clarke, 1892, pl. 4, E).

1 The writer experimented with several floats of modern *Velella and found that they do not tend to shrink appreciably when they become dry, nor do they develop deep or confusing furrows and folds. After all, they are comprised of closely appressed chitinous tubules, and when freed from the mantle, as they easily are, carry with them almost no fleshy tissue which might warp or shrink. Moreover, they are too resilient when embedded in the mantle to make any adjustment to underlying fleshy structures. While the floats might yield to extraneous hard objects in the embedding matrix, it seems quite unlikely that they could be made during fossilization to convey any secondary impressions of their fleshy appearances.

2 According to Ruedemann, 1916, his specimen came from "a quarry one-quarter mile north-east of the fairgrounds" at Ithaca. Although there are no bedrock exposures in any direction from the Ithaca fairgrounds for well over a quarter of a mile, the specimens probably came from the drums of one of the two quarries shown on the Watkins Glen-Cattaraugus small-scale map (1909), to the southeast about half a mile on the hillside. The quarries are in the Middle and Upper Ithaca, but have long since been abandoned.

† See preceding asterisk (*) footnote.
Neither the complete absence of phosphatic substance nor the evidence of a very thin "shell" served as deterrents, for almost all calcareous material is completely leached out of fossils in the near-surface exposure of the Ithaca formation. The giant neotremates appear to have had quite thin shells, but few, if any, orbiculoids are known to have attained, or approached, the size or the elongate, ellipsoidal outline of the Cortland specimens. The resemblance in concentric ornament is revealed by closer scrutiny to be superficial, for the surface of the brachiopods is varicose or rugously foliar, whereas in these, it is excavated by subangular sulci which create the illusion of corrugation. The most telling surface similarity is between molds of the Cortland fossils and the positives of the brachiopods; these are strictly incomparables. It has been urged that the F furrow of the fossils might be the listrium of a neotremate, but this clue proved sterile when the trapezoidal area was excavated. Although somewhat recalling the outline of the brachial adductor scars of *Lindstromella*, this zone in our fossils is on the planate disk, and no such area occurs on the flat, listrium-bearing ventral valve of the brachiopod, nor, to take another tack, is the orientation of the deltoidal adductor cicatrice in relation to the median septum the same as the *L* triangle and the *F* furrow. What is more important, the evidence of preservation shows pretty well that the central area is no muscle scar, but a recumbent, compressed cone, partially filled by matrix.

*Other organisms* were passed in review. There is a certain similarity to cycloid fish scales of the *Naucrates* type, although the disks are far larger than any known unequivocal fish scales of this type, and show no roughening or furrowing such as one rather expects in the region of the fish scale overlap. Or, again, they might be dermal plates of fish, if not scales . . . but this line of speculation, like many others, seemed pointless when the central cone area was revealed. It had been reasoned that the disks might be the apatychi of one of the many large Portage cephalopods, none of whose opercula is known for a certainty; or again, could they be the undivided scutella of large and very primitive hymenocarid crustaceans?

*Coelenterata.*—"Jellyfish" was the first label given the specimens in 1934. Although the concentric banding of the disks superficially resembles the circular muscle sulcation of many fossil scyphomedusae, such as the famous Jurassic ones from Solnhofen (c. g., Walcott, 1898, pls. 41, 43), the elliptical shape and absence of radially symmetrical features, when coupled to the evidence that the disks were originally flexible, cartilagenous plates, rather than yielding gelatinous umbrellas, proved inexplicable.

It was soon realized that ours partook of Ruedemann's *Plectodiscus* enigma, and for a while Ruedemann's suggestion that his problem child might be another (perhaps sole or undersurface) aspect of *Paropsoma*, seemed as good as, if not better than, any other; especially so, since he agreed with Fuchs (1905) in viewing Clarke's fossil as a porpitid siphonophore, and (seemingly contrary to evidence) the Coelenterata had persisted as a most-favored receptacle in the working-hypothesis niche of the writer's mind.
The matter rested until the discovery of the Ordovician disks to be described below. Study revealed that they, like Paropsoneuma, were probably porpitids. Curiosity prompted comparison with the Cortland specimens, whereupon further preparation of the Devonian material quite unexpectedly revealed a Velella-like keel or sail. This clue seems to solve the Plectodiscus problem (or, at least, appears to account for the Cortland specimens). In this light, nearly all of the puzzling factors fall into place.

Assuming for the moment the correctness of this correlation (proof to follow), it now seems that both branches of the disconectate Siphonophora existed side by side on the high seas of the Devonian just as they do today. The radial and concentric fractionation of the float of Paropsoneuma seems to be of the general Porpita type; Plectodiscus seems to have been a Devonian “by-the-wind-sailor.” There is nothing to indicate, however, that these two fossil expressions of the Chori'rophorifie were even as much alike as Velella and Porpita are today.

Comparison with the Siphonophora.—The mature morphology and the larval development of the float of Velella particularly concern us here, for there appear to be important correlations with Plectodiscus cortlandensis at all stages of growth. But in order to understand the ontogeny and function of the polythalamous pneumatophore, we need to know something of the soft anatomy and biology of the living comidia.

As the name implies, the Velellid are wind-blown sailors. They are eupelagic and planktonic organisms of the warmer high seas, drifting with winds and currents. Storms often blow vast flotillas of them ashore or into waters of killing coolness. They are commonly cast up on the British and French coasts (Russell and Yonge) by the Gulf Stream currents, and after storms, Agassiz (1883) and others report them by the thousands on the Florida and West Indian beaches.

The complete life cycle of Velella has been a matter of dispute and ignorance until quite recently. LeLoup (1920) gives a very fine summary of the biologic cycle in his survey of the anatomy and development of Velella velella (spirans) of the Mediterranean. The gonozooids of the mature hordes of Velella give rise to vast numbers of Chrysomitra medusa which sink to the depths. What happens to the newborns has long been a matter of debate. Modern workers have been able to show that only those born on the high seas survive into the next ontogenetic stage. LeLoup says (p. 329) that those born so as to come to rest on the continental shelf are doomed to inevitable destruction. In the open sea the medusa give rise to bathypelagic larvae known as Conaria whose environment is as much as 1000 meters beneath the surface. In time a chitinous pneumatoctyst begins to form in the ctenosarc and as soon as it can be partially distended with gas, the long ascent to the surface commences. This ascendant stage is known as the Ratarula.6

As soon as the Ratarula attains the surface, a tiny two-lobed manticular sail is erected and the larva takes its place as a sailor of the high seas. Further growth

6 All of the larval growth stage terms originated as generic names before their synonymy with Velella was realized. Even so, as early as 1834, De Blainville was urging that Eschscholtz’s (1829) Bacteria was a young Velella. Chun (1897) demonstrated beyond controversy that Velella is the sole representative of the family and that all the many other velellids described are larval stages of Velella.
in this earliest sailing stage, the Rataria, results in additional pneumatophore chambers and some very interesting and important metamorphoses that we will need later to consider in greater detail. After the third or fourth pneumatophore chamber is added, the plan to be pursued in further enlargement of the float is established and the Vellella stage is attained, although the corm is as yet only a few millimeters across. Subsequent changes in the Vellella stage are largely matters of warping of the float disc in conjunction with the perfection of a large sigmoidal sail. Some of these larval changes are shown in figures 4 and 5, and the progressive changes in float symmetry are shown in figure 3.

Figure 2. Generalized morphology of a submature corm of Vellella. Frontal vertical transverse section along the oro-aboral axis. The axis of the stigmata (S.A) has been shifted some 30° to the right in order to clear the sail and for convenience of perspective. Ce- chitinous canals from the central pneumatocyst chambers to the ctenidialia; cp- initial and main gastrozoid; cp- pneumatocyst crest at base of keel; cc- exumbrella; gl- growth lines on keel; gz- gonozooids; hv- hepatic vesels, or cv- vascular system; k- chitinous bifoliate keel; k- vascular sinus at base of crest; mc- central "liver mass" or ctenidialia; mc- collarette of the mantle; ml- free limb of the mantle; ms- sail mantle; pn- pneumatophore or float; pc- pneumatocyst chambers of the float; S.A- stigmata axis; st- external pores of the pneumatocysts (stigmata); tn- tentacles or tentaculozoids. Much modified from Hyman, 1940.
The mature "by-the-wind-sailors" share with the other disconnectate siphonophores a relatively simple organization of the form. The general morphology is shown in text figure 2. From the chitinous, multichambered pneumatophore (pu) embedded in the manticular coenosarc (mc), depends a central (original) feeding polyp (cp). This is eventually surrounded by secondary feeding polypites, reproductive zooids (gs) and circles of peripheral stinging individuals (te), "tentacles". The exumbrellar surface is only partially supported (mc) by the pneumatophore; a wide peripheral zone of mantle, the free limb (ml) surrounds the pneumatophore area. The mantle extends (ms) over the chitinous keel (k) which arises from a sigmoidal crest of the pneumatocysts (cp).

The floats of living or preserved corals are very loosely attached to the coenosarc and are freed from the mantle cover by the slightest rupture. Pneumatophores of capsized "sailors" often wash ashore in vast numbers and when dry, blow about like tissue paper on the beach (Agassiz). In both the living and formalin-preserved corals, the chitinous float has much the appearance and resiliency of cartilage; when dried it is a tough hyaline membrane which retains its air spaces and essential contours. The buoyancy is achieved by tubular pneumatocysts (pc) arranged concentrically about an initial globular air chamber. The early pneumatocyst tubules are lunate in cross-section, but as the disk grows larger they become nearly rectangular in section and much higher and narrower than they are in early annuli. The external effect in the pneumatophore disk of this change in pneumatocyst section is closer peripheral than apical spacing of the surficial corrugations formed by the exposed surfaces of the tubules. The earliest part of the Velella pneumatophore rises in a tiny pointed cone (really bell-shaped originally) while the remainder slopes in gentler angles into the sigmoidal disk of maturity (see below). The maximum peripheral thickness of the largest pneumatophores is probably not much over 2 mm. Over the entire surface of the disk there are extremely delicate, but slightly varying radial corrugations of the chitin in accordance with a multiplicity of vascular vessels crossing the disk from the limb of the mantle.

Since the floats are chitinous, we might expect them occasionally to be fossilized. The Devonian disks show almost perfect correlation thus far in surface details. They were probably entombed while still turgid with the pneumatocysts filled with water. Quite likely the drifting floats of dead corvidia become waterlogged and sink to the ocean floor in the same manner as preserved specimens eventually lose their buoyancy. It requires several hours for a float dissected from a formalin-preserved specimen to achieve its lifetime buoyancy.

Although the average size of Velella floats would probably be about an inch and a half, some do attain, according to Agassiz, to as much as four or five inches in length, which is well within the range of Plectodiscus. There is considerable variation in the nature and amount of convexity of the floats both between "species" and at various growth phases of any one species. In general, the floats are conical or cup-shaped in the earliest phases of growth and gradually become asymmetrical, v-shaped, inverted troughs in maturity, due to a tendency of the otherwise flat disk to fold along the pneumatophore crest at the base of
Ontogenetic and specific modifications in the outline and symmetry of the immature vellicid pneumatozoon. The directions are those of a conventional wind rose with which there is perfect otoconial correlation in the early larval stage. *A. Conaria*, bathypelagic stage of the larva of *Velella velella* (spirans): a single circular pneumatozoon chamber. *B*. *Eataria* ascendant stage of the larva: a single oval chamber, a broad beginning to elongate on the axis where the first bilobed fleshy sail is yet to appear. *C*. Intermediate phase of the *Rutilaria* first sailing stage: ellipsoid central chamber eroded by 8 radial sails supported beneath by sickle-shaped rumparts; second annular chamber formed beneath the first (inward extension on inferior surface indicated by oval dotted line); 8 canals grow upward from the second chamber along the radial furrows of the first (shown by dotted area); bipartite fleshy sail along the N-S axis (diagonal ruling) interrupted at closed aboral pore (central dot); primary external pores (stigmata) indicated by (+ -) on the NNW-SSE axis; first intercommunication pores (pneumatocysts) indicated by (o) on NNE-SSW axis. *D*. *Rutilaria cristata* Haeckel (early *Velella* stage of a corn, the mature phase of which has not yet been identified): several collateral pneumatozoon annular chambers formed; the 8 chamberlets (canals) of the second one have been joined to form a holothoe number chamber about the initial one. N-S as well as the usual E-W x-axis persist in this form; bilaterally symmetrical; *ip* - closed aboral pore; *ip* - first pneumatozoon; *ep* - collateral pneumatozoon; *pp* - pneumatozoon; *lp* - first pair of stigmata; *lp* - second pneumatozoon. *E*. Early *Velella* stage (Armeniella sigmoidea Haeckel): inferior view of the float; showing symmetry developing in contrast to same stage in *Rutilaria cristata*, above; *ss* - primary tentaculaeoids. *F*. More advanced stage of the corn of the vellicid known as *Armeniella sigmoidea*: antero-bilateral and postero-sinistral symmetry further developing out of condition seen in *E*, above. *G*. Float of a young corn of *Velella velella* (natica): showing initial keel developing, sinistrogyrate pneumatozoon crest, and parallelogramoid outline; *st* stigmata; *pp* pneumatozoon crest; *it* initial keel. *H*. Young *Velella velella* (spirans): sigmoidal symmetry of this most specialized sailer is well begun; following the condition seen in *C*, above, there is greatly accelerated growth in the E.S and N.W sectors and consequently the radial axes are twisted into an S and the pneumatozoon chambers become parallelogramoid. By confluence of the canals of the second chamber it has become perfectly concentric with the first, although the location of the first chamber is imposed upon it, but does not appear on the collateral chambers; the axis of the first stig- mata (+ -) makes a cross with the axis of the succeeding ones; in this species, the stigmata of the *Velella* stage nearly coincide with the pneumatozoon; the oval dotted areas on the N-S axis represent the elevations of each pneumatozoon chamber on the pneumatozoon crest at the base of the keel. *A-C* H. de LeMans, 1929; *E* F. from Haeckel, 1889; *G* from Agassiz, 1883.
the sail. As seen in text figure 5, D, the early elevated and conical portion of the disk tends to be flattened so as to have a lenticular cross-section. The high central cone of the early stages is to accommodate a much higher and proportionately larger centradenial “liver” mass at that stage than later exists. Figure 5 shows this early campanulate float and conical liver mass. The modern sailors lose the high, compressed centradenial cone while they are still only a very few millimeters across, yet the rehearsal may have considerable biogenetic bearing, since the proportional height of the cone and general shape is almost precisely that seen in the L area of Plectodiscus. While it is possible that the entire L cone of the fossil is homologous with the temporary centradenial cone of Velella, the three reentrant furrows (a', a", a''' ) suggest, as will come out in discussing the sail, that the “liver” gland may not have invaded the area past the a''' re-entrant. It rather looks at this time as though the compressed float about the centradenial cone served as the main mass of the initial sail in the velellids, and that this was gradually supplanted by the pneumatocyst crest which in turn was replaced in large measure by the keel.

The outline and symmetry of the pneumatophore likewise undergoes considerable metamorphosis between the stage of an initial globular chamber and that of the many-chambered mature float. Three larval stages in the growth of Velella velella (spirans) (AC) and an early mature stage of the same (H) are shown in text figure 3. Figure 3, D, E and G are early phases of maturity in other velellids less specialized than V. v. (spirans). Figure 3, F corresponds in growth stage to H, but illustrates a somewhat different symmetry and outline. The details of these various stages of float growth are rather fully covered in the figure legend. There is every reason to suppose that we may eventually discover fossil siphonophores corresponding in maturity to all of these various growth stages, and to many others rehearsed by other species7 not here shown. The velellids are a protean clan.

Of the eight radial furrows present on the first pneumatocyst, only the E-W one persists onto the subsequent annulations of the Velella stage. Traces of the others sometimes continue in the Rataria and early Velella stages while the float is a caplike cone. The N-S sulcus may continue to be fully as well developed as the E-W one for some time, as for instance in the form described by Haeckel as Rataria cristata (fig. 3, C). The E-W furrow becomes the course of the principal vascular vessel to cross the disk from the limb of the mantle, while the N-S furrow is supplanted by the rising pneumatocyst crest along either side of which hollow vascular furrows attain the center. The E-W furrow eventually continues onto the keel of the sail.

7 Although a large number of species of Velella have been described from Atlantic and Pacific waters, several modern students of the group, notably Chun (1897) and Bigelow (1911), hold that, at best, only two extremely protean species are living today. One species has a tropical Atlantic center of dispersal and the other, the tropical Pacific. Velella velella Linnaeus appears to have priority over all other species proposals for the Atlantic (Mediterranean-Caribbean) velellids. The sigmoidal warping of the pneumatophore (V. spirans) appears to predominate in the eastern Atlantic and Mediterranean, whereas the rectangular float characterizes the “'solders” of the Gulf Stream and the Caribbean. Curiously also, according to Bigelow, “right-handedness” of the sail, which Agassiz showed to be exceedingly rare in the Atlantic realm, is not at all uncommon in the Pacific species and varieties.
Although the outline of _Plectodiscus cortlandensis_ is comparable with the float outline of _Rataria_ larva, there is this important difference: the larval float is elongated on the N-S axis whereas the fossil appears to be elongated on the E-W one. It seems much more likely that the course of the sail has always been in general N-S, as it is today without exception, than that the shape of the disk has remained constant while the orientation of the sail shifted. As a matter of fact, in the _Rataria_, the first sail appears on the N-S line prior to the elongation of the first pneumatocyst. We see today in such forms as the aforementioned _R. cristata_ (text fig. 3, C) only slight polar elongation, and there seems to be no reason why some strains of the velellid stock might not have specialized in obliteration of the E-W arcs rather than the N-S ones. So far as the efficiency of the sail is concerned, the slightly oblique one on the transverse axis of an elliptical disk probably functioned about as well as the usual one on the lesser diagonal of a warped parallelogram. Should the asymmetric tendency now prevalent in the velellids continue, and the lesser diagonal become progressively shorter and shorter (e.g., text fig. 3, F), we may end with an ellipse not unlike that of _Plectodiscus_. But it is not necessarily supposed that the _Plectodiscus_ ellipse originated in this manner.

The furrows of the _Plectodiscus_ disk are radial rather than diametric, a condition without living counterpart. The _F_ groove of the fossil, essentially normal to the course of the keel, would correspond to the _W_ radius of the E-W sulcus, and _G_ may be its continuation. But we need more material before we can speculate with profit on this point. Ruedemann's specimen of _Plectodiscus_ may retain the full complement of larval furrowings and would appear to have been compressed from _E_ to _W_ if the delicate ridge which suggests the keel line is really this axis; otherwise the greatest length of the Ithaca specimen is essentially along the keel line.

There are three types of apertures or ducts from the pneumatocysts of _'elella_. Of greatest systemic interest, but without fossil counterpart, are "tracheal" tubules (text fig. 2, e) which extend downward from the first few pneumatocysts into the centradenial mass. Too delicate for fossilization are the paired intercommunication pores or pneumatopyles (text fig. 3, H) between all of the aeriferous chambers. Beginning between the first and second chambers, the pneumatopyles occur on opposite sides of each annulation on the NNE-SSW axis. On the upper surface there is a diametric series of external, limbate and centrally phialine pores, the stigmata (st, fig. 2). A curious saltation occurs in the location of these apertures from their place in the NNW-SSE axis of the first and second chambers (text fig. 3, D) to essentially the NNE-SSW orientation of the pneumatopyles on all subsequent chambers (fig. 3, H). The stigmata are less regularly developed than the pneumatopyles, and an occasional one, or even pair, may be delayed in development. In the _Comaria_ stage the aboral pore of the first pneumatocyst is permanently closed by a chitinous plug (text fig. 4, _pap_) according to LeLoup (1920). Text figure 3 brings out the orientation of these apertural features.

In _Plectodiscus_ the three poriferous limbate rings (text fig. 1, o) are quite like the rims about the stigmata of _'elella_. Their position in the NW-SE axis agrees tolerably with the larval position of the first two sets of stigmata. The shift in position of these apertures which the larva so vividly rehearses (text fig. 3) may easily correlate with the progressive increase in the growth differential between
the accelerated N.N.E.-S.S.W.W quadrants and the retarded N.N.W.W.-S.S.E.E ones. With the narrowing of the retarded sectors, the stigmata may have been crowded behind the sail and, for greater efficiency, shifted position some 45°. But "whys" are always imponderables.

The sail is the most characteristic structure of the Vellellidae. This has as its core in maturity a bifoliate, triangular and bladelike keel (k, text fig. 2) of chitin. Over this the mantle makes a perfect cover (ms, fig. 2) and extends beyond as a free, flexible margin. The keel rises diagonally from the disk, but on the N-S axis, in a slightly sigmoidal curve. The orientation of the sail on the pneumatophore disk is consistently that of a heraldic bend—from the dexter chief to sinister base. In over 2500 specimens examined off the Tortugas, Agassiz found no exception to this, as he called it, "left-handed" condition. (See preceding footnote.) The proportions of the keel change considerably with astontogeny, but in maturity the baseline and the height of the keel are somewhat greater than the transverse (E-W) axis. The area of one side of the mature keel is usually about half the aboral surface of the float. Growth lines corresponding to some, but not all, of the pneumatocysts appear on the keel. These show modifications in the proportions of the keel at various maturing stages. The surface of the keel carries on each side a median vascular sulcus which appears to be a continuation of the main E-W hepatic furrow of the disk. Anastomosing vascular markings lightly mark the entire keel surface.

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**Figure 4.** Four stages in the development of Vellella velella (spirata). A. Late kataranula stage, N-S vertical section of the aboral area showing first pneumatocyst chamber (ipc) only partially chitinized and barely distended; aboral pore (ap) closed by an erect chitinous plug (pop) which is sometimes spoken of as the first keel; fold of the collarate mantle (sm) rises along the N-S axis to form the first sail, but does not cross the aboral pore area. B. Early Kataria stage; section slightly oblique to the sail; greater distention of the pneumatocyst and showing flattening of the plug of the aboral pore to form a covering over the aboral surface of the float; im—limb of the mantle. C. Kataria stage; chitinization of first chamber of pneumatocyst nearly completed; coronal groove (cg) is beginning to divide the chamber into a float (pf) and a keel (pk). D. Early Vellellia stage; E-W section; first chamber of float now ellipsoidally extended along axis normal to the section and ocellotome (see fig. 2); posterior surface of the chamber is invaginated for reception of the apex of the central one (cd); keel lobe (pk) rising above the crown groove into the fleshy sail (ms) which now crosses the aboral pore without interruption; stigma of first chamber (ist) developing; four collateral chambers of the pneumatophore formed (2-5); note the manner in which 3 and 4 are progressively attached higher on the aboral surface of the first chamber and also how the first few pneumatocyst annuli reflect a high central one. Drawn from larval sections of LeLoup, 1929.
It is obvious from text figure 1 and the photographs, that we have in Plectodiscus cortlandensis a transverse structure which recalls the velellid sail. Before entering into a detailed comparison, it seems advisable to touch upon certain larval developments of Velella which may help for a better understanding of both similarities and dissimilarities that exist between the trapezoidal area of the fossils and pneumatophorous structures of the living organism. LeLoup (1920) has given us the best picture of velellid larval development (text fig. 4). From the paleontologic point of view, it is unfortunate that the highly sigmoidal and therefore derived form, Velella velella (spirans) of the Mediterranean, is the only one as yet studied in such detail, for it would appear that this species tachygenetically eliminates several important steps in recapitulation that lesser-known forms (text fig. 5) appear still to retain. The composite picture that we get from LeLoup's work and from the velellid larva, Rataria cristata of Haeckel (1888), neither the antecedent or ensuing stages of which are known, leaves very little to speculation as to the origin of the pneumatophore features.

As soon as the Rataria attains the surface, the erect chitinous plug of the aboral pore (text fig. 4, A, pap) becomes slightly flattened and elongated on the N-S axis to form a keel-like structure. At the same time the collarette of the mantle, which invests the entire upper surface of the pneumatophore except for the aboral pore, rises in a N-S fold—the first sail (text fig. 4, A). This is bilobed for, like the collarette, it fails to cross the aboral pore. The two-part sail persists for some time, during which the pneumatocyst becomes more and more distended; 8 radial furrows groove its surface (text fig. 3, C); about its base forms a second, ringlike chamber from which 8 chamberlets grow upward in the melonoid furrows on the first chamber; as growth continues the lobes of the second chamber fuse and an annular pneumatocyst, not unlike subsequent ones in appearance, results (text fig. 3, D; 4, D). During most of this development the bilobed sail persists, and a median recéntrant continues for a while after the sail crosses the pore area (e. g., Huxley, 1850, pl. 11, fig. 9). Eventually the erect plug of the aboral pore is flattened and spreads over the upper surface of the lobate first chamber (text figs. 3, D; 4, B: 5, A, cpl). A crown groove (text fig. 4, C, cg) begins to encircle the aboral part of the now elliptical first chamber and slowly pinches off from it a small chamberlet which might be termed the first pneumatocyst crest (fig. 4, C, pk). This crest is gradually compressed and lengthened in the N-S direction to become the first keel structure in the base of the fleshy sail, which by this time grows without interruption across the aboral pore (text fig. 4, D, mks).

Agassiz (1853) observed certain planktonic organisms in the Gulf Stream that showed the typical ratarian radial symmetry, but unaware of the nature of the larval changes that occur in Velella, he assumed that this eight-part organism, with eight chamberlets surrounding the initial flat, despite its possession of a keel and functional sail, must be a Porpita, the adult of which its octomoral symmetry strongly recalled. Although De Blainville suggested as early as 1834, and Haeckel (1888A) some fifty years later showed the Rataria stage to be velellid, the erroneous statement of Agassiz's has persisted to the effect that young Porpita possess only to lose, fully as fine a sail and chitinous keel as Velella. More recent studies have shown that one of the most fundamental differences between the velellids and the porpitas is the fact that the aboral pore of Porpita is always open, and neither keel nor sail ever exists.
This hesitancy of the mantle to cross the closed aboral pore is also reflected by the first few collateral aeriferous chambers. In *Vellella velella (spirans)* (text fig. 4, D) the second chamber, when finally completed, lies as an annulus largely beneath the first. The third nearly completely enwraps the second and extends higher on the flanks of the first; the fourth encloses a large part of the third and extends still higher on the aboral surface of the first chamber than did the third. But the fifth chamber, like all succeeding ones, fails to attain the surface of the first chambers, and begins the construction of a disk rather than contributing to the campanulate cone built by the first few chambers. This is the nature of the E-W growth at right angles to the sail and pneumatoxyst crest. No doubt in the N-S plane of the sail the early enwrapping of the chambers is somewhat greater, judging from the other velellids. One might argue from the mode of chamber addition in *Vellella velella (spirans)* alone that at one time in its phylogeny the early collateral chambers were wrapped rather fully about the first float chamber and that only gradually did a disk develop out of the early campanulate organization. Almost complete substantiation of this reasoning is seen in Haeckel's (1888A) *Rataria cristata* of the "tropical Atlantic" wherein the probably archaic condition prevails (text fig. 5). The differential manner in which

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**Figure 5.** *Rataria cristata* Haeckel, early *Vellella* stage (LeLoup's nomenclature) in larval growth of a *cormidium*, the mature aspect of which has not been identified. Length of float 2 mm. From the "tropical Atlantic." Three views of an individual corm. A. Aboral view: sm- vertical fleshy sail; cpd- lobate central disk of first pneumatoxyst; pc- collateral pneumatoxysts; ml- limb of the mantle, or free edge of the umbrella; ts- tentacles. B. Half lateral, half aboral view: pc- first pneumatoxyst; cd- centradenial cone, "liver mass." C. Slightly eccentric vertical section, parallel to the transverse axis; fp- primary feeding polyp; rz- reproductive zooids; mc- collarette of mantle; st- first stigma. D. Horizontal section showing outline of the centradenial cone and early compression of the float on the E-W axis; hv- hepatic vessels; F- main vascular sulcus across the pneumatoxyst; rm- vessels of the mantle. From Haeckel, 1888.
tachygenesis operates is beautifully demonstrated by comparison of these two sets of larval data: in *L. c. (spirans)* acceleration has all but removed the early enwrapping stage of pneumatocyst growth from the larval rehearsal, the while recapitulating the keel origin quite satisfactorily, whereas in *R. cristata* the palinogenetic rehearsal of the pneumatophore growth is nearly perfect, but the earliest stage of keel development out of the first pneumatocyst is apparently not even intimated.

Astomogeny, in accordance with Jackson's law, intimates that the velellid sail is older than the multicameral float. yet, obviously, it could not originate until the corn was surface dwelling (hyphalmyrophlanktonic). The recapitulation suggests the one-time existence of mature sailors possessing only a single pneumatocyst and that probably having an open aboral pore (as *Porpita* still does). As long as the pore was open, the diametric sail remained bipartite. Possibly the bladelike upward extension of the chitinous plug that eventually closed the pore served as an intermediate wind-catcher between the two lobes of the sail. By the time the plug had degenerated into a plate over the aboral area of the pneumatocyst the sail had probably begun to transgress the pore area.

![Diagram](image-url)

Figure 6. An interpretation of the trapezoidal area of *Plectodiscus cortlandensis* as an archaic pneumatocyst crest and keel of a velellid siphonophore. Restored in accordance with the fundamental lines of the fossil and in the light of recapitulatory evidence seen in larval growth of existing organisms. *a* reentrant apex of the conical area, drawn in accord with the margin of the last inflated pneumatocyst chamber of the crest to invest the antecedent inflated chambers; reentrant reflects primary hesitancy of mantle to cross aboral pore area; *α* concentric reentrants of antecedent inflated investing chambers of the pneumatocyst crest, showing persistence of hesitancy to cross aboral pole; *α* - central conical cone in base of the triangular area, corresponding to the matrix-filled basal part of the cone in the fossil, but not sharply delimited from the remainder of the triangular area; *def* - furrow between the last inflated and completely investing pneumatocyst crest and the unexpanded subsequent investitures; occupied by the N-S vascular vessels, which join the E-W furrow at *a*, thus increasing the depression of the *α* reentrant; *cl* - radial crest-lines, in accord with the morphology of young keels; derived from the compressed upward growth of the pneumatocyst crest on the first pneumatocyst; *gl* - "growth lines" of the keel; contacts of the bifoliolate, unexpanded extensions of the pneumatocyst crest; *ipc* - position of the first pneumatocyst; *ipcr* - expanded and enveloping first pneumatocyst crest; *k* - chitinous keel, formed by uninflated extensions of the pneumatocyst crest; *pe* - annular pneumatocysts of the disk; *pc* - mature pneumatocyst crest, the state seen in modern velellids, inflated part not enveloping preceding crestal portions.
If the ancestral corncs even approached the modern average size, the single-chambered float must have been fairly large, and if it was as frail proportionately in those days as the initial larval chamber is today, it must have often collapsed on the open sea. Perhaps the 8 radial grooves that still develop on the primary axes of the bulb were, with their sickle-shaped internal buttresses, once a bolster against collapse.9

The sail has proved to be the most dominant feature of the colony; after its appearance all structures of the corn were gradually modified to enhance sailing efficiency. Thus we see the initial float lying at the base of the sail, gradually becoming ellipsoidally warped along the sail (N-S) axis, and the entire umbrella and inferior structure correspondingly elongated, and laterally compressed. As we have seen, a crest formed on the N-S axis of the float, became the basal support of the sail, and was eventually compressed into the first section of a bifoliate keel or mast.

When a second chamber was added to the float, it originated beneath the first one and progressively grew upward to enclose it. As might be expected, the upward growth would proceed most rapidly in the radial furrows on the surface of the first. At one stage of growth, the second chamber is markedly lobate in alternation with the lobation of the first chamber. We must be prepared to find this state represented in the fossil record and probably should expect the alternate lobation to be continued for many successive annulations. This archaic trait in the modern larva may explain the alternate lobation of the whole body that we see in the Ithaca Plectodiscus. In ontogeny the eight canal-like lobes of the second chamber merge to form a mature annulation not unlike all subsequent chambers in appearance. We cannot be sure from conflicting data whether the second chamber really completely encloses the first, except for the aboral pore area, as several of Agassiz's (1883) and Haeckel's (1888A) drawings suggest, or if it may not be that the condition observed by LeLoup (1920) really prevails: the second chamber remaining relatively inconspicuous and not reaching very far toward the aboral pole on the surface of the first pneumatocyst. It rather looks as though the third chamber to be formed is the one which sets a new mode in chamber formation, for it appears in most larvae completely to enclose the second chamber and to overlap far toward the aboral pole of the first one. It is this chamber which initiates a new orientation of the stigmata from the NNW-SSE axis, on which they occur in the first two chambers, to the NNE-SSW axis that they are to occupy in all subsequent ones. Once more, we should expect that there once existed antecedents which developed floats in which several chambers nearly or completely encompassed all preceding ones. So long as this continued, the float must have had a compressed pear shape, most likely with an invagination on the oral surface for the apex of the high central mass. Probably the organism was as medusalike as modern Rataria. Presumably the pneumatocyst crest, established on the first chamber, continued in fashion on all subsequent chambers to invest each the preceding.

9 Perhaps some of the Paleozoic lobate Problematica, such as the Cambrian Lantira and Brooksella (Walcott, 1888), were floats of a comparable stage in siphonophore evolution, instead of being scyphomelleae or sea weeds.
All this time the compressive tendency on the E-W axis progressed, and the pear-shaped and then campanulate many-chambered float, became more and more flattened (transverse section, fig. 5, D). Since the float was imbedded in the basal part of the sail (as in _Rataria_, _e. g._, fig. 5, C), which was as flat as possible, the elliptical cross-section progressively became compressed to a biconvex lens. This meant that the investing pneumatocyst crests of later chambers were more and more flattened. Eventually the crestal portion of each annulation was no longer inflated and became wholly a bifoliate keel within the sail. After the first few collateral chambers were added, apparently the tendency to encompass preceding chambers was abandoned by each pneumatocyst ring, except for the small section on the crest, in the interest of building out a discoidal float to compensate for the ever-increasing sail, less and less of which could be retracted as the crests built up into a higher and higher keel. Although probably every buoyant annulation originally contributed to the keel, we see today that only an occasional pneumatocyst crest contributes to the increase of the discoidal keel. This creates the anomaly of many fewer encompassing "growth rings" on the keel than there are pneumatocysts in the discoidal float (e. g., _Agassiz_, 1883, pl. 3).

In accordance with this interpretation of the astomony of _Velella_, a plausible rendition of the trapezoidal area of _Plectodiscus_ has been attempted in text figure 6, the legend of which is sufficiently explanatory. This has been followed in making a restoration of the possible life appearance of _Plectodiscus_ shown as the frontispiece.

It would seem that with so many points of agreement between _Plectodiscus cortlandensis_ and the Vellellide, we may be reasonably sure of genuine biologic relationship. That we are on the right track seems especially probable since not only does the living _Velella_ help us to understand the fossil, but the fossil appears to contribute much toward a clearer understanding of vellelid morphology and ontogeny. These clues indicate that a further search of the fossil record may yield much additional knowledge of the disconectate Siphonophora, for it now seems that we are dealing with an organic plan probably as old as the fossil record itself, and one that has undoubtedly intricately evolved during the millenia of the Phanerozoic.

**Family Porpitidae** Brandt, 1835

**Genus Palaeoscia** Caster, n. gen.

*Genotype._ Palaeoscia floweri_ Caster, n. sp. McMillan formation. Upper Ordovician.*

The new form-genus, being unique, partakes of the characteristics of the genotype described below.

*Palaeoscia floweri._ Caster, n. sp.
Plate 2, figs. 1-4*

All of the characteristics of the new species are shown in the photographs. Two specimens are at hand, one a nearly perfect circle, 75 mm. in diameter, and the other, an incomplete disk some 210 mm. in diameter. Both show rugose corrugation of a delicate, flexible disk. We can infer that it was presumably chitinous in life, but only the imprint remains in the fossils. The smaller (holotype) disk seems to show shrinkage features in the major corrugations.
A porelike depression marks the center of the holotype. Radiating from this aperture are about 16 lines, apparently representing 8 pairs. They can be seen as very slightly depressed grooves on the central 10 mm. of surface. There are very indistinct transverse lines between some of the radii. No evidence of the radii is preserved on the remainder of the disk. The paratype is too poorly preserved to show surface features other than the broad concentric corrugations.

Occurrence.—The two specimens came from the middle of the Corryville member in the McMillan formation (Maysville subseries) of the Cincinnati series, on the upper reaches of Stonelick Creek, approximately 1.5 mi. WSW of Newtonsville, Clermont County, Ohio. This is about ¾ mile down stream from Route 131 highway bridge. The imprints are on the upper surface of an inch thick conchinites that grades upward into fine calcareous mud which has been deposited in undulatory lenses suggestive of inter-cotidal ponding and scouring. This general section of the Corryville carries the usual abundant Maysville fauna. It has recently yielded some gigantic conularids¹⁹ and carries in other layers a rich crinoid fauna. Shallow-water phenomena are commonplace in this part of the local column, including very extensive trilobite burrows and channelings (Cruziana) as well as trails and tracks. Drag marks and other "fucoid" Problematica abound.

Types.—Holotype: University of Cincinnati Museum, No. 24079; paratype: No. 24080.

Discussion.—Among fossils, there is none very closely similar to *Paleoscia*. This is not surprising when it develops that the only generically comparable discoveries as yet are *Discophyllum* Hall (1847) from the Snake Hill Ordovician of eastern New York, and *Paropsonema* Clarke (1900) of the New York Upper Devonian (see Ruedemann, 1934). Both of these agree with *Paleoscia* in showing a delicate radial organization with distinct concentric or transverse lines crossing the radii in such a manner as to suggest either a paired condition of the radii or a radial series of chamberlets. Neither of these fossils shows the strong concentric corrugation of *Paleoscia*, where in turn the delicate radii do not continue (on our specimens) beyond the central area of the disk. *Paleoscia* appears to be unique in preserving a central porelike opening. The similarities are, therefore, closest to the Snake Hill fossils. *Paropsonema* is quite differently constructed in a double or triple series of radial chamberlets, but seems to be an end variation of the same basic organic plan as *Paleoscia*.

Both *Discophyllum* and *Paropsonema* have in recent years been generally conceded to be celereratans despite their quite different original assignments. Following the clue given by Fuchs (1905), Doctor Ruedemann (1916, 1934) showed how very similar the organization of *Paropsonema* is to modern porpidid siphonophores. He also brought out that the paratype of *Discophyllum*, described and illustrated by Walcott (1898, pl. 47, fig. 2) as probably an acraspedote medusa, was almost certainly of the same plan as *Paropsonema*. As Ruedemann (1916, p. 26) summarized their resemblance, "The concentric system of lines in the Discophyllum and young Paropsonema here figured are exactly identical, and there seems to us little doubt that the two are closely related.

¹⁹ The conularids are being described by Mr. G. Winston Sinclair of Ottawa.
organisms belonging to the same class, whatever that may be."

Seemingly akin to Discophyllum and Paropsonema, as well as to Paleoscia, is a Problematicum in the Swedish Cambrian described by Linnarsson (1871) as Astylospoonia radiata. Pursuant to the objections of many of his contemporaries, Linnarsson soon abandoned the assignment of his organism to the sponges. Nathorst (1881) pointed out its ccelenterate aspects and included it in his memoir on Cambrian medusae as Medusites, a rather meaningless but traditional "catch-all" for fossil ccelenterate umbrellas. Walcott (1898, p. 56), with even greater infelicity, assigned this to his Mel'usina, and echoed Nathorst's suggestion that it is a craspedote medusa. The Swedish fossils show radial pores between the radial plicae of one surface and a multiplicity of beaded "tentacles" along the radial plice on the opposite side. Although the fossils are usually preserved as disks, the central half is always distorted or destroyed. One specimen, of exceptional preservation, illustrated without comment by Nathorst (1881, pl. 6, fig. 1), shows part of a high central area, which would appear to give the fossil a campanulate, rather than a discoidal form. The radial pores and corrugation seem to the writer much more like the plan of porpoid siphonophores (e. g., Agassiz, 1893) than any medusa. The "tentacles" on the inferior surface are quite reminiscent of the simple partitioned trachee which extend from the early pneumatocyst chambers of a porpoid float into the centradenial "liver" mass (e. g., Haeckel, 1888A, pl. 46, 48). The seemingly campanulate form of Medusites radiatus recalls the pneumatophores of Porpema and Porpalia of Haeckel (1888A), immature stages of Porpita according to modern students of larval siphonophore development (e. g., Le Loup, 1929).

The delicate surface features of Paleoscia have a remarkable counterpart in the larval porpoids described by Haeckel (1888, p. 30; 1888A, p. 58, pl. 48) as Porpalia prunella from the "tropical Pacific," and reillustrated as fig. 5, Plate 2, of the present paper. With the meager evidence of the Ordovician fossil that we have, it is pointless to do more than intimate this very great similarity to the porpoid siphonophores, and especially to forms, now adduced to be larval, which were described by Haeckel, our greatest student of the class, as phylogenetically simpler than the genus Porpita. Surely here again, as in Plectodiscus and Velella, we have a strong suggestion of biogenetic correlation.

It is quite possible that we may have in Medusites radiatus the campanulate medusoid antecedent of the long Porpoida line, and it may be so primitive as to serve also as the floating ancestor of the sailing Velellida, first known as fossils in the Devonian. In high bell-shaped and general cormidial organization, especially the tentacular trachee over the entire inferior surface of the float, present interpretation being correct, it seems to be almost the perfect paleontologic materialization of the Porpema-Porpalia rehearsal. Discophyllum shows us the line progressed in Trenton times to the state of owning a discoidal float, and
having perhaps more orderly arrangement of the radial pneumatocyst chamberlets. *Paleosciocia* appears to have been of relatively giant size, and is unusual in its rugose concentric corrugation. Apparently the radial elements become evanescent before the periphery of the disk is reached, unless our fossils are only centrally pneumatophorous and the remainder is the imprint of the corrugated limb of the umbrella. Such being the case, however, it seems quite unlikely that the tiny central float could possibly have supported the large coroidium on the surface, but might have been an effective buoy at some depth. *Paropsonema* appears to have at least two series of radial, paired chamberlets—definitely an innovation. That all are archaic disconectate siphonophores seems rather likely.

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EXPLANATION OF PLATE 1 (4)

Figure


Fig. 1. Holotype mold. Lettering corresponds to text figure 1. University of Cincinnati Museum, No. 24081A; X1.

Fig. 2. Holotype cast. University of Cincinnati Museum, No. 24081B; X1.

Fig. 3. Paratype mold. Arrow indicates crumpled edge of disk. Lettering as in text figure 1. University of Cincinnati Museum, No. 24081; X1.

Fig. 4. Reversed lighting on the deltoid area (L) of figure 1, to bring out the lobation concentric with the apical reentrant of the compressed cone; X1.

Fig. 5. Surface detail of portion of figure 2 to show the suggestions of lirate pores (stigmata) (o) of the concentric pneumocytes; X2.

Fig. 6. Enlargement of the corrugate surface of paratype mold; X2.

Fig. 7. Enlargement of surface of holotype mold to show cancellate corrugation of surface on the right side of the furrow; X2.
### EXPLANATION OF PLATE 2 (5)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-4. <em>Palceoscia flowerti</em> Caster, n. gen., n. sp.</td>
<td>26</td>
</tr>
</tbody>
</table>

Upper Ordovician porpital siphonophore. From the Corryville member of the Maysville formation, Cincinnati series, Stonelick Creek, near Newtonsville, Ohio.

Fig. 1. Holotype mold-east. Showing the corrugate disk, apical 'pore' and central rays. University of Cincinnati Museum, No. 24070; XI.

Fig. 2. Enlargement of a portion of the holotype to show detail of corrugation and apparent shrinkage phenomena; X2.

Fig. 3. Enlargement of apical region of holotype to show porelike depression and radial lines; X2.5.

Fig. 4. Paratype slab, a poor mold showing in addition to the concentric furrows of the disk, several burrows made after the disk was impressed in wet beach mud; portion of a *Calymene* head protrudes through the mold. University of Cincinnati Museum, No. 24080; XI.


Pneumatophore detail of an immature *Porpita* from the tropical Pacific, showing radial details very reminiscent of those seen in the apical region of *Palceoscia*; approx. X20.
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NO. 15: TWO ABNORMAL BUSYCON SHELLS

By
Burnett Smith

August 12, 1943

Palaeontological Research Institution
Ithaca, New York, U. S. A.
TWO ABNORMAL BUSYCON SHELLS

By

BURNETT SMITH

INTRODUCTION

The so-called shoulder angle of the gastropod shell is an important site for the development of nodes and spines. Here also is apt to be located a spiral keel when one is formed. Nodes or tubercles have been considered as features distinct from spines (Grabau, 1902, pp. 931, 932, 942, 943) and it is true that they are sometimes separated from the spines by one or more whorls which do not bear either of these structures. Such cases seem to be exceptional for the blunt node of early life is usually followed by, and grades into, the sharper spine of maturity. Node, spine, and keel would appear to owe their origin to shell secretion by the same mantle fold. Presumably this process is nearly uniform and continuous in the making of the keel. Nodes and spines, on the other hand, can only represent periodic expansions of this mantle fold and, in the absence of contrary evidence, it is reasonable to assume that the function which produced the one produced the other.

The shoulder angle is, however, not the only place where periodic expansions of the mantle may occur. A slanting row of spines is sometimes present near the proximal end of the anterior canal. This is apparently a subspecific character in certain Melongenas. The position of this slanting row of spines corresponds with that of the diagonal swollen band on the anterior canal in a number of Busycons (Smith, B., 1905, pl. XXXI, fig. 12; Perry, 1940, pl. 34, figs. 233 b, 233 c, 233 D, 233 E).

Spine rows other than the two already mentioned are not unknown among the Gastropoda. Probably the best examples of such rows are to be found in the Muric group. Of greater interest in the present study is a row of spines not far below the shoulder angle spines listed among the specific characters of Busycon echinatum (Dall) (Dall, 1890, p. 117, pl. 9, fig. 2).

As pointed out long ago by Grabau (1907, p. 616) a second spine row usually begins later in the ontogeny than does the row of shoulder angle spines. The earlier spines of the second row are smaller in each case than their corresponding shoulder angle spines. The later spines of the second row may equal their respective shoulder angle spines in size.

The extra spine row is apparently a much less stable feature than the row of shoulder angle spines. It may, however, be relatively constant within a species or subspecies. It may also occur as an individual character notably in Melongena (Tryon, 1881, III, p. 107; Smith, M., 1937, p. 125; Perry, 1940, p. 151, pl. 33, fig. 235 b) and also again in Muric brandaris (Pelseneer, 1920, p. 44 and fig. 3 after Dautzenberg). It is believed that such individual abnormalities should be noted. With this end in view descriptions and figures of two specimens of Busycon are now submitted as a contribution to the records of teratology.
SECOND SPINE ROW IN A MIocene BUSYCON

The specimen here considered is an example of Busycon contrarium (Conrad) (Conrad, 1840, p. 387; 1861, republication of 1803, p. 81, pl. 43, fig. 11) from the Duplin Miocene of the Natural Well, southwest of Magnolia, Duplin County, North Carolina (Dall and Harris, 1893, pp. 72, 73; Miller, 1912, p. 241). It was collected from the upper or brownish marl. This is Conrad's type locality for the species. His figure represents an immature individual of this very variable species which apparently has not reached the spiny stage of later life. Many individuals from the brownish marl at the Natural Well have already developed spines at the stage of growth indicated by Conrad's figure. However, perhaps a greater number show a more or less rounded outline with few or no nodes or spines in parts of whorls 4 and 5. In spite of such variations the sinistral Busycon shells from the brownish marl of the Natural Well have many points in common and it is believed that most of them, if not all, can be safely included in a single species—Busycon contrarium (Conrad).

The individual to be discussed has attained early maturity, the long dimension of the shell measuring about 14.4 mm. See Plate 1, figures 1-3.

In its early stages this shell is not materially different from the normal Busycon contrarium of the same locality and horizon. Whorl 1 is largely gone and whorl 2 is not sufficiently well preserved for detailed study. Whorl 3, on the other hand, shows the typical youthful features for the species, that is, a definite shoulder angulation studded with perhaps 10 or 20 nodes. In the first half of whorl 4 nodes are quite distinct and about ten in number. In the rest of the whorl they weaken and are vestigial or absent at the whorl's end. The shoulder still has an angular outline at the start of whorl 4 but it becomes more rounded with the whorl's growth. Whorl 3 is not sufficiently well preserved to show spirals but they can be seen on whorl 4. Whorl 5 is rather rounded in outline and is virtually without nodes. Its visible surface is covered with spirals. Shoulder angle spines appear at about the beginning of whorl 6. At the start of whorl 6 its spirals are about like those of whorl 5. Soon, however, the spirals of whorl 6 begin to strengthen above the shoulder angle but to weaken below it. In whorl 6 the second spiral above the shoulder angle is especially strong and about halfway in the whorl it swells into a low spirally elongated node above a shoulder angle spine. After an interval another low node is found on the same spiral and above the shoulder angle spine next appearing. From here on to the end of the individual's growth at about 6½ whorls spines recur at intervals on this second spiral. Counting the two low nodes just mentioned as spines one may say that from the middle of whorl 6 to the middle of whorl 7 (end of individual's growth) there are 13 spines on this second spiral and 13 stronger spines on the shoulder angle. Each weaker spine can be correlated with a former aperture margin which also bears a shoulder angle spine. The weaker spine in each case lies approximately above or slightly forward of its corresponding shoulder angle spine. The last solution is thus provided with two rows of spines, one at the shoulder angle and the other above it.
Interpretation.—The rarity of extra spines, that is, spines other than the shoulder angle spines in *Busycon contrarium* and in other unchanneled Busycons would seem to preclude their interpretation as specific or subspecific characters except in such a case as that of *Busycon echinatum* already noted. The extra spine row of the individual of *Busycon contrarium* here described and figured is viewed as an individual abnormality falling within the field of teratology.

SECOND SPINE ROW IN A PLEISTOCENE BUSYCON

This specimen is referable to *Busycon carica* (Gmelin) which is well figured in the report on the Maryland Pliocene and Pleistocene (Clark, 1906, pls. XLIII-XLV). The shell was collected by Allen L. Midyette, Jr. of Swan Quarter, North Carolina. It came from the spoil banks of the Intra-Coastal Canal between Pungo and Alligator rivers in Hyde County, North Carolina. Richards (1936, p. 1631) refers the marine shells of this locality to the Pamlico formation of the Pleistocene.

The individual is mature and in its present condition the shell has a long dimension of about 160 mm. See Plate 1, figures 4-6. The last whorls is estimated as whorl 7. Whorls 1 and 2 are gone and whorls 3 and 4 are not sufficiently well preserved for detailed study. Whorl 5 has 12 shoulder angle spines and whorl 6 has 14 if incipient spines are counted. Up to this point the shell shows only characters normal for the species. Whorl 7 has 11 shoulder angle spines if one incipient spine is counted and there is nothing unusual in these spines. However, at about the second shoulder angle spine of whorl 7 a strong spiral begins to develop above the shoulder angle. At the old aperture margins corresponding to the third, fourth, and fifth shoulder angle spines of the whorl this strong spiral bears weak nodes which are more or less elongated in a spiral direction. From here on to the end of the individual's growth each shoulder angle spine has above and slightly forward of it a corresponding spine on the strong spiral above the shoulder angle. The last nine shoulder angle spines have accompanying nodes or spines above them. In each case the shoulder angle spine is much stronger than the companion node or spine above it.

Interpretation.—Extra spines, that is, spines other than the shoulder angle spines, are very rare in *Busycon carica*. For this reason the extra spine row just noted in the Pleistocene example of the species is believed to be an individual abnormality. It has no significance in classification but falls within the field of teratology.

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Richards, Horace G.

Smith, Burnett

Smith, Maxwell

Tryon, George W., Jr.
PLATE

PLATE I (VOL. PL. 6)
EXPLANATION OF PLATE I (6)

Figure | Page
---|---
1-3. *Busycon contrarium* (Conrad) | 4
Abnormal individual with two spine rows; long dimension about 144 mm. (1) nonapertural view (2) apical view (3) apertural view. Pal. Research Inst. Number 4121, Number 729 Smith collection. Miocene (Duplin formation). Natural Well, southwest of Magnolia, Duplin County, North Carolina. From the upper or brownish marl at this locality.

1-6. *Busycon carica* (Gmelin) | 5

(Photographs by Ethel Ostrander Smith)
FRONTISPIECE

(See Explanation of Plate I.)
NO. 16, FISH REMAINS FROM THE MIDDLE DEVONIAN BONE BEDS
OF THE CINCINNATI ARCH REGION

By

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## CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Introduction</td>
<td>5</td>
</tr>
<tr>
<td>Middle Devonian bone beds of Ohio, Indiana, and Kentucky</td>
<td>5</td>
</tr>
<tr>
<td>Previous paleontological work</td>
<td>7</td>
</tr>
<tr>
<td>The fish “fauna” of the bone beds</td>
<td>7</td>
</tr>
<tr>
<td>Condition and preparation of the material</td>
<td>10</td>
</tr>
<tr>
<td>Taxonomic note</td>
<td>11</td>
</tr>
<tr>
<td>Bone bed localities cited</td>
<td>12</td>
</tr>
<tr>
<td>Systematic descriptions</td>
<td>14</td>
</tr>
<tr>
<td>References cited</td>
<td>45</td>
</tr>
<tr>
<td>Plates</td>
<td>47</td>
</tr>
</tbody>
</table>
FISH REMAINS FROM THE MIDDLE DEVONIAN BONE BEDS OF THE CINCINNATI ARCH REGION

By

John W. Wells
The Ohio State University

There is a vast deal of skillful carpentry exhibited... in the coverings of... ancient ichthyoliths.

Hugh Miller: The Cruise of the Betsey

INTRODUCTION

The purpose of this study is to describe and illustrate the long known but heretofore only vaguely identified fish remains, mostly microscopic in size, which occur in enormous numbers in the bone beds of Middle Devonian formations flanking the Cincinnati arch. In another paper the writer has discussed the stratigraphy, paleoecology, lithology, and genesis of these beds; therefore only a brief résumé of these aspects is included here.

THE MIDDLE DEVONIAN BONE BEDS OF OHIO, INDIANA, AND KENTUCKY

The Middle Devonian limestones of central Ohio consist of two formations, the Columbus (late Ulsterian) and the Delaware (early Erian). Within these are at least four thin bone beds: the First bone bed, 10 feet below the top of the Columbus in Franklin and southern Delaware counties, central Ohio; the Second bone bed, at the contact of the Columbus and Delaware, extending from central Ohio north to Lake Erie; the Third bone bed (Hadrophyllum zone), 25-30 feet above the base of the Delaware in Franklin and Delaware counties; and the Fourth bone bed, two feet above the Third and known only at Delaware, central Ohio. The Rocky Branch bone bed lies at the approximate horizon of the Second Ohio bone bed at or near the top of the Jeffersonville limestone in southeastern Indiana on the opposite flank of the Cincinnati arch from the Ohio bone beds. These bone beds exhibit considerable variation in development and stratigraphic relations with the surrounding rocks. They are absent in some places; in others they may be a foot or more in thickness; commonly they are several inches in thickness. They are clastic accumulations of rounded sand grains, much pelmatozoan debris, innumerable tiny scales, plates, teeth, and bones of fishes, some conodonts, ostracods, Foraminifera, and rare plant spore exines (Frontispiece, Plate 1). Macrofossils are fewer in number but may bulk large and comprise rugose corals, bryozoans, brachiopods, pelecypods, and gastropods; Crustacea and cephalopods are notably absent.

Another Ohio bone bed, the East Liberty bone bed, lies between the Columbus formation, the upper part of which, as seen in the central Ohio outcrops, is missing, and the Upper Devonian Ohio shale in the Bellefontaine Devonian outlier in Logan County, west central Ohio, about 50 miles west of the central Ohio outcrops. It consists largely of rounded sand grains with some fish material and a few phosphatic nodules. On paleontological grounds it is thought to be some-
what younger than the other Ohio bone beds and the Rocky Branch bone bed of Indiana—probably of Olentangy (post-Delaware, latest Erian) age.

The Kiddville layer in the lower part of the Boyle limestone formation of east central Kentucky is similar lithologically and faunistically to the East Liberty bone bed and probably represents approximately the same late Middle Devonian horizon.

The apparent relations of the bone beds and associated rocks are suggested in figure 1.

Figure 1.—Stratigraphic relations of Devonian bone beds in the Cincinnati arch region.

These bone beds all occur on the flanks of the Cincinnati arch and none is known in equivalent formations away from this structure in Michigan, Ontario, New York, Pennsylvania, etc. The source of nearly all of their fish remains is believed to have been the fresh-water environments of the middle Paleozoic lowland area, Cincinnati. These remains are not only concentrated in the bone beds but are also thinly diffused throughout the enclosing limestones. The bone beds do not, as do some bone beds, represent catastrophic annihilations of indigenous marine fish communities, but are concentrates accumulated during diastems resulting from fluctuations of the bottom with respect to wave base, of the very shallow sea bordering Cincinnati. In places they represent lag concentrates, in others, rapid subaqueous accumulations of coarser material transported from areas of lag concentration, with by-passing of finer particles, and in still others, aeolian deposits derived from subaerial exposures of lag concentrates.
PREVIOUS PALEONTOLOGICAL WORK

The presence of fish remains in the Ohio bone beds has been noted in all the descriptions of them since the Second bone bed was first described by Edward Orton in 1878 (p. 610) as "one of the most remarkable layers, indeed, in the entire series of American Paleozoic deposits." But beyond the fact that they consist of fragments of plates, teeth, spines and dermal denticles or scales, practically nothing is known of their further identity and relationships. Newberry indicated (1880, p. 31) the presence of the ichthyodorulites Machacaonthus and Acanthaspis, of scales resembling Coelolepis and Nostolepis, and "elasmobranch teeth, probably coming under Chonelodus Agassiz." The latter possibly being Ohiolepis of the present work. Eastman mentioned and figured "Thelodus-like scales" from the Second bone bed (1908, p. 72, figs. 7, 8, 15; pl. 2, figs. 4, 11); his figures are not good, but represent acanthodian scales. Recently Romer and Grove (1935, p. 816) mentioned Eastman's statement and in a footnote wrote Stetson who says (in litt.) that the scales referred to by Eastman "appear from section to resemble acanthodian scales." This seems to be all regarding the identity of the bone bed fish remains.

One scale type similar to one found commonly in the bone beds was described by Strauffer (1928, p. 442, pl. 53, figs. 21-24, 31-34) from the Olentangy shale in Delaware County, central Ohio, as Acanthodes dublinensis, together with unnamed fish teeth (p. 442, pl. 53, figs. 38-41), some of which pertain to Onychodus and Phoebodus.

THE FISH "FAUNA" OF THE BONE BEDS

The vertebrate remains of the bone beds are wholly a thanatocenotic assemblage, in this case an assemblage of mostly fragmentary parts of fishes from freshwater environments that were accumulated in a marine environment. None is found in direct association or articulation, and after dispersal consequent upon decomposition or consumption of the carcasses few escaped the triturant and solvent effects of nekrophages and detritivores as they were carried into the sea. It is unlikely that all these remains represent the fauna of a single environment, but rather that in the bone beds are mingled representatives of several contemporaneous environments—fluvial, lacustrine, estuarine, and possibly marine. Therefore the use of the term "fish fauna of the bone beds" should not be understood to signify the fish fauna of the waters in which the bone beds were deposited but rather the fish thanatocenose of those lithologic units.

The following groups of fishes have been recognized in the bone beds, represented for the most part by microscopic but not necessarily incomplete skeletal parts:

Subclass Ostracodermi
   Order Heterostraci
      Family Drepanaspidae (indeterminate plates)
   Order Osteostraci
      Family Cephalaspidae (3 species)
Subclass Placodermi
   Order Acanthodii (14 species)
   Order Ithrodira
Suborder Euarthrodira
Family Coccomeridae (1 species)

Suborder Ptychodonta (3 species)

[Order Macropetalichthyidae] 1
[Order Stegaschelii]

Suborder Rhinonida (Asterosteus)]

Subclass Chondrichthyes
Order Selachii

Suborder Pleuropterygii
Family Cladoschelichidae (4 species)
Suborder Pleurocoelodii (2 species)

Subclass Osteichthyes
Division Crossopterygii
Order Rhipidistia

Family Osteoleontidae (1 species)

[Order Dipnoi]
Family Dipnoiidae

From this listing it is seen that of the 12 major groups of fishes known to have been living in Middle Devonian times, six are represented in the bone beds of the Cincinnati arch region, and if the Middle Devonian formations of this region as a whole are included, nine are represented. The orders missing from the roster are:

Anaspida—almost exclusively Upper Silurian
Palaeospondyloidae—known only from Middle Devonian of Scotland.
Antiarci
Coccacanthini
Palaeconiformes

The distribution of the types indicated in the outline above in the bone beds 2 is indicated by the following table.

From an inspection of this distribution it develops that the bone bed fishes fall into two groups: one, which includes those found in the four central Ohio bone beds and the Rocky Branch bone bed of Indiana, in all of which are found, with some degree of uniformity, 26 of the 29 types listed; and a second which includes the Kiddville bone bed (or bone beds) of central Kentucky and the East Liberty bone bed of the Bellefontaine outlier of west central Ohio, in both of which are found three forms, all selachians, not found in the other bone beds, together with ro that do but are believed to be remanent and derived from older and now probably nonexistent beds. The three exclusive types of the second group are significant, for they suggest that the Kiddville and East Liberty bone beds are considerably younger than those of the first group. They are related to types elsewhere not known in beds older than latest Middle Devonian or early Upper Devonian (State Quarry beds of Iowa; Geneseo shale and Conodont bed of New York; Wildrieglen beds of Germany).

1 Bracketed groups have not been found in the bone beds but are found in the associated Columbus or Delcambre formations.
2 The fish remains in the Kiddville and East Liberty bone beds exist in two states—often broken but unwarmed and unweathered remains. It is not likely that the fish-looking specimens are types found only in these beds, whereas the remains material is found fresh-looking only in the supposed older Ohio and Indiana bone beds.
3 There are fragments of three or four additional distinct types that are unassigned and undescribed at this time. Three of these are figured (Plate 4, figures 9, 10, 12).
<table>
<thead>
<tr>
<th>TYPE</th>
<th>CENTRAL OHIO BONE BEDS</th>
<th>Rocky Branch</th>
<th>East Liberty</th>
<th>Kidville</th>
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<tr>
<td></td>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Indet. drepanaspid plates</td>
<td>X</td>
<td>X</td>
<td></td>
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<tr>
<td>Ohioaspis tumulosus, n.g., n.sp.</td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
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<tr>
<td>forma typicus</td>
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<td></td>
<td>X</td>
<td>X</td>
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<tr>
<td>forma turritus</td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
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<tr>
<td>forma clavulus</td>
<td></td>
<td></td>
<td>X</td>
<td></td>
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<tr>
<td>forma hystricosus</td>
<td></td>
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<td>X</td>
<td>X</td>
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<tr>
<td>Ohioaspis impositus, n.sp.</td>
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<tr>
<td>Ohioaspis lamellatus, n.sp.</td>
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<tr>
<td>Cheiracanthoides comptus, n.g., n.sp.</td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
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<tr>
<td>Cheiracanthoides comis, n.sp.</td>
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<td>X</td>
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<tr>
<td>Cheiracanthoides venustus, n.sp.</td>
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<tr>
<td>Cheiracanthoides breviplicatus, n.sp.</td>
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<td>Helolepis bellarugosus, n.g., n.sp.</td>
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<td>X</td>
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<tr>
<td>Helolepis venustuloides, n.sp.</td>
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<tr>
<td>Acanthoides hardyi, n.sp.</td>
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<td>X</td>
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<tr>
<td>Acanthoides sciotoensis, n.sp.</td>
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<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Acanthoides dublinensis (Stauffer)</td>
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<td>X</td>
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<tr>
<td>Plectrodus ohioensis, n.sp.</td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Plectrodus multidentatus, n.sp.</td>
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<td>X</td>
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<tr>
<td>Plectrodus aculeatus, n.sp.</td>
<td></td>
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<tr>
<td>Machaeracanthus major Newberry</td>
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<tr>
<td>Gyracanthus ? eastmani, n.sp.</td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
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<tr>
<td>Coccosteus spatulatus Newberry</td>
<td></td>
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<td>X</td>
<td>X</td>
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<tr>
<td>Ptyctodus, sp.</td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
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<tr>
<td>Rhynchodus, sp.</td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
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<tr>
<td>Palaeomylus, sp.</td>
<td></td>
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<td>X</td>
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<tr>
<td>Cladolepis gunnelli, n.g., n.sp.</td>
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<tr>
<td>Ohiolepis newberryi, n.g., n.sp.</td>
<td></td>
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<td>X</td>
</tr>
<tr>
<td>Ohiolepis stewartae, n.sp.</td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Deirolepis carinatus, n.g., n.sp.</td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
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<tr>
<td>Phoebodus floweri, n.sp.</td>
<td></td>
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<tr>
<td>Phoebodus ? bryanti, n.sp.</td>
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<tr>
<td>Onychodus sigmoides Newberry</td>
<td></td>
<td></td>
<td>X</td>
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</tr>
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</table>
CONDITION AND PREPARATION OF BONE BED MATERIAL

Where the bone beds are fresh and unweathered they are solid and commonly dark bluish gray in color, with a peppering of black fish remains. The latter are phosphatic, colored black by finely disseminated iron sulphide, as is commonly the case in most Paleozoic vertebrates where preserved in limestone. Upon weathering the bone beds become crumbly, saccharoidal, or shaly, the limy parts being tinted light brown or buff, the vertebrate remains oxidizing to rich mahogany, brown or yellow shades. In this latter condition the microscopic fossils can be picked out with a needle or moistened brush tip. But in either case the writer found it simpler to digest the samples in dilute acetic acid (one volume of glacial acetic diluted with two of water). This has the effect of dissolving the calcitic cement, limestone, and most invertebrate remains without affecting in the least the vertebrate fossils or conodonts. Nor does it destroy the pyritized or limonitized ostracods, arenaceous Foraminifera, or vegetable spore exines. After digestion, the residues were washed to remove the clayey constituents, dried without sieving, the size range of the fish remains being considerable, and finally picked over under the microscope.

Naturally, none of the fish remains retains any of its original coloration, but they do have a range of coloration as a result of fossilization or weathering that is worth noting. Brotzen (1934, p. 2) noted that the acanthodian scales found in the bone bed erratic studied by him showed very fine infiltrated colored substances in the cavities and tubules which largely determine the color of the specimens; in larger cavities black to dark red brown, in smaller ones light red, yellow, or yellow brown. The substance itself, according to Brotzen, is opaque and amorphous—hematite or some similar mineral. The range in color is from black to ivory white through all shades of red, brown and yellow.

The Ohio bone bed fish remains are similarly colored by infiltrated substances, and most of the tints evidently are due to the effects of some degree of weathering particularly the oxidation and hydration of the iron sulphide of the unweathered bone. Specimens of the Third bone bed can be collected in the Scioto quarry (locality 7) which are relatively unweathered. In them the scales and bone fragments are a very dark gray, practically black, but near and on weathered surfaces they are a rich red brown. Many of the scales in this bed are strongly pyritized, especially those of Onychodus, and gleam brassily in the light from crystal facets. Rare fragments are found replaced by iridescent opal. Some of the acanthodian scales are especially colorful. One tiny specimen of Ohiolepis ste wartae has a brilliant ivory base with bright vermilion tubercles. Another of O. newberryi has a pearly gray base with deep brown tubercles. Scales of Cheiracanthoides often seem to have been carved from ivory, with flecks of pale salmon red on the translucent enamelled coronal surface and edges. Pieces of the scales of Onychodus show a range from ebony-like tones to translucent pearl-gray tubercles on an opaque gray base, or tubercles of red jasper set on waxy gray flint.
TAXONOMIC NOTE

The taxonomy of the 29 distinct types of scales, dermal defenses, bones, and teeth, presently to be described from the bone beds, presents an awkward problem. Some few, such as the scales, dermal studs, teeth, and bony plates of *Onychodus sigmoideus*, gnathal elements of *Ptyctodus*, *Palcomylus*, *Rhynchosus*, armor plates of *Coccocestus*, and *Macharacanthus* spines, can be placed with reference to fairly well-known fish, but most of the material, usually that of very small size, obviously belongs to forms peculiar to the fresh waters and estuaries of Cincinnati and are known only from isolated bits which can hardly be assigned with any satisfaction to established categories of less than subordinal or familial rank, much less to genera and species. Nor is it likely that there will in the future be found well-preserved, tolerably complete remains of the fishes to which they pertain, when one considers the probable conditions of sedimentation during Middle Devonian times in the Cincinnati arch region. For such material one is tempted to disregard classical taxonomic procedure and to use some such scheme as the *Ordo militaris* proposed by Croneis (1938; 1941, p. 1239) for just such incomplete but not necessarily imperfect specimens. There is much merit to this proposal, especially when it is a question of such an isolated group as the conodonts, but it can hardly be satisfactorily employed simultaneously with the orthodox Linnean system, as is more or less necessary in the present instance, where mingling of *manipuli* and *genera* would be more confusing than a mingling of Linnean genera, organ genera, and form genera.

The names used in this paper for certain types are to be regarded in the same tolerant way as those applied to conodonts (perhaps more so since the writer has refrained from multiplying the species far more than is customary in describing conodonts)—convenient tabs for recognizable units whose systematic relationships are, and may ever remain obscure insofar as the larger entities to which they pertain, in this case, fishes. Wherever the category departs from the usually conceived status of a genus, it is so indicated, as an organ genus or form genus.

In making the foregoing reservation concerning certain of the names herein employed, the writer is aware of the recent anguished polemic of Arkell and Moy-Thomas (1940, p. 4) against

... the impossible situations produced by erecting new genera on single more or less unidentifiable fragments such as fish scales. Brotenz (1934) has made 4 genera and 59 species on single acanthodian scales, some of which are even dubiously acanthodian (Watson, 1937, p. 115). The erection of these genera and species is valueless. Many of them are almost certainly synonymous with known forms, but it can hardly be considered worth while to find out.

From this eclectic view the writer heartily dissents. It does seem as though Brotenz has overdone the making of species in the case mentioned, but the fish scales and teeth upon which he based them are scarcely "unidentifiable fragments"; they are individually complete parts of a structure whose identity as a taxonomically distinguishable organism extends more or less equally to all its parts. Scales are difficult to identify according to the "species" to which they belong.

*Using these last two in the sense proposed by Jollmans, Halle, and Goethe in 1935 (Croneis, 1938, p. 194): *ornit genus* for detached parts belonging to the same morphological category, and *form genus* (or artificial genus) for forms with generically unrelated species.*
belong, but may this merely seem only so because they have not yet been as intensively studied as they could be? Mammalian teeth are considered sufficiently expressive of the entire organism to which they belong to the extent that only one-quarter of all mammalian species of extinct quadrupedal organisms be identified. Is the erection of these also valueless? Some of them doubtless are synonymous with "known forms", and they are, it is believe study of them, forms worth while finding out. Bone bed material rarely if ever displays even partially complete organisms but it does present invaluable clues to some of earth's paleobiota that otherwise would be only vaguely known. The writer believes that if only parts (not "fragments") of an extinct organism are likely to be the only representatives of genera and species, they may just as well be named as its entire skeleton. After all, a skeleton in all its completeness is in its turn only part of an organism.

**BONE BED LOCALITIES CITED**

1. Arlington, Franklin County, central Ohio: O. S. U. No. 3818, probably from one of the now-filled quarries near Marble Cliff Station: *Second bone bed*.
2. Marble Cliff Station, Franklin County, Ohio: *Second bone bed* (Stauffer, 1909, p. 44).
3. 1. 4th quarry, Marble Cliff Quarries Co., west 1/2 of Scioto River, across from Marble Cliff Station, Franklin County, Ohio: *First bone bed*, along west wall (Stout, 1942, p. 215).
4. Same as 3, along west and north walls: *Second bone bed*.
4a. Same as 3, but in Columbus limestone, 2 feet below *Second bone bed*.
5. Scioto (Main, or North) quarry, Marble Cliff Quarries Co., north of Hobo quarry: *First bone bed*, along west wall (Stout, 1942, p. 215).
6. Same as 5: *Second bone bed*.
7. Same as 5: *Third bone bed*.
8. Junction of McCoy Road and Scioto River Road, east side of Scioto River, one mile north of Fishinger bridge, Franklin County, Ohio: *Third bone bed*.
9. J. and L. Snouffer quarry, east of Scioto River, one mile south of Dublin, Franklin County, Ohio: *Second bone bed*, near top of east quarry wall.
10. Farholomew run, west side of Olentangy River, southern Delaware County, central Ohio: *Third bone bed*, at elevation 815 feet (Stauffer, 1909, p. 76).
11. Miami Stone Co. quarry, west side of Olentangy River, one mile northwest of Deep run, Delaware County, Ohio: *First bone bed*, at top of exposure in lower and abandoned quarry.
12. Same as 11: *Third bone bed*, near top of exposure in upper quarry.
12a. Deep run, east side of Olentangy River, 2 1/2 miles north of Delaware-Franklin county line, Delaware County: *Third bone bed* (Stauffer, 1909, p. 79).
13. Case run, east side of Olentangy River, Delaware County, Ohio: *Third bone bed*, one-quarter mile upstream from river (Stauffer, 1909, p. 80).
14. Abandoned quarry just north of abandoned schoolhouse, west side of Olentangy River, one mile north of Stratford, southern Delaware County, Ohio: *Third bone bed*, at top of exposure (Stauffer, 1909, p. 85).
15. Abandoned quarry just west of Hocking Valley R. R., on Delaware run, western part of city of Delaware, Delaware County, Ohio: Third and Fourth bone beds. All references to this locality are to the Fourth bone bed) (Westgate and Fischer, 1933, p. 1162).

16. Abandoned quarry just east of Owen, five miles southwest of Marion, Marion County, Ohio; Second bone bed near top of exposure along east side of quarry north of road (Stauffer, 1909, p. 92).

17. J. M. Hamilton and Sons quarry, east of highway, 1.75 miles north of Marion, Marion County, Ohio: Second bone bed, near top of exposure.

18. National Lime and Stone quarry, on Broken Sword Creek, one mile northwest of Spore, about six miles northwest of Bucyrus, Crawford County, Ohio: Second bone bed, near top of exposure along east wall (Stauffer, 1909, p. 109).

19. France Stone Co. quarry, 1.5 miles east of Bloomville, Seneca County, Ohio: Second bone bed, floor of west end of quarry (Stauffer, 1909, p. 110).

20. Quarry two miles south of Venice at end of railroad spur, Erie County, northern Ohio: Second bone bed, above coral bed along east wall (Stauffer, 1909, p. 129).


East Liberty Stone Co. quarry one mile west of East Liberty, Logan County, west central Ohio: East Liberty bone bed, at top of exposure.

Rocky branch, three miles northwest of Scipio, northern Jennings County, southeastern Indiana: Rocky Branch bone bed, in bed of creek. (Collected by C. A. Malott.)

Near Hargett, Estill County, east Central Kentucky: Kiddville bone bed. (Collected by C. C. Branson.)
SYSTEMATIC DESCRIPTIONS

The classification used follows that of May-Thomas in his recent book on Paleozoic fishes (1936). The numbers are those of the catalogue of the Ohio State University Geological Museum, where the material is deposited. The localities are referred to by the numbers used in the preceding list of localities.

Class Pisces
(Agnatha)
Subclass Ostracodermi
Order Heterostraci
Family Drepanaspidae
Indeterminate drepanaspid plates

Plate 2, figure 45; Plate 4, figures 6, 7; Plate 5, figures 14; Plate 6, figure 1

Localities and material.—First bone bed: 5. Third bone bed: 8, 13: Rocky Branch bone bed, Indiana. Nos. 10401-10404.

Remarks.—Fragmentary specimens probably represent body plates of drepanaspid fishes. They are badly broken up and retain none of their original outline although the surface ornamentation and internal structure may be well preserved. The ornamentation consists of smooth, dome-like, highly polished tubercles, 0.25 to 0.45 mm. in diameter, completely separated from each other basally by less than half their basal diameters, with the intertubercular space pitted by many canal openings—so many that the bases of the tubercles appear root-like, as in Ganosteus and Pycnoasteus. Occasionally two tubercles are fused and some are worn flat on top. The internal structure is distinctive and distinguishes these plates from the arthrodiran fragments which they resemble so closely externally and which are associated with them in the bone beds. The basal laminar layer is very thin and dense. There is no cancellous layer, and the reticular layer contains well-developed horizontal canals with vertical diverticulae opening on the surface between the tubercles through the superficial tubercle layer. The tubercles of the superficial layer contain tufts of fine dentine tubercles which extend from a well-developed pulp cavity to the thick enamel layer. The openings of the pulp cavities are small and connect with canals of the superficial layer and occasionally are joined directly with the intertubercular surface by canals. The reticular layer contains dentine structures similar to those regarded as unerupted tubercles in Tessaraspis by Wills (1935, p. 438, pl. 3, fig. 2; pl. 5, figs. 1, 2). They may, however, not be unerupted tubercles but instead what Gross (1935, p. 13) described as secondary filling of the cavities of the spongiosa by dentine in cornua plates of psammosteids. There is no trace of bone cell cavities.

Several specimens (Plate 2, figure 45; Plate 6, figure 1) may represent the fulcral scales of the posterior trunk region. When complete they seem to have been elongate oval in outline, strongly arched, and bearing an axial series of conical, posteriorly disposed spines, with here and there small lateral supernumerary spinules. In Drepanaspis gemindensis, the fulcral plates bear only a single spine.

One specimen (Plate 4, figure 8) is suggestive of an oral arch or gnathite of Drepanaspis, as it is figured in restoration by Patten (1932, fig. 6).
Order COELOLEPIDA

Remains of fishes of this problematical order, so abundant in stratigraphically older bone beds such as the Ludlow (Rohon, 1893) bone bed, consist of placoid-like dermal scales or denticles, easily recognized by the existence of a more or less well-developed pulp cavity and basal pulp-opening. None has yet been found in any of the Middle Devonian bone beds of the Cincinnati arch region. The supposed coelolepid scales figured in Eastman (1908, pl. 1, figs. 7, 8, 15; pl. 2, figs. a, 13) from the Columbus limestone are acanthodian scales, probably Chirracanthoides comptus, n. sp.

Order OSTEOSTRACI

Family CEPHALASPIDE

Genus OHIOASPIS, n. gen. (organ genus)

Diagnosis.—Small isolated tuberculated tesserae up to 3 mm. in diameter, oval to subpolygonal in outline, consisting of a dense inner laminar layer with bone cell cavities, a vascular middle layer, and an outer superficial dentine layer confined to the tubercles. Mucous canal openings from the vascular layer distinct over the intertubercular surface, with mucous grooves and pores arranged roughly at right angles to the tubercle-free borders. Tubercles stellate, erect, conical or cylindrical, in the latter condition supported by ridges, striations, or buttresses of dentine. In some cases the tubercles are flattened and imbricated but are more commonly well isolated, exposing the mucous canal openings in the interspaces. No pulp cavity in the tubercles.

Genotype.—Ohioaspis tumulosus, n. sp.

Remarks.—The affinities of the fish represented by these dermal tesserae are naturally uncertain, since we have no definite idea of the body form, orbits, electric fields, or other structures important for close determination. Relationship with the cephalaspids, however, is established by the close correspondence between the microscopic structure of the tesserae and that of the corresponding exoskeletal elements of more completely known forms—the arrangement of the skeletal layers, the presence of bone cell cavities, and the mucous canals, grooves, and pores. In cephalaspids, with few exceptions, the exoskeleton is continuous rather than broken up into independent tesserae. Traquair considered the exoskeleton in Atelaspis (genotype: A. tessellata from the Downtonian of Scotland) to be made up of separate tesserae (1899, p. 854), but Stensiö (1932, p. 151), on the basis of Traquair's figures, concluded that the tesserae were simply polygonal areas rendered apparently independent by fracture and weathering. Patten described a specimen which he ascribed to Atelaspis (1912, p. 163, figs. 199, 200B, 242) from the Lower Devonian of Miguasha, Quebec, in which the entire body seems to have been covered with small polygonal tuberculated tesserae very similar to those of Ohioaspis. He emphasized that this specimen exhibited the tendency, in an undoubted cephalaspid, for the exoskeleton to break up into separate polygonal plates. It may be doubted whether his specimen is congeneric with A. tessellata, but no further and more detailed descriptions or figures have yet been published of the Miguasha cephalaspid and its possible relationships with the form represented by Ohioaspis cannot be established.
Independent tesserae, but with heterostracan micro-structure, seem also to occur in *Astraspis*, an Upper Ordovician agnathan (Bryant, 1936). They are found also in *Camptaspis*, described by Branson and Mehl (1931, p. 510, pl. 1, figs. 1-3, fig. 1) from the Lower Devonian Jefferson formation of Utah. According to these authors, this was a primitive arthrodir representing "a stage before appreciable progress had been made toward the reduced number of plates in the capsule" but the entire aspect of the specimens and the tessellated median-crested cranial shield are strikingly like the cephalaspids, a group with which no comparisons were made by Branson and Mehl. Unfortunately no description of the microscopic structure of the skeleton was given and the writer received no reply from a request to study the type specimens. The figure and description of the tessera indicate a close similarity with *Ohioaspis*.

There remains a possibility that the affinities of these tesserae lie elsewhere than amongst the heterostracans, for instance, among the stego-cladids as exemplified by *Gemindina*. In these peculiar types of primitive gnathostomes much of the cephalic part of the body is covered by separate stellately tubercled studs or tesserae in superficial aspect very much like those of *Ohioaspis*, *Drepanaspis*, and *Psammostrus* (Brönni, 1933, p. 273, fig. 2). Indeed, there is already known from the Delaware formation of Ohio a rhenanid very close to, perhaps even identical with *Gemindina—Asterosteus*, known from one or two very poorly preserved central parts of the cranium (Newberry, 1875, p. 35, pl. 54, fig. 1). Thus there are circumstantial hints of a connection between *Asterosteus* and *Ohioaspis*, but if Brönni's observation that the macroscopic structure of the dermal studs of *Gemindina* corresponds to that of *Drepanaspis* and *Psammostrus* be eventually corroborated by the still unknown histologic structure of the bones of *Gemindina*, the likelihood of this relationship will be considerably diminished.

The spinelike plates from the Columbus and Delaware formations named *Acantholepis* (Plate 4, figure 10) by Newberry (1875, pp. 38-40, pl. 56, figs. 1-6) may represent cornua plates pertaining to the same fish as *Ohioaspis*. Their enamelled tubercles are formed by dente eruptions containing tufts of fine dentine tubules with practically no pulp cavities (Plate 7, figure 5). They rest on a thick superficial layer containing many bone cell cavities. The spongiosa is highly canaliculated and the basal layer is very thin.

*Ohioaspis tumulosus*, n. sp.

Plate 2, figures 1-10; Plate 5, figures 5-8

Text figure 2 a-f, h

*Description.—* Small tuberculated tesserae, rhomboidal, quadrangular, oval, or irregularly circular in outline. Surface bearing 2 to 30 stellate tubercles up to 1 mm. high. Centrally the middle vascular layer is thicker so that the whole surface of the tessera below the tubercles is convex. The tubercles may extend
practically to the edges of the tessera but commonly the periphery is marked by a zone of well-defined mucous grooves arranged roughly at right angles to the margin. Centrally the tubercles are higher above the surface than near the margins and their bases are usually closely approximated with very little of the intertubercular surface exposed between them. Mucous canal pores commonly occur on the tubercles between the tubercle ridges. Base flat, convex, or even slightly excavated.

**Dimorphus.**

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**Locality and material.**

a. Forma typicus: First bone bed—5, 11. Second bone bed—1, 2 (holotype, 19405, paratype, 19406), 4, 6, 16, 17, 19. Third bone bed—7, 8 (19407, 10418), 10, 12, 13, 14. Fourth bone bed—15; East Liberty bone bed, Rocky Branch bone bed.

b. Forma turritus: First bone bed—5. Second bone bed—2 (19411), 6, 17, 18–20. Third bone bed—7 (holotype, 19409), 8 (19410), 12, 13, 14; Rocky Branch bone bed.

c. Forma clavulus: First bone bed—5. Second bone bed—2, 16, 17; East Liberty bone bed, Kiddville bone bed.

d. Forma hystricosus: First bone bed—3, 5 (holotype, 19413). Second bone bed—6, Third bone bed—12; East Liberty bone bed.

**Remarks.**—These tesserae exhibit wide range in outline, shape of the base, and structure and form of the tubercles. In very small specimens the base is thin and flat, the bottoms of the mucous grooves often being perforated with a netlike effect. In larger specimens, of average size, the base is convex, the convexity being mostly in the dense laminar layer although in some large specimens it is shallowly concave and consists only of the middle vascular layer with many centrally ascending tubules, radiating peripherally (Plate 2, figure 6). In such specimens the dense laminar layer has apparently been detached or abraded, and it is notable that they also show effects of attrition on the upper surface—post-mortem attrition, whereas unworn specimens, except for the very smallest ones, almost always have a laminar convex base.
The greatest variation exists in the external structure of the tubercles, and on the basis of this, the following *forma* may be recognized:

a. *forma typicus.*—Tubercles broad, low, rounded, with low ridges radiating from the summits; closely packed basally. (Pl. 2, figs. 1-3, 5-7).

b. *forma turritis.*—Tubercles subcylindrical, with blunt, rounded tips and 5-8 narrow buttress-like lateral supporting ridges of dentine. Ridges notched at upper edges, expanding outwards basally, separated by deep grooves. (Pl. 2, figs. 4, 8, 10).
c. *forma hystericosus*.—Tubercles similar to those of *forma turritus* but taller, slenderer, with tips produced to an acute point, rarely more than three in number.

d. *forma clarus*.—Tubercles bulbous, striated or with low ridges, set on constricted stellate bases. Mucous grooves very weak. Top of tubercles usually worn flat, suggestive of a ventral situation on the body for this type. (Pl. 2, fig. 9).

One specimen from locality 18, consists of an elongate plate, 1 x 1.7 mm., which is asymmetrically folded a little to one side of the longer axis so that the limbs from an angle of about 60° with each other. This tessera, with typical tubercles, is interpreted as having occupied a marginal position on a depressed body, its asymmetric folding and lack of tubercles on the shorter side removing the possibility of its having been a fulcrum of texta or a median plate of the dorsal surface.

*Ohioaspis impositus*, n. sp.

Plate 2, figures 12-16
Text figure 2 g

*Description.*—Small tesserae, subtriangular, rhombic or trapezoidal in outline, with a convex, often very thick, base. Center of the plate bearing a compact knot of 5-18 subequal, elevated, striated, stellate tubercles rising abruptly from the base. Surface of the base appearing as a broad flat rim of mucous grooves or pores. Tubercles often very closely appressed and compressed in imbricating series. Diameter across surface of base from 0.5 to 1.5 mm.

*Localities and material.*—Second bone bed—2 (10417), 19. Third bone bed—7 (holotype and paratype, 19415). S (10418); Rocky Branch bone bed (10416); Kiddville bone bed.

*Remarks.*—This type of tessera is relatively uncommon and so far has not been found in the First and Fourth bone beds. Its general aspect, with the central compact cluster of distorted tubercles, is strikingly different from that of either *O. tumulosus* or *O. lamellatus*.

*Ohioaspis lamellatus*, n. sp.

Plate 2, figure 11
Text figure 2 i

*Description.*—Small, thin, subcircular, flat plates, from 0.4 to 0.6 mm. in diameter, bearing one or two tubercles 0.5-0.6 mm. high. Surface of basal part marked by mucous grooves and pores. Tubercles relatively very tall, with no marked central axis and consisting of three or four broad, thin, buttresslike ridges fused along their inner edges, their outer upper edges being rounded.

*Localities and material.*—First bone bed: 5 (holotype, 19419); 11.

*Remarks.*—This rare form, marked by the reduction of the tubercles to mere fragile clusters of buttresses, so far has been found only in the lowest of the four central Ohio bone beds. The constant lack of more than four ridgelike buttresses suggests this is not merely an early stage in the development of the tessera of the *O. tumulosus* type.
GNATHOSTOMATA
Subclass PLACODERMII
Order ACANTHOID

Seven species of acanthodians have been described from the Lower and Upper Devonian of Quebec and New Brunswick, but the American Middle Devonian has so far yielded only fin spines (Machacanthus) and occasional isolated scales. The first reference to scales was by Dr. Burnett Smith (1910, p. 663) who mentioned "relatively large four-sided and apparently unsculptured" scales (like Acanthoides dublinensis?) from the Marcellus formation in central New York. More recently Stauffer (1938, p. 242, pl. 53, figs. 21-24, 31-32) described Acanthodes dublinensis from scales found in the Olentangy formation of central Ohio, stratigraphically a few feet above the Third bone bed of the Delaware formation. The first mention of their occurrence in the Columbus and Delaware formations was given by Romer and Grove in 1935 (p. 816) who noted, on the authority of Stetson, that the scales assigned by Eastman (see note, page 7) to Thelodus and Coelolepis are probably acanthodians.

Fragments of the acanthodian fin spine organ genus Machacanthus (Watson, 1937, p. 126) are found occasionally in the bone beds. Small fragmentary specimens of M. major Newberry may be found in the Second bone bed in the Marble Cliff quarries. But tiny acanthodian scales in bivalvular bodies are excessively abundant in all the bone beds at all localities, and by far outnumber all the other types of fish remains. Much less common are the dental elements supposed to be acanthodian, and in less variety, provisionally placed in Plectodus Agassiz, 1839.

While much work has been done on this interesting and perplexing group of little Paleozoic fishes, the most important recent publication being that by D. M. S. Watson (1937), the scales have scarcely been studied at all, the greatest attention naturally having been paid to the morphology of the head and fins. It is almost impossible to obtain data from the literature on the scales themselves in the various families and genera. Broten (1934, 1934a) has made a start on the study of them and his lead is followed here. He points out (1934, p. 19; 1934a, p. 5) that each acanthodian genus has a characteristic scale type which in general make-up and style of ornamentation is nonvarying, except for size and a certain variability of ribbing and outline, over the whole body except the head, and that the scale type can be used for systematic purposes. Broten has also for the first time accurately described the microscopic structure of the older acanthodian scales. Similar results were obtained by Gross (1935). Thin sections of the Ohio bone bed acanthodian scales made by the writer show the same structures (Plate 6, figures 2-5) and these are not further discussed in view of the detail already available in the papers cited.

Mention should be made here of the work by Gunnell, who in two papers (1931, 1933) mainly devoted to conodonts, described nine new genera based upon iso-
lated scales, dermal studs, and teeth of Pennsylvanian fishes. Most of these pertain to selachians, but *Holmesella* is acanthodian. Gunnell recognized the acanthodian affinities of this form in 1933 (p. 288) and included in it scales with smooth (*H. quadrata*, genotype) and ridged coronal surfaces, although he still seems to have regarded them as teeth or oral fixtures. *Holmesella* is here restricted as an organ genus of short-crowned, smooth-surfaced scales, and is the scale type characteristic of the well-known Carboniferous genus *Acanthodes*, several species of which are known from the Pennsylvanian of the United States (Eastman, 1902).

A new point in the squamation of these fishes is the discovery of several specimens (Plate 2, figures 25, 35, text fig. 5c) consisting of two or three ordinary acanthodian scales fused solidly, in each case the fusion having taken place between the posterior edge of a forward scale and the anterior edge of the scale diagonally behind it.

The terminology applied to scales of the acanthodian type is illustrated by text figure 3.

![Generalized acanthodian scale](image)

**Figure 3.—Generalized acanthodian scale**

**KEY TO BONE BED ACANTHODIAN SCALE TYPES**

1. Coronal surface bearing ridges:
   A. Ridges diagonal, radiating  
      1. Coronal surface equal or wider than base:
         a. Ridges distinct over entire coronal surface  
            *Cheiracanthoides*
         b. Ridges developed only along anterior edge:
            aa. Coronal surface rhomboid in outline,  
               base thick, inflated  
               *C. comis*
            bb. Coronal surface broader than long,  
               base thin, flat  
               *C. breviplicatus*
2. Coronal surface narrower than base; posterior corner prolate.  
   \[ C. \text{venustus} \]  
B. Ridges parallel to longer axis.  
   1. Coronal surface rounded quadrangular, nearly as wide as base.  
      \[ H. \text{hellarugosus} \]  
   2. Coronal surface elongate rounded triangular, much narrower than base.  
      \[ H. \text{venustuloides} \]  
II. Coronal surface smooth.  
   A. Coronal surface practically flat, outline rhomboid.  
      1. Coronal surface regularly rhomboid.  
         \[ A. \text{dublinensis} \]  
      2. Coronal surface elongate rhomboid.  
         \[ A. \text{sciotoensis} \]  
   B. Coronal surface convex, rounded quadrate in outline.  
      \[ A. \text{hardyi} \]  

**Genus: Cheiracanthoides, n. gen. (organ genus)**

*Diagnosis.*—Scales with nearly flat or slightly convex crown, well-developed neck, and a thick, inflated base. Coronal surface equal to, wider, or narrower than the base, its posterior corner usually projecting back beyond the base. Surface marked by 4 to 24 fine, radiating, occasionally bifurcating rounded ridges, convergent towards the posterior corner. Internal structure like that of scales of Acanthoiide.  

*Genotype.*—Cheiracanthoides comptus, n. sp.  

*Remarks.*—This is the scale type of the genus Cheiracanthus. In general form it is similar to Acanthoides, from which it is distinguished by the fine coronal ridges. The ridges show much variation but are always much finer than those of Diplacanthoides and the grooves between them are never so deeply excavated as to notch the anterior margin deeply. They are most strongly developed anteriorly but usually extend at least halfway to the posterior corner; in some specimens they are distinct over the whole surface, and in others they are supplemented by a second set radiating toward the posterior corner from the scale center which is posterior in position. Supernumerary ridges occur in a few instances at the lateral corners. In a few types the ridges are subparallel and run off the posterior edge; these are often very difficult to distinguish from the associated scales described below as Helolepis.  

There is much variation in the proportions of Cheiracanthoides scales,—in outline of the crown, height of the neck and thickness of the base. On the basis of these together with the number and arrangement of the coronal ridges, several species can be distinguished.
Cheiracanthoides comptus, n. sp.
Plate 2, figures 17-25; Plate 6, figures 3-4
Text figure 4 a-g

Figure 4.—Acanthodian scales, Cheiracanthoides—a-g, C. comptus Wells, n. g., n. sp.; a-e, × 15 (19420); d, × 20 (19422); e, f, g, × 10, × 10, × 30 (19421)—h, C. comis Wells, n. sp., × 20 (19425)—i, j, C. venustus Wells, n. sp., × 15 (19430, 19428)—k, C. brevlicatus Wells, n. sp., × 15 (19431).

Description.—Small to relatively large scales, thick, with crown about the same width as the base, a constricted short neck, and a thick, inflated base. Crown nearly flat, regularly subrhomboidal to broadly triangular in outline symmetrical, overhanging the posterior corner of the base, surface bearing from 5 to 30 small, subacute ridges which converge towards the posterior corner. Lateral corners often reflected slightly upward.

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Specimen | Ridges | Length | Width | Height
---|---|---|---|---
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11 | 15 | 1.1 | 1.5 | 0.7
12 | 16 | 2.0 | 2.2 | 1.1
13 | 19 | 2.3 | 2.75 | 1.0
14 | 22 | 1.4 | 2.2 | 1.2
15 | 29 | 2.5 | 3.0 | 1.5

Localities and material.—First bone bed: 3, 5, 11. Second bone bed: 1, 2 (19422), 4 (19423), 6, 9, 10, 12, 18, 19, 20 (19424), 21. Third bone bed: 7 (holotype and paratypes, 19420), 8 (19421), 10, 12, 13, 14. Fourth bone bed: 15; Rocky Branch bone bed, Indiana; East Liberty bone bed, Ohio.

Remarks.—Wide but continuous variation exists in this type of scale, which is the commonest fish remain in the bone beds and which has been found at every locality. The most striking deviation from the normal type is found in occasional specimens (Plate 2, figures 18, 21) which have a second set of ridges radiating posteriorly from a point about one-third the distance from the posterior to the anterior corner. In most specimens the ridges are straight except near the lateral corners where they bend slightly toward the posterior corner. The ridges are usually simple, but in larger specimens they show a tendency to bifurcate toward the anterior edges. One exceptionally well-preserved specimen (Plate 2, figure 19) has very thin notched posterior edges, each projection between the notches bearing a posterior prolongation of an anterior ridge; ordinarily well-preserved specimens have evenly rounded posterior edges.

A single specimen from the Second bone bed at locality 4 consists of two scales fused solidly by the antero-posterior sides of the crowns, necks, and bases. The posterior edge of one scale overlaps one-third of the crown of the scale behind it. Another fused pair (Plate 2, figure 25) from the Third bone bed at locality 7 is like the other except that the coronal surfaces are so completely merged that the overlapped edges are wholly indistinguishable.

**Cheiracanthodes comis, n. sp.**

Plate 2, figures 26-27; Plate 6, figure 2

Text figure 4 h

**Description.**—Medium-sized scales like *C. comatus*, except that the ridges are weakly developed and occur only along the anterior edges.

**Dimensions.**—

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<td>11</td>
<td>1.0</td>
<td>1.1</td>
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</tr>
</tbody>
</table>
Localities and material.—First bone bed: 1, 11. Second bone bed: 1, 6, 16 (holotype, 19425), 17. Third bone bed: 8 (19426), 10, 14. Fourth bone bed: 15.

Remarks.—This scale can be mistaken for *Acanthoides dublinensis*, especially when the normally faint ridges have been abraded, but the coronal surface of *A. dublinensis* is smooth and glistening whereas that of *C. comis* is dull and shows faint scallopings along the anterior edges. *C. comis* is evidently very close to *C. comptus* but unabraded specimens show that the ridges are never developed for more than a third of the distance towards the posterior corner.

**Cheiracanthoides venustus**, n. sp.
Plate 2, figures 28-32
Text figure 4 i

Description.—Medium to large scales, with proportionally small crown, an almost unconstricted neck, and a broad, thick base. Crown varying in outline from symmetrico-thombic to asymmetrico-quadrangular, the posterior corner prolonged to a sort of snout but rarely extending backwards beyond the corner of the base; anterior corner rounded. Edges of crown reflected basally and continuous with the neck which is expanded basally. Base wider than the crown, often very much wider and at least equal to the combined thicknesses of crown and neck. Surface of crown with 4 to 10 stout, rounded, occasionally bifurcating, radiating ridges.

Dimensions.—

<table>
<thead>
<tr>
<th>Specimen</th>
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<th>Length</th>
<th>Coronal width</th>
<th>Basal width</th>
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</tr>
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<td>1.4</td>
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</table>

Localities.—First bone bed: 5, 11. Second bone bed: 1 (19429), 2 (19430), 4, 6, 9, 16 (holotype and paratype, 19427), 17, 18, 19, 20. Third bone bed: 7, 8 (19438), 10. Fourth bone bed: 15; Rocky Branch bone bed, Indiana; Kiddville bone bed, Kentucky.

Remarks.—This scale is very striking in its very general aspect, with the large, broad base and relatively small crown with its prolate posterior corner. The normal examples show a nearly even petaloid coronal outline. Some of the largest and thickest scales found in the bone beds are included here.

**Cheiracanthoides breviplicatus**, n. sp.
Plate 2, figure 33
Text figure 4 f, k

Description.—Moderate-sized scales with broad, transversely rounded rectangular or broadly ovate crown, the anterior edge of which is turned sharply
downward partially covering the neck which is short and constricted. Base low, almost flat. Surface of crown very thin, smooth, and glistening, bearing 9 to 22 low, rounded ridges which are developed only along the anterior edge, usually wider than the base, posterior edge considerably overhanging the base.

**Dimensions.**

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</table>

**Localities and material.**—First bone bed: 3. Second bone bed: 1 (holotype, 19431), 17, 18. Third bone bed: 8, 14.

**Remarks.**—Distinctive characters of this species are the glistening coronal surface with numerous faint anterior ridges, the broad crown with reflected anterior edges, and low flat base. It is uncommon.

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Figure 5.—Acantboliian scales, *Heloplepis* and *Acantboliodes*—a. H. renostatooides Wells u. sp., × 15, × 25 (19436, 19435); b. H. bellarugosa Wells, n. g., n. sp.; c. triple fused scale, × 15 (19434); d. a. × 25, × 15 (19432, 19433); e. A. hardyi Wells, n. sp., × 15 (19439); f. A. scitoensis Wells, n. sp., × 15 (19438); g. A. dublinensis (Stauffer), × 20 (19440).
One variant from locality 3, apparently belonging to this type, has an asymmetricto-rhomboid outline, with the sloping anterior ridge-bearing portion sharply delimited from the flat, lustrous coronal surface, suggesting that the ridges were developed only on that part of the scale protected by the overlap of the posterior edge of the preceding scale, or that they originally covered more of the coronal surface but, being on a part of the trunk exposed to some wear, the ridges were abraded and the coronal surface polished.

Genus HELOLEPIS, n. gen. (organ genus)

Diagnosis.—Small acanthodian scales with quadrangular to subtriangular elongate crown, short neck, and a well-developed, thick base. Coronal surface inclined very slightly anteriorly towards the basal plane, and bearing a few relatively coarse parallel ridges.

Genotype.—Helolepis bellarugosus, n. sp.

Remarks.—This scale type is distinguished from Cheiracanthoides by the faintly inclined coronal surface on which the relatively fewer ridges are parallel rather than radiating. It resembles the selachian dermal denticle later described as Deirolepis, but has a more completely developed base and less inclined coronal surface.

Helolepis bellarugosus, n. sp.

Plate 2, figures 34-36
Text figure 5 c-e

Description.—Small scales having the characters of the genus as diagnosed above. Coronal surface elongate-ovoid to ovoid, nearly flat, nearly equal to the width of the base, and bearing 4 to 7 relatively coarse anterior parallel ridges which rarely extend more than halfway to the posterior corner.

Dimensions.

<table>
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<th>Coronal width</th>
<th>Basal width</th>
<th>Height</th>
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Localities and material.—Second bone bed: 1 (holotype, 19432), 2 (19433), 4, 17 (19434). 10, Third bone bed: 7, 12, 14.

Remarks.—This species is marked by its elongate-rounded rectangular crown with relatively few parallel ridges. One specimen from locality 17 consists of three scales fused solidly, with distinct coronal margins overlapping about one-fourth of the next scale in the series (Plate 2, figure 36).

Helolepis venustuloides, n. sp.

Plate 2, figures 37-38
Text figure 5 a-b

Description.—Like H. bellarugosus, but the coronal surface is elongate-rounded
subtriangular in outline and much narrower than the base, and bears only 2 to 4 coarse, well-developed, parallel ridges.

**Dimensions.**

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<th>Length</th>
<th>Coronal width</th>
<th>Basal width</th>
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**Localities and material.**—Second bone bed: 1. Third bone bed: 7 (10436), 8 (holotype, 10435). Fourth bone bed: 15.

**Remarks.**—This species approaches some specimens of *Cheiracanthoides venustus* in its general form, but the coronal surface is inclined and its ridges are parallel rather than radiating.

**Genus ACANTHOIDES** Breith, 1931 (organ genus)

**Diagnosis.**—Acanthodian scales with smooth, glistening, usually more or less convex crown, translucent on edges, quadrangular to rhomboidal in outline, with short neck and thick, rounded inverted pyramidal base.

**Remarks.**—This type is like that of the scales of the well-known Carboniferous genus *Acanthodes* (*Holmesella*), but differs by the posterior overhang of the crown and the more or less convex rather than flat or concave coronal surface.

*Acanthodes* hardyi, n. sp.

Plate 2, figure 39

Text figure 5 f
description.—Small, moderately thick scales with convex crown, short neck, and moderately inflated base. Outline of crown rounded quadrangular, oval, or even rectangular. Anterior edges of coronal surface reflected basally; posterior edge prolonged beyond the base.

**Dimensions.**

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</table>

**Localities and material.**—First bone bed: 3. Second bone bed: 1, 2, 16. Third bone bed: 7, 8 (holotype, 10437).

**Remarks.**—Readily distinguished by its elongate-quadrangular to oval, never rhombic, convex, coronal surface. It is an uncommon form and less than 10 specimens have been found so far.

*Acanthodes sciotensis* n. sp.

Plate 2, figures 40-41

Text figure 5 g
description.—Small, relatively thin scales, with faintly convex coronal surface, short neck, and low base. Outline of crown sharply elongate-rhombic, posterior edge prolonged back from the base, usually centered a little to one side of the base.
Devonian Fish Remains: Wells

which therefore projects from under one anterior edge. Anterior edges of crown slightly reflected basally.

Dimensions.—

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Localities and material.—First bone bed: 3, 5. Second bone bed: 1, 2 (19439), 6, 16, 18. Third bone bed: 7, 8 (holotype, 19438). Fourth bone bed: 15, Rocky Branch bone bed, Indiana; East Liberty bone bed; Kiddville bone bed, Kentucky.

Remarks.—The uniform, elongate diamond-shaped outline and proportional thinness of this scale render it distinct from other species of this genus.

Acanthoides dublinensis (Stauffer)

Plate 2, figure 42

Text figure 5-h

Acanthoides dublinensis Stauffer, 1938, Jour. Paleont., vol. 12, p. 442, pl. 53, figs. 21-24; 31-34.

Description.—Small thick scales with nearly flat crown, more or less regularly rhombic in outline with rounded corners, especially the anterior one. Posterior corner extending slightly beyond the base. Neck short and thick. Base thick, strongly convex, centered a little anterior of the center of the crown, occasionally slightly broader than the crown.

Dimensions.—

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Localities and material.—First bone bed: 3, 5, 11. Second bone bed: 1 (19440), 2, 6, 16, 17, 18, 20, 21. Third bone bed: 7, 8, 12, 13, 14. Fourth bone bed: 15, East Liberty bone bed; Kiddville bone bed; Olentangy shale, central Ohio (Stauffer); Marcellus formation, central New York.

Remarks.—Stauffer’s material came from the lower part of the Olentangy shale, stratigraphically a few feet above the Third bone bed. The type is fairly common in the bone beds, and is readily distinguished by its thickness and regularly rhomboid outline.
In his description of this scale, Stauffer failed, as did Gunnell with similar forms, to orient it correctly, hence his figures show only lateral and basinal aspects.

The possible reference of the scales described by Burnett Smith (1910, p. 663) from the Marcellus of New York to this form has already been mentioned.

Genus PLECTRODUS Agassiz, 1838 (organ genus)

Remarks.—Small, slightly porous plates bearing inset conical denticulations, resembling the acanthodian teeth or dental elements known as Plectrodus, occur with some frequency in the bone beds. Like the acanthodian scales the fishes to which they pertain are unknown, and they are here recognized as three species.

**Plectrodus ohioensis**, n. sp.

*Description.*—Small dental elements consisting of a more or less oblong, straight or bent convex base of porous bony tissue, along the crest of which is set a series of 3 to 5 conical, nearly straight denticles. The under side of the base is concave. On one side of the main row of denticles there may be one or two smaller ones. The main denticles are taller and larger at one end and decrease toward the other. They are expanded basally within the porous base from which they are distinct, with pores regularly arranged around their bases, giving them a stellate effect. Length of base: 0.7 to 2.0 mm.; height, from under side of base to tip of highest denticles, 0.6 to 1.5 mm.


Remarks.—This form differs from *P. mirabilis* Agassiz (in Murchison, 1839, pl. 35, figs. 3-8) of the Ludlow bone bed (Downtonian of England), by its much smaller size and denticles which are nearly circular rather than subtriangular in cross section. Descriptions and figures of Devonian teeth known to be acanthodian (Dean, 1907), show that they commonly consist of one large, grooved denticle flanked by several smaller cusps or denticles on either side arranged en echelon.

**Plectrodus multidentatus**, n. sp.

*Description.*—Small dental elements like *P. ohioensis* in size and structure, but bearing a large number of denticles which are arranged in three and four irregular rows faintly en echelon, the larger denticles forming an alternating double row along one side with a diagonal series of two or three smaller ones corresponding to each larger one. The smaller denticles, where not broken off, usually show signs of ante-mortem wear. In thin section, the denticles are seen to consist of dentine with numerous very fine dentine tubules and a large pulp cavity with many small pulp canals leading into the basal canal system.

*Localities and material.*—First bone bed: 5 (holotype, 19446). Third bone bed: 7 (19449). 8: Rocky Branch bone bed, Indiana.

Remarks.—This species is distinguished from *P. ohioensis*, which is about the same size, by the several rows of proportionally smaller denticles. On one specimen there are two rows of denticles on one side of the main row, and one on the other. The aspect is similar to that of the jaw element of *Ischnacanthus* figured by Dean (1907, fig. 10).
Devonian Fish Remains: Wells

Placodus aculeatus, n. sp.
Plate 4, figures 5, 6

Description.—Very small dental elements consisting of a thin, slightly porous, circular or elongate-oval base, bearing from one to three slender, acute, curved denticles which are compressed triangular in cross section. Where only one denticle is present, the base is circular, measuring from 0.6 to 0.8 mm, across and the denticle is from 0.6 to 0.7 mm, high. Where three denticles are developed, the base measures about 0.3 x 0.8 mm, flat on the bottom, and the denticles are about 0.5 mm, high, the two end ones being slightly larger than the middle ones and all are curved towards one long side.

Localities and material.—Second bone bed: 9 (19448), 16. Third bone bed: 7 (holotype, 19447).

Remarks.—Distinguished by the angularity of the denticles and relatively small size. The shape of the denticles is more nearly like that of previously described acanthodian teeth than in either of the two preceding species. Internally their structure is like that of the others, although the base is denser and bears very few canaliculae.

Genus MACHACRACANTHUS Newberry, 1887 (organ genus)
Machacracanthus major Newberry
Plate 7, figure 1


Localities and material.—Second bone bed: 4 (19450), 6.

Remarks.—Small, incomplete specimens of this large paired fin spine are found in the Second bone bed. This is not uncommon and is widely distributed throughout the upper part of the Columbus formation and its stratigraphic equivalents in Indiana, Ontario, and New York, and in the Delaware formation. If it really pertained to an acanthodian fish, as is deemed probable by Hussakof and Bryant (1910, p. 140) and Watson (1937, p. 126), then individuals of unusual size—as much as 2 m in length—for this group are indicated.

The microstructure of a specimen from the Second bone bed shows numerous longitudinal pulp canals with dense walls of dentine in which lie myriads of fine dentine tubules. The tissue between the dentine cylinders is dense and packed with clusters of large dark bone cell cavities. The axial cavity as seen in cross section has the same shape as the exterior of the spine.

Genus GYRACANTHUS Agassiz, 1837 (organ genus)
Gyracanthus ? eastmani, n. sp.
Plate 2, figures 46, 47

Description.—Very small, elongate, slightly tapering, nearly straight spines. Cross section subelliptical, compressed, with subcylindrical pulp cavity about one-third the total diameter. Exterior nearly smooth, with faint longitudinal ridges where unorn.; anterior edge very faintly carinated; posterior edge strongly carinated. Carina bearing a single row of widely spaced, downwardly projecting thornlike denticles on its edge, with occasional enamelled low smooth tubercles along its sides. Diameters of type specimen: 1.5 x 2.2 mm.
Localities and material.—First bone bed: 5 (?). Third bone bed: 7, 8 (holotype, 19451): Rocky Branch bone bed, Indiana (19452); Kiddville bone bed, Kentucky.

Remarks.—This ichthyodorulite probably represents a new acanthodian organ genus, although it broadly corresponds with the distal part of *Gyracanthius primaeus* Eastman (1908, p. 114, fig. 17) from the Marcellus formation of New York. The material is too fragmentary for better discrimination, but it is named because it can easily be recognized in bone bed material. A specimen from the Rocky Branch bone bed of Indiana shows an irregular series of pores along either side of the carina and one or two on the carina between the pore series.

Order ARTHRODIRA

Suborder EUARTHRODIRA

Family COCCOSTEIDÆ

Genus COCCOSTEUS Agassiz, 1844

COCCOSTEUS spatulatus (Newberry)

Plate 4, figures 12-18; Plate 8, figure 1


*Protititanocanthus fossatus* Eastman, 1889, N. Y. State Mus., Mem., vol. 10, p. 144, pl. 10, fig. 2; text fig. 30.

Localities and material.—Delaware formation, Delaware, Ohio:


Bone bed material: Second bone bed: 2 (19454). Third bone bed: 7 (19453).

Remarks.—Several small fragments of an exoskeletal arthrodiran armor plate, ornamented with small stellate tubercles, probably belong to this poorly known species. In thin section (Plate 8, figure 1) they are characteristically arthrodiran in structure. Externally they are much like those of *Rhyuchodus secans*, except that the tubercles are smaller and dull rather than enamel-like. Only one specimen is sufficiently complete to be identified with certainty as to position in the head and trunk armor.

Median basal

Incomplete but uncrushed and retaining intact the right posterior and part of the right lateral margins. Original width across the posterior side, 17 mm.; length at least 29 mm.; convexity at posterior end nearly 5 mm. From side to side it is arched, the central part more so than the sides. Posterior edge bevelled
and smooth, partly enclosed by the externo-basal plates. Inner posterior surface deeply grooved on each side, the groove passing into a socket about three-fourths of the distance to the middle, the groove and socket serving to lock the plate on either side to the overlapped parts of the externo-basals. The under surface of the sides is shallowly grooved for articulation with the externo-basal. The internal surface of the center of the plate is marked by a pair of broad shallow grooves converging from the anterior edge and ending near the posterior end in two deep pits which nearly penetrate upwards to the external surface. Tubercles over entire external surface, faintly concentric in pattern, very small over the posteriorly located center of ossification.

The aspect of this plate is clearly cocceostean and it probably represents a young individual of C. spatulatus. There is some resemblance to the corresponding plate of the contemporary species C. halmodeus Clarke of the New York Marcellus formation.

Right antero-ventro-lateral:

Only parts of the outer lateral and posterior edges are preserved. It must have belonged to a somewhat larger individual than the MB.

Other plates are wholly fragmentary and not worth further remarks. One bears a well-defined sensory groove but none of the margins is preserved.

Suborder PTYCTODONTIDA

Genus PTYCTODUS Pander, 1858 (organ genus)

PTYCTODUS, sp.

Locality and material.—Third bone bed: 13 (19456).

Remarks.—PTYCTODUS has not hitherto been reported from the Middle Devonian in Ohio. One small piece representing a short stretch of a Ptyctodont tritoral surface bearing very feebly developed transverse ridges is referred to this organ genus of gnathal elements. It evidently was from an immature fish in which the lamellar plates of the dental elements had not developed any considerable depth. It does not appear to have undergone much wear and at one end (anterior?) the transverse striae pass into a nearly smooth flat surface.

Genus RHYNCHODUS Newberry, 1873 (organ genus)

RHYNCHODUS, sp.

Plate 3, figure 1; Plate 4, figure 11; Plate 7, figures 2-4, 7, 8

Locality and material.—Second bone bed: 1, 2, 4, 6, 9, 17, 19, 21. Third bone bed: 7 (19458), 8, 12, 13, 14; Rocky Branch bone bed, Indiana (19457); East Liberty bone bed.

Remarks.—One species of this organ genus of gnathal elements occurs in the
Columbus and Delaware formations—R. secans 8 Newberry (1873, p. 316, pl. 38, figs. 1, 1 a; pl. 29, figs. 1-2 c). Fragments of the sectorial edges of tiny gnathal elements of this genus, marked by striations and gouges due to masticatory activities (Plate 3, figure 1), are common in the bone beds, especially the Third, but they cannot certainly be identified with R. secans because of their imperfect condition. The exterior layer is thin, but very dense and externally polished, and the internal part very spongy or openly cellular.

Genus PALÆOMYLUS Woodward, 1891 (organ genus)
Palæomylius, sp.
Plate 6, figures 8, 9

Localities and material.—Second bone bed: 10. Third bone bed: 8 (19461), 10.
Remarks.—Several small worn fragments of dense dental material show in section the typical structure of packed minute tubules or columns of dentine normal to the tritural surface of the gnathal elements known as Palæomylius (genotype: Rhynchodus frangens Newberry, of the Columbus and Delaware formations) and Ptyctodus. In the latter genus the columns are usually modified into laminar plates transverse to the length of the jaw element (Plate 6, figure 7), whereas in Palæomylius, which lies between Rhynchodus and Ptyctodus, they are packed so that they form scattered puncta on the surface (Eastman, 1898, p. 545). Two species of Palæomylius are known from the Ohio Middle Devonian—the genotype mentioned above, and P. crassus (Newberry), but the bone bed specimens can be identified with neither until more complete material is found.

Order MACROPETALICHTHYDA
Genus MACROPETALICHTHYS Norwood and Owen, 1846
Macropetalichthys rapheidolabis Norwood and Owen, 1846
Plate 8, figure 2

(For synonymy see Hay, 1902, p. 349, and 1929, pp. 644-645)

Remarks.—Fragments of the crania upon which this species rests are not uncommon in the Middle Devonian limestones of the eastern United States, but so far none has been definitely identified from any of the bone beds. This may be due to the lightness of the bony structure of M. rapheidolabis as contrasted with the uniformly dense and abrasion-resistant structure of most of the fish material in the bone beds—a condition consistent with their accumulation in these layers.

A photomicrograph of the structure of a specimen (19462) of cranial bone of this species from the Columbus limestone is included here for comparison with that of coccostral and Ptyctodontid cranial plates.

8 The external body armor of the fish to which this type of jaw belonged is ornamented with rounded tubercles with stellate bases and thick, polished, transverse caps, as indicated by the remains of a badly mangled ecrass (19459), still mostly embedded in matrix, collected from the Delaware formation in the old Wagner No. 4 quarry near Sandusky (Staufer, 1909, p. 127) in the summer of 1941 by C. T. Hardy (Plate 7, figure 6). Fragments bearing a similar ornamentation occur occasionally in the bone beds (Plate 3, figure 11; Plate 7, figures 2-4, 7-8); they resemble the associated dragon-spid plate fragments but the tubercles are much larger and coarser. Fragments of the plates of Macropetalichthys and Coccosteus also bear similar tubercles but without the highly polished caps.
Subclass CHONDRICTHYES

Order SELACHII
Suborder PLEUROPTERYGII
Family CLADOSELACHIDÆ

In descriptions of Devonian sharks such as Cladoselache, occasional mention has been made of the existence of patches of shagreen or of scattered shagreen denticles, but there are very few descriptions of these tiny dermal defenses. Dean (1909, pp. 214-215, figs. 1-3) referred to and figured shagreen denticles of C. jylcri and other species from the Upper Devonian Cleveland shale of northern Ohio. He noted that in these forms, as in modern sharks, the denticles on the same fish are very different in appearance on different parts of the body, ranging, for instance, in Ctenacanthus clarki from unsculptured to richly ornamented with cusplike points or ridges (text fig. 6 c). Gross (1933, p. 63, fig. 17) described and figured the teeth and dermal defenses of Cladodus (Protacrodus) wildungensis Jaekel from the Upper Devonian of Germany (text fig. 6 h). He states that these “scales” are regularly arranged in diagonal series as in acanthodians and that their sculpture is in swinging curves with small swellings (“Schüppchen”) at the anterior tip like tiny overlapping scales. The ornamentation is considerably coarser than that of the denticles described below. Recently, Smith Woodward and White (1938) figured and described the internal structure of a dermal tubercle of Cladoselache from the Cleveland shale like the larger one figured by Dean. It is composed mostly of dentine and corresponds closely to Ohiolepis and Cladolepis of the bone beds.

Gunnell has described (1931, 1933) a number of selachian scales from the Pennsylvanian under the organ generic names Cooleycella, Cooperella, Hammondella, Idiacanthus, Kirkella, Moreycella, and Williamsella. The last approaches Cladolepis but the ornamentation consists of rounded rather than grooved ridges. Moreycella, is very similar to the shagreen denticles of some Recent sharks (see Ulrich and Basler, 1926, pl. 9, fig. 3), as are also specimens of Cooperella (op. cit., pl. 9, fig. 8.—Platyodon). Idiacanthus resembles closely the mouth denticles of the Recent Chlamydoselachus (Smith, 1937, fig. 10). At least one of Gunnell’s species of Holmesella, the acanthodian scale organ genus, pertains to Cladolepis (H. ornamenta) (text fig. 6 h).

Whether the shagreen types described below pertain entirely to cladoselachids is uncertain, although it seems probable. Some Cladolepis scales are known to belong to this group (i.e., those of C. jylcri and C. clarki) or to fish with cladodont teeth (i.e., C. wildungensis). Cladolepis gunnelli, however, occurs in the Kidville and East Liberty bone beds with no associated selachian skeletal remains other than Phoebodus floweri and P. ? bryanti, the latter a dubious pleuracanthid. In the Geneseo shale and Conodont bed of New York Cladolepis occurs with both cladodont and dittodont teeth. Deirolepis and Ohiolepis occur in formations that so far have yielded but one described selachian tooth—Cladodus prototypus Eastman (1907, p. 61, pl. 1, fig. 15) of the Columbus formation.
Genus CLADOLEPIS, n. gen. (organ genus)

Diagnosis.—Dermal siagreen denticles pertaining to cladodont sharks, consisting of nearly flat, thin, oval to subrhomboid crown which is attached to a small, thin, cushionlike base by a nearly nonexistent neck. Posterior part of crown considerably overhanging the base; anterior part of base protruding beyond crown. Surface of crown ornamented by narrow ridges originating at the anterior end and curving outwards towards the sides and converging towards the posterior end, giving an imbricating petaloid aspect. Tops of the ridges grooved upwards from the base. Anteriorly the ridges may be very short and resemble partially recumbent grooved spines.

Genotype.—Cladolepis gunnelli, n. sp.

Remarks.—The petaloid grooved ridges of this scale type seem to have resulted from the laying over and fusing of clusters of originally nearly upright or somewhat backwardly inclined placoid denticles. In thin section (Plate 8, figure 4) each is formed by a layer of dentine containing dendritic masses of tubules arising from a very small pulp cavity. Beneath the ridges the canalicate pulp cavities form a sort of reticulate layer which is underlain by the dense laminar base which is penetrated by innumerable very fine canalicate radiating outwards and downwards from the “scale center” somewhat as in the acanthodian scale.
Cladolepis gunnellii, n. sp.
Plate 3, figures 2-6; Plate 8, figure 4
Text figure 6 a, b, d

Description.—Small denticles, 1 to 2.5 mm. wide, having the characters of the genus as diagnosed above. Outline subrhomboidal to oval, occasionally rounded quadrangular, with posterior end often slightly prolate. Coronal surface nearly flat, thin, bearing from 7 to 14 grooved ridges (counted across from the widest part). Anterior end often with one or two tiny subsidiary onlapped crownlets. Base usually thin, but convex and acanthodianlike in some specimens.

Locality and material.—Kiddville bone bed, Kentucky (holotype and paratypes, 10.603); East Liberty bone bed, Ohio (10.604).

Remarks.—This type is less coarsely sculptured than C. wildungensis and the ridges are less individualized and more interfused and recumbent than in the denticles of Cladoselache, spp. of the Cleveland shale.

Scales very similar to, if not identical with this species, occur in the State Quarry beds of the early Upper Devonian of Iowa (Plate 3, figure 7) and in the upper part of the Geneseo shale and Conodont bed of the late Middle Devonian (Taghanic) of New York (text figure 6 c).

Genus OHIOLEPIS, n. gen. (organ genus)

Figure 7.—Cladoselachian dermal denticles of Ohiolepis and Deirolepis—a, d, f, g, O. newberryi Wells, n. g., n. sp.; a, c, X 15, X 12. (19467); b, g, X 15, (19409); d, X 15, (19466); f, X 7, (19470); e, h, O. stewarti Wells, n. sp., X 15, X 20, (19472, 19471); i, O. stewarti ? X 20, (19502); j, D. carinatus Wells, n. g., n. sp., X 15, (19473).

Diagnosis.—Small to relatively large shagreen denticles, rounded rhombic, quadrangular, or irregularly elongate or transversely oval in outline, consisting of a broad crown ornamented by numerous spinelike tubercles with enamelled anteriorly indented, anteriorly sloping faces and acute, posteriorly inclined tips, resting directly on an often internally convex, lamellar base. Scale center very fine, irregularly branching tubules. Base containing innumerable very fine straight tubules which radiate horizontally from the scale center when the base is flat, or peripherally when it is convex. Very small pulp cavities beneath the tubercles
which contain highly developed, ramifying dentine tubules. Pulp cavities united by feeble horizontal meshwork of intercommunicating canals opening on the outer surface between the tubercles but none of them apparently penetrating the dense basal layers. Anterior sides or edges of denticles devoid of tubercles over a narrow strip where overlapped by preceding denticles.

Genotype.—Ohiolepis newberryi, n. sp.

Remarks.—The distinctive character of these dermal scales or denticles lies in their ornamentation of inclined, indented, acute tubercles which are not recumbent, highly elongated, broadly grooved and interfused as in Chadoslepis.

Ohiolepis newberryi, n. sp.

Plate 3, figures 8-15; Plate 8, figures 3, 5, 6
Text figure 7 a-d, f, g

Description.—Scales having the structure of the genus as diagnosed above; regularly rhombic, elongate-rhombic, or irregularly oval in outline, with a thick, convex base. Surface ornamented with rows or series of posteriorly inclined spine-like enameled tubercles, each bearing a deep groove on the anterior slope. Axes of the spines commonly parallel with the antero-posterior diagonal of the denticle. A narrow, plain margin surrounds the ornamented central area, usually broader on the anterior, overlapped edges.

Dimensions.—

<table>
<thead>
<tr>
<th>Shape</th>
<th>Tubercles</th>
<th>Length and Width</th>
<th>Height</th>
</tr>
</thead>
<tbody>
<tr>
<td>rhombic</td>
<td>7 to ca. 130</td>
<td>0.5 x 2.5 mm.</td>
<td>0.3 - 0.7 mm.</td>
</tr>
<tr>
<td>elongate-rhombic</td>
<td>6 to ca. 100</td>
<td>0.5 x 0.35 to 2.5 x 1.5</td>
<td>0.25 - 0.7</td>
</tr>
<tr>
<td>irregularly oval</td>
<td>20 to ca. 120</td>
<td>1.8 x 0.8 to 3.5 x 1.5</td>
<td>0.4 - 0.7</td>
</tr>
</tbody>
</table>

Localities and material.—First bone bed: 3 (19407), 5, 11. Second bone bed: 1, 2 (holotype and paratypes, 10466), 4, 6, 17, 18, 10, 20. Third bone bed: 7 (19469), 8 (19470), 9, 12, 13. Fourth bone bed: 15. Rocky Branch bone bed, Indiana (10468).

Remarks.—This scale type is relatively common in all the Ohio bone beds. The spined-like tubercles show differences in form in different specimens. The commonest is an inclined acute cone, subtriangular in cross section with a deep groove in the anterior face. The depression may be so extensive as to leave only a rim on the anterior face, and the tubercles resemble those on the scales of Onychodus sigmoioides except that they are less inclined, narrower, and the rim is not horse-shoe shaped. On some specimens the anterior tubercular groove is very shallow and developed only near the base, the upper two-thirds or so being half-conical and strongly curved backwards, often overlying the next tubercles and even fused to it. In a few specimens the tubercles are blunt and nearly club-shaped, usually very closely set and more or less fused basally. Very rarely specimens have tubercles compressed with their longer axes.
lying in a dorso-ventral plane, and closely packed or imbricat in two or three antero-posterior series, or forming a tangled mat.

The arrangement of the tubercles follows a fairly distinct pattern in most specimens. In rhombic and elongate-rhombic scales the dorso-ventral diagonal is marked by a row of tubercles which tend to be larger distally from the scale center. In front of and behind this series are roughly parallel, shorter ones, their marginal tubercles tending to be concentrically arranged. In the irregularly oval scales the tubercles seem to form series radiating from the scale center.

Most specimens are relatively unworn, or at least were so before becoming detached from the cadaver, but a few show visible signs of ante-mortem wear especially in the center of the scale where it is thickest. Such worn specimens evidently occupied a ventral position on the depressed body of these bottom dwellers.

**Ohioolepis stewartae**, n. sp.

Plate 3, figures 19, 20
Text figure 7, e, h, i

**Description.**—Small dermal denticles consisting of a very thin, broad, flat base, rounded rectangular in outline, commonly with a central anterior tonguelike extension; bearing a relatively small number (3 to 10) of spinelike tubercles similar to those of *O. newberryi* in shape and structure, arranged in a single transverse series, the central ones smaller and often with one or two adventitious tubercles here and there between them.

**Dimensions.**—

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Length</th>
<th>Width</th>
<th>Tubercles</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.0 mm.</td>
<td>0.4 mm.</td>
<td>3</td>
</tr>
<tr>
<td>2</td>
<td>0.2</td>
<td>0.5</td>
<td>5</td>
</tr>
<tr>
<td>3</td>
<td>0.3</td>
<td>1.0</td>
<td>5</td>
</tr>
<tr>
<td>4</td>
<td>0.5</td>
<td>0.8</td>
<td>6</td>
</tr>
<tr>
<td>5</td>
<td>0.4</td>
<td>0.6</td>
<td>7</td>
</tr>
<tr>
<td>6</td>
<td>0.4</td>
<td>0.8</td>
<td>8</td>
</tr>
<tr>
<td>7</td>
<td>0.7</td>
<td>0.7</td>
<td>9</td>
</tr>
<tr>
<td>8</td>
<td>0.5</td>
<td>0.75</td>
<td>10</td>
</tr>
</tbody>
</table>


**Remarks.**—This rather uncommon scale type is readily distinguished by its very thin, flat base and relatively few tubercles. There is some individual variation in outline and development of the anterior tongue. In a few specimens a posterior tongue may appear. Some depart strongly from the transverse shape and are long and narrow with very strongly compressed tubercles with merely a trace of the antero-basal groove (number 1 above). One specimen, quadrate in outline, bears two antero-posterior rows of thin, imbricated tubercles.
Genus DEIROLEPIS, n. gen. (organ genus)

*1 Cooperella* Gunnell, 1933, non Carpenter, 1861

Diagnosis.—Small shagreen denticles with thin, slightly convex crown sloping anteriorly sharply with respect to the plane of the base; proportionately very long neck; and a flat, subcircular, very thin base. Coronal surface with a few relatively coarse, rounded, parallel ridges.

Genotype.—Deirolepis carinatus, n. sp.

Remarks.—Distinguished by the angular rather than sub-parallel relationship between the coronal and basal planes, by the long neck, very thin base, and by the relatively few, coarse, simple, parallel ridges. In some specimens the inclination of the crown is such that its anterior edge is nearly merged with the base.

*Cooperella* Gunnell includes at least one species—*C. ceroida* (1933. pl. 31, figs. 73-75)—which falls within this scale type.

Deirolepis carinatus, n. sp.

Description.—Dermal denticles having the characters of the genus as diagnosed above. Coronal surface elongate-oval in outline, often flaring posteriorly and bearing 2 to 5 parallel ridges, its width equal to or greater than the width of the base.

Dimensions.—

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Ridges</th>
<th>Length</th>
<th>Width</th>
<th>Height</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
<td>0.3 mm.</td>
<td>0.3 mm.</td>
<td>0.3 mm.</td>
</tr>
<tr>
<td>2</td>
<td>3</td>
<td>0.3</td>
<td>0.5</td>
<td>0.4</td>
</tr>
<tr>
<td>3</td>
<td>3</td>
<td>0.7</td>
<td>0.7</td>
<td>0.4</td>
</tr>
<tr>
<td>4</td>
<td>3</td>
<td>0.8</td>
<td>0.75</td>
<td>0.6</td>
</tr>
<tr>
<td>5</td>
<td>3</td>
<td>0.5</td>
<td>0.6</td>
<td>0.3</td>
</tr>
<tr>
<td>6</td>
<td>4</td>
<td>0.6</td>
<td>0.5</td>
<td>0.4</td>
</tr>
<tr>
<td>7</td>
<td>4</td>
<td>0.9</td>
<td>0.6</td>
<td>0.4</td>
</tr>
</tbody>
</table>

Localities and material.—First bone bed: 3. Second bone bed: 1, 2 (holotype, 10473), 6, 9, 20. Third bone bed: 7, 8, 10. Rocky Branch bone bed, Indiana (?).

Remarks.—This distinctively marked form is uncommon in the bone beds, less than a dozen specimens having been found.

One specimen from locality 6 is doubtfully included here. It has the flat base and long neck of *Deirolepis*, but the coronal surface is larger than normal and bears 10 ridges convergently arranged as in *Cheiracanthoides*. A similar specimen with 12 ridges was found in the Rocky Branch bone bed of Indiana.

Suborder PLEURACANTHODII

Genus PHOEBODUS St. John and Worthen, 1875 (organ genus)

Remarks.—Although Phoebodus may be only a variant of *Dittodus* ("Diplo-odus") (Hussakof and Bryant, 1919. p. 138), species of it are commonly sufficiently distinct to warrant retention of the name for teeth with well-developed intermediate denticles between the median and lateral cusps.
Figure 8.—Pleuracanthian teeth—a, *P. (?) bryanti* Wells, n. sp., Kiddville limb bed, anterior, lateral, and posterior aspects, × 12, (19476); b, c, d, *P. floweri* Wells, n. sp.; b, c, East Liberty limb bed, × 20, × 10, (19474); d, Kiddville limb bed, × 10, (19475).

*Phoeodus* *floweri*, n. sp.

Plate 3, figures 22, 23

Text figure 8 b-d

Description.—Small teeth, 1.5 to 4.5 mm. wide and 1 to 3 mm. high, with three principal cusps, the median one slightly shorter than the laterals, with single minute denticles between the median and each lateral. Cusps subconical, compressed antero-posteriorly with sharp lateral keels, curved backwards, the laterals also curved slightly outwards, posterior surfaces smooth, anterior surfaces marked by 3 to 5 strong, slightly spiral striations, some of them bifurcating basally. Elongate, rough "button" on posterior part of base.

Localities and material.—East Liberty limb bed (holotype, 19474); Kiddville limb bed (hypotype, 19475).

Remarks.—This tooth is probably very closely related to *P. sophia* St. John and Worthen (1875, p. 251, pl. 1, fig. 14 and *P. macisaacsii* (St. John and Worthen) (1875, p. 252, pl. 1, figs. 12, 13) from the lower Upper Devonian Cedar Valley limestone of Iowa, but it is smaller, with more sharply striated cusps. *P. priscus* (Eastman) (see Hussakof and Bryant, 1919, p. 145, pl. 44, fig. 3; text fig. 51) from the lower Upper Devonian of Illinois and upper Middle Devonian (Conodont bed) of New York is much larger, with twice as many striations on each cusp, but otherwise very much like *P. floweri*.

This is one of the very few records of the dittodont-phoebodont type of shark teeth in the Middle Devonian. They occur in the "Tully pyrite" bed in western New York (Hussakof and Bryant, 1919, p. 149; Bradley, 1866, p. 71) together
with *P. sophiae* (collected by the writer). A specimen referable to *D. grabau H.* and B. has been collected by the writer in central New York from the upper part of the Tully formation. One of the teeth from the lower Olentangy shale of central Ohio figured by Stauffer (1938, pl. 53, fig. 38) probably pertains to *P. floweri*. Others figured by him (pl. 53, figs. 45, 46) are less determinable but seem to be *Phoebodus*, but neither *P. flozveri* nor *P. ? bryanti*, described below.

**Phoebodus? bryanti**, n. sp.  
Plate 3, figures 24-27

**Description.**—Very small teeth, 1 to 3.5 mm. in width and about the same in height, with three principal cusps, the median one shorter and slenderer than the laterals, with one, or more commonly two, minute denticles between the median and each lateral. All cusps smooth, ovoid in cross section, with obtuse or sharp lateral edges and curved strongly backwards from their point of origin, the laterals also being curved outwards. Base thin, wider than high, convex anteriorly, strongly concave posteriorly, forming a strongly curved plate; no "button"; two small pores in the lower center of anterior side, and a narrow slotlike pore opposite these on the posterior surface. Substance of cusps and denticles polished and translucent; that of the base dull and opaque.

**Localities and material.**—Kiddville bone bed, Kentucky (holotype and paratype, 19476); East Liberty bone bed, Logan Co., Ohio (hypotype, 19477).

**Remarks.**—This tooth is marked by the peculiar shape of the base which is unlike that of normal cladodont, dittodont, or phoebodont teeth, and at first glance the cusps seem to be inclined strongly forward rather than backwards as usual. For these reasons the reference to *Phoebodus* is tentative and provisional—a new genus may very well be involved. *Dittodontus grabau* Hussakof and Bryant (1910).

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**Figure 9.**—*Onychodus* scales—a, b, c, fragments of scales, × 10, × 15, × 15 (19479, 19480, 19503); d, e, f, small dermal elements, × 15, × 20, × 20 (19479, 19480, 19482).
Devonian Fish Remains: Wells

p. 147, text fig. 52) from the uppermost Middle Devonian (Conodont bed) of western New York, is a variable smooth-cusped form, some specimens of which are phoebodont, and very small specimens of which resemble P. bryanti closely except for the base and cusp relations.

Sub-class OSTEICHTHYES
Division CROSOPTERYGH
Order RHIPIDISTIA
Family ONYCHODONTIDEAE
Genus ONYCHODUS Newberry, 1857
Onychodus sigmoides Newberry

Plate 3, figures 28-38; Plate 4, figures 19, 20; Plate 8, figures 7-11
Text figure 9 a-f


Locality and material.—Remains of Onychodus occur in the bone beds at every locality in Ohio, Indiana, and Kentucky, as well as scattering throughout the Middle Devonian limestones of the Cincinnati arch area. The supposed dermal denticles or scales described below, inter alia, have been noted from the First bone bed, 11 (19482); Second bone bed, 19 (19480); Third bone bed, 7, 8, 14 (19479).

Remarks.—Isolated parts of this powerful and well-armed fish, which must have attained very large proportions, are among the commonest fish remains throughout the upper part of the Columbus formation (Klonidike member) and the Delaware formation, in the form of dentaries, scales, symphysial teeth, and isolated cranial bones. Scarcely a specimen of the bone beds can be found that does not contain many small conical teeth and little scraps of bone and scales.

These small fragments are classified as follows:

b. Fragments of fin rays.
c. Body scales, large and small.
d. Dermal denticles
   aa. With keeled base and broad flange.
   bb. With flat or concave base and very narrow flange
      aaa. With a single drumloid tubercle.
      bbb. With 1 to 10 horse-shoe shaped tubercles.
e. Teeth
   aa. Symphysial teeth.
   bb. Laniary teeth, with fluted base.
   cc. Interlaniary teeth, with subconical base.

The bone and scales are easily identified, even from very small bits, by the

If the body proportions of Onychodus were approximately those of Heloptychius, then a fragment of the anterior portion of a left dentary in the Ohio State University Geological Museum (11489), indicating a dentary originally at least 35 cm. long, belonged to a fish no less than four meters long. Or, if it had the slenderer build of Ostrolepis, at least 51 meters long. In either case individuals of this genus were by far the largest fish of Middle Devonian times, although smaller than the climax arthrodires Dinichthys and Titanichthys of the Upper Devonian Ohio and Cleveland shales.
characteristic ornamentation of close-set, often anastomosed, small, enamelled, broadly grooved tubercles. These resemble plastic cones that have been flattened by pressure applied diagonally downward from one side just below the apex, or more simply they are horse-shoe shaped 3. In some places, especially on cranial and gnathal bones and large body scales, the tubercles are drumloid with ridges radiating backwards from the forward apex, and resemble those of the bone fragments from the Upper Silurian bone beds of Oesel named \textit{Lophastinus superbus} by Rohon (1893, pl. 1, figs. 38, 39), and whose structure he compared with that of the scales of \textit{Hololopychius} (1893, p. 74). In size the tubercles range from 0.2 to 0.3 mm. in diameter and about half as high. The surface of dentary and cranial bones and very large scales is dense, with tiny granulations between the tubercles. The surface of smaller scales, however, is usually not dense, and the tubercles arise from a series of fine parallel ridges which in turn overlie a dense laminar layer. Small bits of these scales lacking any tubercles and showing only a basal layer with fine parallel granulated ridges occur occasionally in bone bed residues.

In thin section the scales and bone show the structures of the cosmoid type, with a thick basal isopenic layer overlain by the exposed vascular layer on which are the scattered cosmine tubercles (Plate 8, figures 7-9). The reduction of the cosmine layer in \textit{Onychodus} is similar to that found in the other cosmosterigians, \textit{Hololopychius} and \textit{Glyptolepis}, and in the dipnoan \textit{Dipterus} (Forster-Cooper, 1937, figure 32) the lower part of the cosmine tuberculated layer is continuous and the vascular layer is rarely exposed. One specimen from the Third bone bed shows large drumloid tubercles overlying the small horse-shoe shaped tubercles (Plate 3, figure 36).

Three kinds of very small dermal elements have been found sparingly in the bone beds, all of them bearing the \textit{Onychodus} type of tubercle ornamentation. The first is a single multi-ridged drumloid tubercle about 0.5 mm. long resting on a thin flange-like plate about 1 mm. in diameter, below which projects a stout obusely rounded keel (Plate 3, figures 31, 32). In one specimen the flange is turned up on one side. These denticle-like studs may have been set in the fleshy tissues around the symphysial whorl of teeth between the tips of the dentaries. The second type is similar but has a very narrow flange and no basal projection— the base being flat or slightly concave. The third type is a small, thin subellipsoid stud with several horse-shoe shaped tubercles surrounded by a relatively broad, thin flange of cosmine, with a slightly convex base (Plate 3, figure 34).

Two types of very small curved conical teeth, both belonging to \textit{Onychodus}, are very abundant in the bone beds (Plate 3, figures 37, 38). One is long and slender, with a fluted, hollow, flaring base; the other is proportionally shorter and thicker, with a constricted, tapering, nonfluted base. The first type represents the laniary teeth between which in the dentary are set the slightly more numerous short, fat, interlaniaries. In thin section the teeth consist of a simple cone of den-

---

3The tubercular ornamentation is almost exactly like that of some species of \textit{Glyptolepis}, especially the specimens identified as \textit{Glyptolepis, sp. cf. G. papilliferus} Agassiz by Kner (1915, p. 46, pl. 6, fig. 1) from the Upper Devonian of Ellesmere Island.
Devonian Fish Remains: Wells


Arkell, W. J., and Mayo-Thomas, J. A.

Bradley, F. H.

Branson, E. R., and Mehl, M. G.

Brett, E.

Breitzen, E.

Bryant, W. J.

Cronin, C.

Dean, Bashford

Eastman, C. R.

Forster-Cooper, C.

Foss, W.

Gunnell, F. H.

Hay, O. P.

REFERENCES CITED


1938. Utillitarian classification for fragmentary fossils. J. Geol., 46, 973-984.


1931. Conodonts from the Fort Scott limestone of Missouri. J. Paleont., 5, 244.

1933. Conodonts and fish remains from the Cherokee, Kansas City, and Wabounee groups of Missouri and Kansas. J. Paleont., 7, 261-297, pls. 31-33.


The fin overlaid by a very thin, minutely striated layer of enamel, with a large, open pulp cavity (Plate 4, figures 16, 20; Plate 8, figures 10, 11).

One small specimen (Plate 3, figure 33) is thought to be part of a fin ray. It is a hollow rod, quadrangular in cross section, 0.75 mm. across a side, with a shallow longitudinal groove along the middle of two opposite sides. Small pores in the bottom of these grooves communicate directly with the internal longitudinal cavity. The resemblance to the fin rays of Eusthenopteron is very close.
PLATES

PLATE I (VOL. PL. 7)

Plates furnished by the Bownocker Fund, The Ohio State University
EXPLANATION OF PLATE I (7)

**Frontispiece**

<table>
<thead>
<tr>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Above. Residue of bone material from sample of First Ohio bone bed, Scioto quarry, Franklin County, Ohio, × 6. (19486).</td>
</tr>
<tr>
<td>Below. Thin section of sample of Second Ohio bone bed, Marble Cliff, Franklin County, Ohio, × 6. (19487). The gray and nearly white areas are fragments of brachiopods, pelmatozoan ossicles, and bryozoans; the very dark gray and black areas are fish material—bones, teeth, and scales.</td>
</tr>
</tbody>
</table>
PLATE II (VOL. PL. 8)
**EXPLANATION OF PLATE II (8)**

1-10. *Ohioaspis tumulosus* Wells, n. g., n. sp. .................................................. 16

- Figure 1, forma *typicus*, holotype, Second bone bed, Loc. 2, × 6, (19405).
- 2, 3, forma *typicus*, Third bone bed, Loc. 8, × 6, (19407).
- 4, forma *turritus*, Third bone bed, Loc. 8, × 6, (19410); 5, 7, forma *typicus*, Third bone bed, Loc. 8, × 6, (19407); 6, forma *turritus*, Third bone bed, Loc. 7, × 6, (19406).
- 9, forma *clavatus*, holotype, First bone bed, Loc. 3, × 6, (19414); 10, forma *turritus*, Second bone bed, Loc. 2, × 14, (19411).

11. *Ohioaspis lancillatus* Wells, n. sp. .................................................. 19

- Holotype, First bone bed, Loc. 5, × 14, (19419).

12-16. *Ohioaspis impositus* Wells, n. sp. .................................................. 19

- Figures 13, 16, holotype and paratypes, Third bone bed, Loc. 7, × 14, × 6, (19415).
- 12, Rocky Branch bone bed, Indiana, × 14, (19416); 14, Second bone bed, Loc. 2, × 14, (19417); 15, Third bone bed, Loc. 8, × 6, (19418).

17-25. *Cheiracanthoides complatus* Wells, n. g., n. sp. .................................................. 23

- Figures 17, 18, Second bone bed, Locs. 4, 2 × 6, (19413, 19417); 20, 23, holotype and paratypes, Third bone bed, Locs. 7, × 6, × 14, × 6, (19406).
- Second bone bed, Locs. 1, 2 × 6, (19420, 19425).

26-27. *Cheiracanthoides comis* Wells, n. sp. .................................................. 24

- Figure 25, Second bone bed, Loc. 14, × 14, (19425); 27, Third bone bed, Loc. 8, × 14, (19426).

28-32. *Cheiracanthoides crenustus* Wells, n. sp. .................................................. 25

- Figure 28, Third bone bed, Locs. 8, × 14, (19428); 29, 30, paratypes and holotype, Second bone bed, Loc. 17, × 6, (19427); 31, 32, Second bone bed, Locs. 1, 2 × 6, (19428, 19429).

33. *Cheiracanthoides brevificatus* Wells, n. sp. .................................................. 25

- Holotype, Second bone bed, Loc. 1, × 14, (19431).

34-36. *Helolepis bellarugosus* Wells, n. g., n. sp. .................................................. 27

- Figure 34, holotype, Second bone bed, Loc. 1, × 14, (19432); 35, Second bone bed, Loc. 2, × 6, (19423); 36, Second bone bed, Loc. 17, × 14, (19434).

37-38. *Helolepis crenustuloides* Wells, n. sp. .................................................. 27

- Figure 37, Third bone bed, Loc. 7, × 6, (19436); 38, Third bone bed, Loc. 8, × 14, (19435).

39. *Acanthoides hardyi* Wells, n. sp. .................................................. 28

- Holotype, Third bone bed, Loc. 8, × 14, (19437).

40-41. *Acanthoides sciotocnus* Wells, n. sp. .................................................. 28

- Figure 40, Second bone bed, Loc. 2, × 6, (19436); 41, holotype, Third bone bed, Loc. 8, × 14, (19438).

42. *Acanthoides dublinensis* (Stauffer) .................................................. 29

- Second bone bed, Loc. 1, × 14, (19440).

43. *Plectrodus ohioensis* Wells, n. sp. .................................................. 30

- Third bone bed, Loc. 7, × 14, (19442).

44. *Plectrodus multidentatus* Wells, n. sp. .................................................. 30

- Holotype, First bone bed, Loc. 5, × 14, (19446).

45. *Drepanaspis fulcular scale* (?) .................................................. 14

- First bone bed, Loc. 5, × 14, (19463).

46-47. *Gyracanthus ? castmani* Wells, n. sp. .................................................. 31

- Figure 46, holotype, Third bone bed, Loc. 8, × 6, (19451); 47, Rocky Branch bone bed, Indiana, × 6, (19452).
PLATE III (VOL. PL. 9)
EXPLANATION OF PLATE III (9)

Figure 1. Rhynchodus, sp. — Rocky Branch bone bed, Indiana, × 6, (19457).

2-7. Cladolepis gunnelli Wells, n. g., n. sp. — Figure 2, East Liberty bone bed, × 6, (19464); 3-6, holotype and paratypes. Kiddville bone bed, Kentucky, × 6, (19463); 7, (this species), State Quarry limestone, Iowa, × 6, (19465).

8-18. Ohiolepis newberryi Wells, n. g., n. sp. — Figures 8, 11, 12, holotype and paratypes, Second bone bed, Loc. 1, × 14, (19466); 9, 16, First bone bed, Loc. 3, × 6, × 14, (19467); 10, Rocky Branch bone bed, Indiana, × 6, (19468); 13-15, 17, 18, Third bone bed, Loc. 7, × 6, × 6, × 6, × 14, (19469).

19, 20. Ohiolepis stewarti Wells, n. sp. — Figure 19, holotype, First bone bed, Loc. 11, × 14, (19471); 20, Second bone bed, Loc. 1, × 14, (19472).

21. Deirolepis carinatus Wells, n. g., n. sp. — Holotype, Second bone bed, Loc. 2, × 14, (19473).

22, 23. Phoebodus floweri Wells, n. sp. — Figure 22, Kiddville bone bed, Kentucky, × 6, (19475); 23, holotype, East Liberty bone bed, × 6, (19474).

24-27. Phoebodus ? bryanti Wells, n. sp. — Figure 24, East Liberty bone bed, × 14, (19477); 25-27, holotype and paratype, Kiddville bone bed, × 14, × 6, × 6, (19476, 19477).

28-38. Onychodus sigmoides Newberry — Figure 28, scale fragment, Third bone bed, Loc. 7, × 6, (19478); 29, scale fragment, Third bone bed, Loc. 14, × 6, (19479); 30, skin denticle, Third bone bed, Loc. 14, × 14, (19472a); 31, skin denticle, Second bone bed, Loc. 2, × 14, (19480); 32, scale fragment Delaware form., Delaware, O., × 14, (3794); 33, fin ray (?), Second bone bed, Loc. 6, × 6, (19481); 34, skin denticle (?), First bone bed, Loc. 11, × 14, (19482); 35, scale fragment, Third bone bed, Loc. 8, × 6, (19483); 36, scale, Third bone bed, Loc. 7, × 6, (19478); 37, 38, interlabial and labial teeth, Third bone bed, Loc. 8, × 6, (19483).
EXPLANATION OF PLATE IV (10)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-4. Plectrodus ohioensis Wells, n. sp.</td>
<td>30</td>
</tr>
<tr>
<td>Figure 1, Second bone bed, Loc. 17, × 25, (19443): 2, holotype specimen from Columbus formation, 24 inches below Second bone bed, Hoio quarry, × 25, (19411); 3, Second bone bed, Loc. 2, × 25, (19444); 4, Second bone bed, Loc. 9, × 25, (19445).</td>
<td>31</td>
</tr>
<tr>
<td>5-6. Plectrodus aculeatus Wells, n. sp.</td>
<td>14</td>
</tr>
<tr>
<td>Figure 5, Second bone bed, Loc. 9 × 25, (19448); 6, holotype, Third bone bed, Loc. 7, × 25, (19447).</td>
<td></td>
</tr>
<tr>
<td>7. Drepanaspis plate fragment</td>
<td>14</td>
</tr>
<tr>
<td>Third bone bed, Loc. 8, × 15, (19401).</td>
<td></td>
</tr>
<tr>
<td>8. Drepanaspis gnathie (?)</td>
<td>14</td>
</tr>
<tr>
<td>Third bone bed, Loc. 8, × 15, (19402). (Not figure 6 as stated in text.)</td>
<td></td>
</tr>
<tr>
<td>9,12. Indeterminate plates</td>
<td>16</td>
</tr>
<tr>
<td>Third bone bed, Loc. 7, × 6, (19488). (Not figure 10 as stated in text.)</td>
<td></td>
</tr>
<tr>
<td>10. Acantholepis pastilusus Newberry</td>
<td>32</td>
</tr>
<tr>
<td>Fragment of spine, Third bone bed, Loc. 2, × 6, (19506).</td>
<td></td>
</tr>
<tr>
<td>11. Rhynchodus, sp.</td>
<td>33</td>
</tr>
<tr>
<td>Surface of indeterminate plate, Third bone bed, Loc. 7, × 6, (19458).</td>
<td></td>
</tr>
<tr>
<td>13-18. Coccocestus spatulatus Newberry</td>
<td>43</td>
</tr>
<tr>
<td>Third bone bed, Loc. 7, (19453); 15, 16, external and internal aspects of basal plate, × 6; 15, fragment of indeterminate plate, × 6; 16, 17, external and internal aspects of right antero-ventro-lateral (?), × 2; 18, indeterminate plate fragment, Second bone bed, Loc. 2, × 6, (19451).</td>
<td></td>
</tr>
<tr>
<td>19,20. Onychodus sigmoides Newberry</td>
<td>43</td>
</tr>
<tr>
<td>Figure 10, longitudinal section of laniary tooth, Third bone bed, Loc. 8, × 15, (19483); 20, vertical section through upper part of dentary tooth, Delaware formation, near Delaware, × 15, (19484).</td>
<td></td>
</tr>
</tbody>
</table>
PLATE V (VOL. PL. 11)
EXPLANATION OF PLATE V (11)

Sections

<table>
<thead>
<tr>
<th>Page</th>
<th>Sections</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-4.</td>
<td>Drepanaspis plate &lt;br&gt; Third bone bed, Loc. 8, (19401). 1, vertical section, X 45; 2, 3, 4, parts of same section, X 180.</td>
</tr>
<tr>
<td>5-8.</td>
<td>Ohioaspis tumulosus Wells, n. g., n. sp. &lt;br&gt; Figure 5, forma territus, vertical section, X 45, Third bone bed, Loc. 8, (19412); 6, 7, 8, forma tephrarum, 6, vertical section, paratype, X 45, Second bone bed, Loc. 2, (19401); 7, 8 horizontal basal and vertical sections, Third bone bed, Loc. 8, X 45, (19408).</td>
</tr>
</tbody>
</table>
PLATE VI (VOL. PL. 12)
EXPLANATION OF PLATE VI (12)

Sections

1. Drepanaspid fulcral scale ........................................... 14
   Transverse vertical, Third bone bed, Loc. 8, × 45, (19424).

2. Cheirocanthoidea comites Wells, n. g., n. sp. ..................... 24
   Longitudinal vertical, Third bone bed, Loc. 8, × 45, (19429).

3,4. Cheirocanthoidea comptus Wells, n. g., n. sp. .................. 33
   Second bone bed, Loc. 9, longitudinal vertical section: 3, × 45; 4, × 180, showing bone cell cavities, (19424).

5. Section of Second bone bed, Marble Cliff .......................... 39
   Showing in center and at bottom arenthodian scales; center section filled through base and shows bone cell cavities, × 45, (19487).

6. Plectrodus multidentatus Wells, n. sp. .............................. 49
   Transverse section through lower part of tooth and enclosing arenthodian scales, Third bone bed, Loc. 7, × 150, (19449).

7. Ptyctodus caleculus Newberry and Worthen ........................ 34
   Section parallel to tritellar surface, State Quarry beds, Iowa, (19460).

8,9. Paleomythus, sp. .................................................. 54
   Sections parallel and perpendicular to tritellar surface, Third bone bed, Loc. 8, × 45, (19461).
PLATE VII (VOL. PL. 13)
EXPLANATION OF PLATE VII (13)

Sections

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. <em>Macracoanthus major</em> Newberry</td>
<td>31</td>
</tr>
<tr>
<td>Transverse section of axial part of spine, Second bone bed, Loc. 4, × 45, (19450).</td>
<td></td>
</tr>
<tr>
<td>2-4. <em>Rhynchodus</em>, sp.</td>
<td>33</td>
</tr>
<tr>
<td>Vertical sections through plate, Third bone bed, Loc. 7, × 15, × 45, × 180, (19458).</td>
<td></td>
</tr>
<tr>
<td>5. <em>Acantholepis pustulosus</em> Newberry</td>
<td>16</td>
</tr>
<tr>
<td>Vertical section of spinelike plate, Columbus form., Marion, O., × 45, (11481).</td>
<td></td>
</tr>
<tr>
<td>6. <em>Rhynchodus secans</em> Newberry</td>
<td>34</td>
</tr>
<tr>
<td>Vertical section of cranial plate, Delaware form., Sandusky, O., × 45, (19459).</td>
<td></td>
</tr>
<tr>
<td>7,8. <em>Rhynchodus</em>, sp.</td>
<td>33</td>
</tr>
<tr>
<td>Vertical sections of plate, Third bone bed, Loc. 7, × 45, × 180, (19458).</td>
<td></td>
</tr>
</tbody>
</table>
### EXPLANATION OF PLATE VIII (14)

#### Sections

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td><em>Coccosteus spatulatus</em> Newberry</td>
<td>32</td>
</tr>
<tr>
<td></td>
<td>Vertical section of cranial plate, Third bone bed, Loc. 7, X 45, (19455).</td>
<td></td>
</tr>
<tr>
<td>2.</td>
<td><em>Macroptelichthys rajchikolabia</em> Norwood and Owen</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td>Vertical section of cranial plate, Columbus formation, Columbus, X 45,</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(19462).</td>
<td></td>
</tr>
<tr>
<td>3.5.6.</td>
<td><em>Onolepis newberry</em> Wells, n. g., n. sp.</td>
<td>38</td>
</tr>
<tr>
<td></td>
<td>Figure 3, longitudinal vertical, Third bone bed, Loc. 8, X 45, (19470);</td>
<td></td>
</tr>
<tr>
<td></td>
<td>5-6, longitudinal and transverse verticals, Second bone bed, Loc. 1, X 45,</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(19466).</td>
<td></td>
</tr>
<tr>
<td>4.</td>
<td><em>Cladolepis gunneli</em> Wells, n. g., n. sp.</td>
<td>37</td>
</tr>
<tr>
<td></td>
<td>Transverse vertical section, Kidville bone bed, Kentucky, X 45, (para-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>type, 19463).</td>
<td></td>
</tr>
<tr>
<td>7-11.</td>
<td><em>Onychodus sigmoides</em> Newberry</td>
<td>43</td>
</tr>
<tr>
<td></td>
<td>Figures 7, 8, vertical section of small scale, in ordinary light and with</td>
<td></td>
</tr>
<tr>
<td></td>
<td>crossed Nichols, Delaware formation, Delaware, O., X 45, X 49, (1944);</td>
<td></td>
</tr>
<tr>
<td></td>
<td>9, vertical section of large scale, Delaware form., Delaware Co., O., X 40,</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(19485); 10, 11, transverse sections of incus teeth, Third bone bed, Loc.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>8, X 180; 10, marginal, showing striated enamel of exterior; 11, internal,</td>
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</tr>
<tr>
<td></td>
<td>showing dentine, (19483).</td>
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</table>
NO. 17. TWO SPINE ROWS IN A FLORIDA BUSYCON CONTRARIUM

By

BURNETT SMITH

September 28, 1944

Paleontological Research Institution
Ithaca, New York, U. S. A.
TWO SPINE ROWS IN A FLORIDA BUSYCON CONTRARIUM

By

Burnett Smith

INTRODUCTION

Nodes or tubercles on the shoulder angle are present in the early conch stages of Busycon. In the unchanneled Busycons the blunt nodes usually grade into relatively sharp spines on the mature shoulder angle. As a rule these Busycons have spines on the shoulder angle only. Exceptionally there may be an additional spine row. Such a row below the shoulder angle is a specific character in Busycon echinatum (Dall) (Dall, 1890, p. 117, pl. 9, fig. 2). Occasionally an extra spine row occurs as an individual abnormality in a species which normally has only the shoulder angle spines. A spine row of this type above the shoulder angle has been found in a Miocene specimen of Busycon contrarium (Conrad) and in a Pleistocene specimen of B. carica (Gmelin) (Smith, 1943). Hackney (1944, p. 143) reports similar occurrences for the Recent B. carica of the “Sound” in the Beaufort, North Carolina region. As individuals with an extra spine row, whether in Recent communities or in fossil assemblages, are associated with far greater numbers of normal individuals it is only reasonable to interpret them as freaks. In the belief that such cases should be recorded, the following note is presented.

DESCRIPTION OF SPECIMENS

The normal and abnormal specimens of Busycon contrarium (Conrad) (Conrad, 1840, p. 387; 1861, republication of 1893, p. 81, pl. 45, fig. 11) described and figured in this paper were collected at Sanibel Island, Florida, by Katherine V. W. Palmer.

In the normal specimen (Pl. 1, figs. 1-3) whorls 1 and 2 are somewhat worn but whorl 3 is sufficiently well preserved to show both spirals and shoulder angle nodes. Whorls 4 and 5 have about 15 shoulder angle nodes each; those on whorl 5 have become spinelike. Eleven shoulder angle spines are counted for whorl 6 but shell growth is estimated to have stopped at 5 3/4 whorls. Three of the spines on whorl 6 are small. On whorl 6 spirals are well developed above the shoulder angle. Spirals are also present below the angle but here they tend to weaken with the progress of the ontogeny. There are probably 6 primary spirals above the shoulder angle. On whorl 6 about 7 spirals of a later cycle or cycles have been added. Above the shoulder angle there is no one primary spiral which greatly exceeds the others in strength. This normal specimen has a
long dimension of about 159 mm. It has been considered here to facilitate the discussion of the next specimen.

In the abnormal specimen of *Busycon contrarium* from Sanibel (Pl. 1, figs. 4-6) whorl 3, though not well preserved, shows spirals and shoulder angle nodes. Whorl 4 bears about 14 nodes. At about the start of whorl 5 the nodes have become spinelike. Whors 5 and 6 have each about 14 shoulder angle spines. Shell growth is estimated to have ceased at 61/4 whorls. There are three shoulder angle spines on the quarter whorl assigned to whorl 7. The last whorl (parts of whors 6 and 7) shows well-marked spirals above but weakening spirals below the shoulder angle. At about the start of whorl 6 one spiral above the shoulder angle is seen to be much stronger than its fellows. Followed toward the aperture this relative strength increases. Disregarding very fine spiral markings this strong spiral is the sixth above the shoulder angle at the aperture. If the strong spiral is traced backward from whorl 6 it can be identified as the second primary spiral above the shoulder angle. At about 51/4 whors this strong spiral bears a weak spine whose growth line proves that it is contemporary with a much stronger shoulder angle spine. This double-spined condition of the aperture is repeated at intervals during the remainder of the animal's life. If incipient spines are counted, 15 such double-spined apertures were developed. In no case does the spine of the upper row attain the size of its corresponding shoulder angle spine. On account of aperture angulation the upper spine may be slightly forward of the corresponding shoulder angle spine. This abnormal specimen has a long dimension of about 167 mm.

**COMPARISONS**

The Recent Sanibel specimen of *Busycon contrarium* with an extra spine row has 15 spines on this row if one counts incipient spines. The Miocene example of the same species noted by Smith (1943, pp. 4, 5, pl. 1, figs. 1-3) has 13 spines in the extra row. Two of these are incipient. If the whorl counts have been estimated correctly in each case the extra spines begin a little earlier in the Recent example. In each specimen the extra spines appear first in whorl 6. In each specimen the spiral bearing the extra spines becomes conspicuous before the spines appear. The spines in the extra row of the Pleistocene *Busycon carica* described by Smith (1943, p. 5, pl. 1, figs. 4-6) appear early in whorl 7 if the estimated whorl count is correct. Counting 2 incipient spines there are 9 spines on the extra row and its spiral is conspicuous before the spines develop on it. The extra spines noted by Hackney (1944, p. 143) in Recent examples of *Busycon carica* are stated to be on the "body whorl". She writes: "Usually, **,** they are noticeable only in this position on the shell, but sometimes a definite ridge is apparent in the same relative position on the spire."

In the abnormal Miocene and Recent examples of *Busycon contrarium* it is rather surely the second primary spiral above the shoulder angle which bears the extra spines. In the Recent specimen spirals of a later cycle or of later cycles are introduced between the spine-bearing spiral and the shoulder angle. The
spine-bearing spiral thus becomes the sixth spiral above the shoulder angle at the aperture. No such addition of secondary or later spirals takes place in this part of the shell in the Miocene specimen. Here the spine-bearing spiral is separated from the shoulder angle by the first primary spiral only. The first primary spiral degenerates markedly toward the aperture.

Preservation of the Pleistocene example of *Busycon carica* is not regarded as sufficiently good to justify an attempt to determine the cycle and number of the spiral bearing the extra spines. However, there is a strong probability that this spiral is one of the primary spirals.

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## EXPLANATION OF PLATE 1 (15)

**Figure** | **Page**
--- | ---
1-3. *Busycon contrarium* (Conrad) | 3

- Normal individual with spines at the shoulder angle only; long dimension about 159 mm.; (1) nonapertural view, (2) apical view, (3) apertural view. P. R. I. No. 20038. Recent. Sanibel Island, Florida.

4-6. *Busycon contrarium* (Conrad) | 4

- Abnormal individual with two spine rows, one at the shoulder angle and the other above it; long dimension about 167 mm.; (4) nonapertural view, (5) apical view, (6) apertural view. P. R. I. No. 20039. Recent. Sanibel Island, Florida.

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Forrest Kirkland
Artist, Amateur, Archeologist, and Paleontologist
NO. 18, A NEW JELLYFISH (KIRKLANDIA TEXANA CASTER) FROM THE LOWER CRETACEOUS OF TEXAS

By

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March 15, 1945

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CONTENTS

TEXT

Abstract .......................................................... 5
Introduction ......................................................... 5
Fossil analysis ...................................................... 6
Order Trachyomedusa (? Haeckel, 1866 ................................ 7
Family Kirklandiidae Caster, new ................................ 7
Genus Kirklandia Caster, new ..................................... 7
Kirklandia texana Caster, new .................................... 7
Discussion ........................................................... 10
Neontologic comparisons .......................................... 19
Paleontologic comparisons ....................................... 26

ILLUSTRATIONS

TEXT FIGURES

1. Generalized plan of the structures of *Kirklandia texana* Caster .......... 10
2. Alternative symmetry scheme for *Kirklandia texana* Caster .............. 11
3. Detail of the "manubrial area" of *Kirklandia* ................................ 12
4. Axial section through the restored disk of *Kirklandia* ....................... 13
5. Axial profile sections through perradii and interradii of *Kirklandia* to illustrate variations in the topography of the oral surface .......... 14
6. Morphologic details of *Ptychogastria antarctica* (Haeckel) for comparison with *Kirklandia* ........................................... 22
7. Composite representation of *Rhizostomites admirandus* Haeckel of the Solnhofen Upper Jurassic of Bavaria ........................................ 34
8. Vertical sections through Narcomedusa showing the potentiality of these hydrozoan jellyfish to explain the features of *Rhizostomites admirandus*, s. s., and possibly of *Kirklandia texana* ...................... 37

PLATES

1-5. Illustrating oral and aboral surfaces of *Kirklandia texana* Caster and associated biota and Problematica.
A NEW JELLYFISH (KIRKLANDIA TEXANA CASTER) FROM THE LOWER CRETACEOUS OF TEXAS

By

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ABSTRACT

Medusoid fossils from Denton County, Texas, found in the Pearsop formation (Waschita series) of the Comanchian, Lower Cretaceous, appear to belong to the Trachylna (Hydromedusa), a group whose paleontologic record is very little known. A new family, Kirklandididae, is proposed to accommodate the new genus and species, Kirklandia texana Caster. Kirklandia is unique for America, but appears to shed light on several European Problematica of analogous aspect.

INTRODUCTION

A "letter to the editor" of Natural History from Forrest Kirkland (1941) of Dallas, Texas, first called my attention to the curious fossils to be described in this paper. He was reporting certain jellyfishlike curiosities that he and his wife had turned up in pursuing their avocation of fossil-hunting. The photographs accompanying the letter were convincingly medusoid and immediately intrigued my curiosity because of their similarity in certain respects to Problematica from the Wyoming Upper Cambrian on which I was then working (Caster, 1942).

Through Kirkland's generosity, the University of Cincinnati Museum acquired some of his "jellyfish". Cursory examination verified unique traits indicated by the photographs, and Kirkland was urged to submit the material to one of the specialists in Mesozoic paleontology for description. However, Kirkland had already recognized the importance of his discovery and had sent part of his material to the United States National Museum in the hope that someone there would find the opportunity to study it. By a chain of emergency circumstances, the job devolved on me in 1942, only immediately to be delayed by Army teaching responsibilities at the University.

The real misfortune in this postponement was the unexpected death of Mr. Kirkland. Not only was it unfortunate that he did not live to see the project completed and his opinion concerning his discovery vindicated, but it left us without adequate materials to complete the study. With all the ardor of a true amateur he had undertaken to secure new materials, most of his original collection having been generously distributed. Kirkland's early death may be in part attributable to zeal beyond physical strength.

Soon after, wartime travel restrictions were invoked, and it became imperative to assemble as much of Kirkland's original collection as possible, if the study were to be done at this time. This ganoering has proved to be a large task. But with the kind services of Mrs. Kirkland and several fossil-hunting colleagues in Dallas the search has been fairly successful, and apparently most of the original collection is now at hand. In the course of the quest, several important supplementary specimens have also come to light.
The United States National Museum material was made available through the courtesy of Drs. R. S. Bassler and J. B. Reeside, who also generously waived prior rights to describe the jellyfishes. Other specimens in the original suite were loaned by Dr. B. F. Howell of Princeton University, Dr. Gayle Scott of Texas Christian University, Dr. Archie MacAlpin of the Pan-Handle Plains Museum of West Texas State Teachers College, and Mr. F. V. Studer of Canyon, Texas. The Bureau of Economic Geology of the University of Texas, through the courtesy of Drs. F. B. Plummer and H. B. Steenzel, loaned a suite of topotype material and furnished information leading to several private collectors.

A very large part of the success of the hunt came from the wholehearted cooperation of various Texas amateur geologists. Mr. William T. Watkins of San Antonio loaned his collection of topotype material and three important natural casts from a new locality; Messrs. Fred T. Moseley and Thomas D. Copeland of Dallas made their collections of Pawpaw mollusks available. Mr. Eugene Davis of the same city was most helpful in securing new data, as were also Mr. J. P. Conlin of Ft. Worth and Dr. M. A. Stainbrook of Texas Technological College.

It will be clear from the ensuing pages that there is much yet to be learned about these curious fossils. We have had perforce to depend on materials incidentally, rather than specifically or professionally collected. And, indeed, it was not until the study was well under way that anyone was in a position to judge what supplementary structures or features ought to be sought. This is the usual difficulty in studies of the Problematica. Thorough collecting of the topotype site and the surrounding area ought to yield many new details of both disk surfaces. We need further data on the peripheral zone of the umbrella; clinching evidence of bell margin; material to settle the matter of oral arms vs. marginal tentacles, etc. Above all we need geologic data on the occurrence of the fossils, both physical and biologic. There are spoor of creeping and crawling and walking creatures commingled with the jellyfish. We need badly to know more about these associates. Such matters may well be a challenge to the enthusiastic "dry-dredgers" of the Dallas area.

The text figures were prepared by my wife, Aimeliese S. Caster, who has also assisted in the preparation of the manuscript. The cost of engraving and collotyping has been met by the Faber Fund for Paleontology of the University of Cincinnati Museum.

FOSSIL ANALYSIS

The assignment of these Problematica to the higher systemic categories is a tentative arrangement, and might even be viewed as a challenge to prove or disprove the designation. In most branches of invertebrate paleontology such assignments are in the main inferential, due to the absence of critical soft-part anatomy. In the present instance we must argue from inference and analogy all the way to specific characters. Closest contact with known organisms comes at the family level; from these similarities, in the main, the Hydrozoa and Trachylina are inferred.
Class HYDROZOA
Subclass TRACHYLINA

(? ) Order TRACHYMEDUSAE C. Haeckel, 1866

As will be brought out in the neontologic discussion at the end of the species analysis, Kirklandia does not fit with complete satisfaction in the order Trachymedesse. From familiar similarities there does not appear to be much doubt of the Trachylina assignment, but there seems to be a subordinate three-way mingling of narcomedusid, trachymedusid, and novel traits. Although currently our data require the emphasis on traits of the second category, the combination of features may eventually warrant the erection of a new order of the Trachylina. This would in all probability contain, as well, certain other fossil Problematica which are now homeless.

Family KIRKLANDIIDAE Caster, new

Since neither fossil nor Recent acalceph families will accommodate the new medusae, it seems advisable to point out their distinctness by coining a new family for them. Like the monotypic new genus, the family Kirklandiidae shares the characters of the new species, because there is now no need to stratify features. Probably one should think of the fleshy gastric disk with insert and exsert lobes, pendant sex sacs (if such they be) and absence (external at least) of mesenterial walls, as family attributes. These seem to be adequate for separating the new family from the most similar medusids, the Ptychogastridae.

Genus KIRKLANDIA Caster, new

Genotype—Kirklandia texana Caster, new species. Pawpaw formation; Washita division of the Lower Cretaceous (Cenomanian) in Denton County, Texas.

Being monotypic, the new genus shares the species traits described below. When better known, and in the eventuality that new species are discovered, the generic characteristics of that analysis probably should include the central (manubrial) zone; the orally protuberant gastric cone; the tubular (?) radial canals in the mouth vicinity; and perhaps the circlet of cesophageal outpouches. Comparisons between Kirklandia and related genera will be found at the end of the species description.

Kirklandia texana Caster, new species

Plates 1-5.

About 40 specimens of this curious fossil have been available for study. All of the topospecies, main mass of the collection, are external molds, and all but one specimen are imprints of the same side of the organism—here termed inferior. Three natural casts, presumably of the same medusae are known from a separate locality.

1 Mayer (1910, vol. 2, p. 371) defines the "Ptychogastridae" as having numerous more or less isolated clusters of tentacles some of which bear adhesive tentacles; numerous free lithostyl clubs; 8 radial canals; 4 lips; 8-lobed stomach; stomach lobes lie in the radii of the radial canals and are bound to the subumbrella by means of 8 mesenterial partitions; the gonads lie upon the stomach lobes and each is more or less divided by the mesentery so that there may be 8 double (16) gonads. These features italicized in the above description are shared with the Kirklandiidae, and bespeak the trachymedusid radicide—the one best developed in the Cretaceous fossils.

2 Named in honor of Forrest Kirkland of Dallas, Texas, original discoverer of the fossils.
The study has been greatly facilitated by the use of latex rubber casts taken from the natural molds. Most of the photographs are of such "elastocasts". In the following description, unless otherwise specifically stated, reference is constantly made to the original form of the organism, as judged from the casts.

Whatever the systematic compartment to which the fossils are eventually referred, their features are so very medioid that the coelenterate system of orientation and radial terminology greatly facilitates their description. These matters are shown on text figures 1 and 2. The plates illustrate some of the better preserved specimens and show something of the form and mutability of the material.

The fossils consist primarily of the imprints of scalloped disks ranging from 44 mm. to about 100 mm. in diameter and up to 35 mm. in thickness. Topography, proportions, and dimensions are best conveyed by the photographs. The natural and rubber casts are irregularly biconvex or planoconvex, radially grooved, and complexly inflated in the sectors, one side—apparently the oral one—being much more distended. Nearly all of the specimens show preservational distortion suggesting auctious or gelatinous flow, the while consistently showing evidence of original turgidity. Plate 4, figure 5, reveals a section of disk surface which seems to have shrunken and wrinkled before burial. Other specimens (e.g., Plate 2, fig. 2) show suggestions of what Kieslinger (1939) calls "cramp" (rigor mortis) in Jurassic medusae.

From the limited number of specimens available, it is dangerous to make very sweeping generalizations as to radial plan, especially when dealing with such variable material—and by no means all of the variation is due to geological accident. It does seem reasonably certain, however, that a basic four-part radial symmetry characterizes the "master plan", as shown in text figure 1. Probably by coincidence, the best preserved specimens adhere to this scheme. Apparently all symmetries, odd and even, from 5 to 16 are represented in the collection. These variations seem to be attributable to various degrees of fission (complete or incomplete) of the four basic radial parts. Six and especially seven radii are common. In many, if not most, specimens there is asymmetrical and unequal growth (or perhaps distortion) of the radial elements.

**Oral or subumbrellar surface.**—We have many data on the aperture-bearing side of the disks, since this is the more spectacular and consequently commoner imprint collected. The plates give the general impression of this surface. It is a billowy, out-pouched, convex surface, the central area of which is rather deeply concave. At the center of the concavity is an ovoid or subpolygonal and commonly subquadrate area of bas-relief, analogous to the manubrial zone in the simpler acalephs. This area, (the M area on figure 1) is elevated as a low mound above the general central concavity. Its center is excavated to varying depths, but usually to the common level of the concavity, in a ring fossa (Of) which surrounds a persistent and very characteristic tiny emergent cone (Co). The apex of the cone barely surmounts the "manubrial" area. Its base is about 1.5 mm. across in largest specimens. The diameter of the ring-groove
in the same specimens is about 4 mm. This annular furrow appears to represent the opening into the central chamber of the disk and probably reveals oral structures impressed against opposing aboral ones. Outside the fossa is a framing swell (Mf). The angles of this swell are slightly produced (Ol) and are seemingly a bit roughened and wrinkled, though the entire surface of the swell seems to be finely lined, parallel to the sides. The frame (Mf) is up to 1.5 mm. wide. Since the best preserved eight-part specimens show a quadrate central mound area, analogous to the coeleterate manubrium, its orientation is taken to be perradial (Fr), and other radial positions are derived therefrom as in figure 1.

Although most specimens seem to show the lobes of the disk in perradial and interradial position as depicted in figure 1, at least one specimen seems to bear the lobes in adradial positions, as shown in figure 2. In the present discussion the condition shown in figure 1 is arbitrarily chosen for purposes of description. Better material may require modification in line with figure 2. These matters in no way alter the general concept of disk arrangement, but do show the variability of the material. In this case it is probable that the manubrial quadrangle is shifted one-sixteenth of a circle one way or another by geologic distortion, and that in life was consistently in one or the other of these positions.

A few specimens, such as the one seen on Plate 1, figure 5, and Plate 2, figure 1, seem to show, most imperfectly, and not altogether convincingly, a shadowy circlet of small globular pouches or sacs (Gap) which lie contiguous to the oral fossa and apparently beneath the framing swell, wherefore perhaps their inconspicuousness. The sacs, if such they be, seem to be directed centrifugally, and probably opened on the aperture. In no specimen is the circlet complete, and the dimensions are hard to ascertain. The average “sac” seems to be about 2 mm. in diameter. The number of these ghost-pouches is likewise hard to determine, for they appear to be in series with the disk petals in some instances while in others, and perhaps this is the more common state, they appear to be twice the petal number and lie on either side of the perradial and interradial (Ir). If these writhes at the limits of perception are bona fide they fit very intimately into the trachyline hypothesis later espoused. On the other hand, they are exceptional features to-day in the Trachylina, and dissipation of the “ghosts” will in no wise jeopardize the hypothesis. Details of the manubrial region are shown in figure 3.

Leaving the manubrial swell, on the perradial and interradial of eight-part specimens, but on the primarily insert radii (see below) of all specimens, are semiterete costa, presumably radial, (i.e., canaliculate) tubular conduits (Ggo) from the ring fossa. In the largest specimens these conduits maintain their tubular state for about 5 mm. centrifugal from the swell, and then rapidly expand into the pendant pouches (Gap). Each tubule is about 2 mm. in diameter where it leaves the manubrial swell.

In adradial (Ar) position, between the elevated conduits (Ggo), and extending from the margin of the polygonal frame (Mf) are primary sulci (S). In the most perfect specimens there are eight of these. Each sulcus is centripetally expanded so as to create a stellate depressed zone (Ss) or circlet as the deepest
part of the central concavity of the disk. In some specimens the expanded sulci form depressed isosceles triangles rather than the more usual lancelate areas. Both are shown in the plates. In the archetypical (four-part symmetry) specimens the four primary sulci (primary adradii) divide centrifugally to form secondary sulci ($S_2$). The alternating four manubrium-reaching adradii expand into broad subtrigonal depressed zones ($Nr$) on the disk margin, or continue without modification as "melon-grooves" around onto the aboral side of the disk.

This is the regular plan, the oral aspect of which is shown in text figure 1. The

Figure 1.—Generalized plan of the structures of Kirklandia texana. Oral or subumbrellar view. This seems to be the basic four-part symmetry from which by asymmetrical centripetal insertion of exsert (Ex) lobes and perhaps by the splitting of the canaliculate radii the mutability of the species is attained. Exsert lobes stippled; gastrogenital pouches ruled; outermost margin entirely hypothetical. Manubrial orientation in relation to the lobes is problematical, but the condition here represented seems to fit the majority of Texas specimens. In this form there is complete schematic accord with the Trachymedusae, Ptychogastridae. See, however, figure 2. Ar- adradius; Cd- central disk (oral or gastric disk); Cm- delicate circular corrugations or rugae of the peripheral zone (possibly ring-muscles or velar muscles); Ex- exsert lobe (fails to attain the manubrial zone); Gg- internarial and perradial subteete carinae (radial canals, or gastrogenital canals); Gg- swollen protuberances on the primarly insert lobes (gastrogenital sacs on the radial canals); In- insert lobe (sector which attains the manubrial zone); Ir- internarines; M- quadrate or polygonal central elevated area of central disk concavity (manubrial zone); Mm- low carina between ovoid depressions on the swollen protuberances (possibly an internal remnant of the mesogonial wall); Nr- negative area of alternate adradii; Pd- paired depressions on the swollen protuberances (perhaps indications of the gonads within the gastrogenital pouches); Pf- peripheral field (subumbrella or velum); Pr- perradius; S- primary sulcus; Sr- secondary sulcus; St- concentric rugae of the peripheral zone (muscle traces or shrinkage lines); Ss- ray of the subcar star.
regular condition seems, however, to be exceptional among the specimens. Non-
alternative bifurcation of the basic sulci is commonplace. There seems to be an
added complicating factor of centripetal migration of the point of sulcar splitting,
so that in some instances additional sulci, originally secondary, attain the manu-
brium.

The sharp and deep sulcar furrows by splitting divide the disk into insert and
exsert lobes or "sectors". Here again the atypical (archetypical perhaps) plan
is that represented in text figure 1, with eight insert petals and four exsert. As
we have seen in the discussion above, the centrad migration of the secondary
sulci \((S_2)\) leads to an increase in the number of insert elements, and to asym-
metry or odd-number symmetry. There seems also occasionally to be an extra
exsert lobe; presumably brought about by other than original primary sulci
dividing. This radial and asymmetrical fractionation of the disk seems to be a
fundamental characteristic of *Kirklandia*. The question might arise as to how
one can distinguish between originally insert and secondarily insert lobes. This
is possible only on the basis of other symmetries or asymmetries of the disk, or
more positively where the central features are preserved. Apparently radial canals
connect only with originally insert lobes, or those derived by fission of the original

![Figure 2](image-url)

**Figure 2.**—Symmetry of *Kirklandia* disk suggested by Princeton University specimen
No. A794. In this specimen the lobes seem to lie in anadial position to the perradially
placed mouth as in the *Narcomedusa*. This is in contrast to the condition shown in figure
1, which seems to be the commoner condition of the Cretaceous material. Labels as in figure 1.
canaliculate radii. When an insert lobe does not connect with an oral duct it seems to be a fair assumption that it is a centripetal migrant. The difficulty of course comes from the fragmental nature of the material, and no great store is placed on these as the only interpretations to account for increased lobes.

All of the molds show the lobes to be broadly swollen, but the natural casts are inflated in rotund billows. The greatest inflation, aside from the pendant sacs, lies in the outer (peripheral) third. On the more perfectly preserved material the arcs of the lobation on the circumference are subequal, whether insert or exsert. In others there is a great discrepancy in arc from lobe to lobe. This, as well as the differential topography, can best be portrayed by photographs. The surface of the lobes in some specimens is closely wrinkled concentrically with the periphery. Most specimens show undulatory deformation such as one would expect of a turgid yet yielding jelly buried in sand.

Figure 3.—Detail of the "manubrial" region of Kirklandia. The possible position of buccal pouches (Bp), which seem to be faintly suggested by some of the fossils, is indicated by dotted etchels. Cf projecting central cone (probably aboral gastric wall forced downward by cone of umbilal jelly); Mf, rounded swell surrounding the ring aperture (manubrial structure); Of, oral furrow (circular mouth or stomodeum); Ol, perradial angles of the manubrium. Other labels as in figure 1.

In marked contrast to the natural casts, all of the molds (K. texana, s. s.) preserve impressions of disks which were lanceolate in axial section at the periphery, (text figure 4). One natural cast appears to be bulbously inflated at the margin. This condition is possibly exaggerated by erosion. The others are broadly lanceolate. In the molds the margins are often a bit deflexed, i. e., bent toward the
oral side. This may be a shrinkage or preservational phenomenon. The perimeter of the natural casts is smoothly rounded, with no sign of peripheral extension, cicatrice or adhesion. This smoothness is, again, quite possibly due to erosion. In contrast, the perimeters of nearly all of the disk-molds so preserved as to show this region, seem centripetally to taper off in rugose wrinkles. These intimate that the disks evanescently continued into a thinner layer of substance. Wherefore the restoration as given in figure 4:

![Figure 4](image_url)

Figure 4.—Axial section through the restored disk of Kirklandia. Known features are shown in solid outline; all others inferred from similarities to the trachyline Hydrozoa. It is quite possible that the gastric features were somewhat more inflated in life than here shown, judging from three natural casts. The natural molds, much the commoner occurrence of the fossil, suggest proportions as here shown. It is problematical how large the umbrella may have been, and whether the aboral portion shown in diagonal ruling was in life a thickly invested gastric wall or represents the shrunken umbral jelly. Ae, oral concavity (when mud-filled often forced aborally through the soft tissues to stand up as an aboral cone projecting through the aboral gastric wall). Ac, aboral (umboral) surface of the disk (supposed gastric wall); Bp, exterimities of the gastric lobes (often dependant in the molds); G, inferred internal gonads on the basis of the paired depressions (Pd, fig. 1); Gv, inferred gastric cavity; Gw, implied gelatinous umbrella; Gs, gastric wall or shrunken residue of Ga (thickness implied from evidence of rigidity in the molds and casts); Gp, oral surface of disk; Gt, umbral concavity of aboral surface. Other labels as in figures 1, 2, and 3.

As we have seen, the total number of peripheral lobes (exsert and insert) is difficult to determine due to the fragmental state of the material. Not a single mold specimen preserves the complete perimeter, and the casts are somewhat worn. Many of the specimens clearly carry more than the "basic" 12 lobes (fig. 1) (eight insert, four exsert). Some of the specimens show no exsert lobes, but this may be due to imperfect preservation or erosion on the outcrop. However, if the hypothesis of lobe increase is correct, one should expect occasionally to find an eight-lobed specimen (four insert and four exsert) as is the case. At least one specimen appears to have only six lobes and all insert. Odd numbers of lobes from 7-13 can be counted, but on these specimens it is very difficult to determine which are insert and which exsert lobes, due to their crumpled or otherwise altered condition.

The normal insert lobes are pedunculate toward the quadrate (manubrial) zone where they narrow almost to coincide with the radial canals. The calyculate or pedunculate portion of lobes in the largest specimens is about 4.5 mm. in radial length.
The most striking feature of the new medusae is the circlet of ancillary protuberances on the insert (or most insert) lobes (Gpg) of the oral surface. As seen in the illustrations, these lie on the inner half of the disk; they vary from merest mounds to enormous, pillowy, broadly sessile inflations. Most curious of all, in many specimens these structures are centrifugally pendant, stalked bags. They seem to be evaginate distentions of the radial canals (Ggc). By axial sections across several disks, shown in figure 5, the main variations in the profile of these sacs are illustrated. In a few specimens the pockets are split, two to an insert lobe, (Plate 3, figs. 2, 3) but this seems to be an aberrancy. Random lobes in many of the disks (Plate 3, fig. 2) fail to develop (or at least now to show) these sacs or pouches. Maybe they are newly inserted lobes, and had no radial canal (at least centrifugal canal) connection and were therefore sexless. In most individuals there is considerable variation in the shape of the pendent sacs, —but perhaps no more than one ought to expect considering their original substance and geologic vicissitudes. The greatest regularity of shape and size exists in the smallest disk...e.g., Plate 1, figure 4.

Figure 5.—Axial profile sections through perradial or interradii of Kirklandia disks to illustrate wide topographic variation of the oral surface of the disk. Variation within individuals and from specimen to specimen.
Several specimens (for example, Plate 2, figs. 1, 5) show small ovoid paired depressions (Pd) on the oral surface of the pendant sacs. A narrow carina separates the depressions. They appear to have been formed by differential shrinkage of the wall and may reflect the position of sex organs (G) within the sac. Perhaps the carina occupies the position of an internal wall or mesentery between the organs, separating the sac internally into two radial compartments.

A few individuals show minor constrictions of the petaloid lobes about half the distance between the pendant sacs and the periphery, thus creating tribolobate sectors, (Plate 1, fig. 3). These constrictions could have been caused by cramping of circular muscle strands in the oral wall of the disk during burial.

**Aboral surface of the disk.**—Our knowledge of this surface is restricted to what we can learn from one excellent mold and the three somewhat weathered natural casts. Probably the most inflated natural mold (Plate 1, fig. 5) gives the most faithful picture; the others, thus recalling the originals of all of the molds, were probably somewhat flattened due to shrinkage and vertical pressure. The least altered cast (Plate 1, fig. 4) shows a broadly concave, scalloped aboral disk on which the sulcation of the oral surface is repeated, except that the four primary sulci seem to cross at the center. It is unfortunate that none of the present collections establish these central relationships definitively. It is of greatest importance to note the continuation and duplication on the aboral surface of the oral sulcation plan. Therein may lie one of the most important clues to fossil affinities. (See *Rhizostomites admirandus* in the paleontologic comparisons, below). Only one out of the four aboral records at hand is well enough preserved to suggest the relationships at the center of the disk; erosion and the breaking through of oral features obscure this region in the other specimens. **Better preserved aboral surfaces are our greatest need for establishing paleontologic relationships of Kirklandia.**

One natural cast and the sole aboral mold show the broad central umbral concavity (Um), in the very center of which rises a cone. The apex of the cone is eroded away in the cast, but more completely preserved in the mold. In the latter (Plate 2, fig. 1) it shows the eight descending canals (Gge) of the oral surface, proving that they are terete tubules, as might be supposed. At the apex of the cone is a truncated quadrato area, obviously broken across. This state seems beyond doubt to have been caused by an aboral rupture of the disk surface opposite the mouth by the mud-filled central concavity (Ue) of the oral disk. Such an accident might easily arise during compaction and settling of a medusa. The cast (Plate 5, fig. 1) seems to reflect the same condition, but probably wasn't actually ruptured.

In the aboral mold the surface is more rugosely wrinkled (SL) than in the oral ones. This suggests longer exposure to the air. Differential shrinkage may thus account for the umbralulbial rupture. The periphery of the mold as in the oral disks, seems to continue into a thinner, more tenuous zone of greatly shrunken tissue.

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3 A somewhat analogous state is described by Kieslinger (1939) for radial features of medusa in the Solnhofen Jurassic of Bavaria.
Peripheral zone and accessory features.—Fragments of a thin sheet of tissue (Pij) lying outside the disk are preserved on several molds. This is concentrically rugose (Cm) in the same manner as, but to a greater degree than, the surfaces of the disks and seems to be a continuation of them, (e.g., Plate 4, fig. 5; Plate 2, fig. 5). None of the specimens preserve this zone entirely around a disk or to the original outer periphery. Thus the over-all size of the organisms and the nature of their perimeter are unknown.

Most curious of the accessory structures are molds of nodose much wrinkled sheets or columns of soft substance, (see Plate 4, figs. 1-4). Although these structures occasionally lie upon the lobate imprints, it cannot be definitely established that they were in life connected with them. The natural implication is that they were. As shown by Plate 4, figures 2, 3, the surface of these masses is closely covered by regularly ovate papilike, arranged in an irregular manner. In one specimen the masses are distributed in an arc of about the same radius as the usual disks (Plate 4, fig. 3) and in another slab (Plate 4, fig. 4) the masses seem to be in the form of eight or nine rather thick short arms distributed in an ovate plan and embedded nearly vertical to the bedding planes. On these “arms” the nodes seem to cover all surfaces. This distribution suggests that they were peripheral structures of the living organisms, possibly utriculating tentacles around the margin of a medusa bell. Some of the tiny nodes suggest a concave, cuplike surface.

Two specimens, one of which is illustrated on Plate 1, figure 6, show either arms or worm burrows emanating from the central area of the mold. In one the burrowlike structure enters the rock and its termination is unknown. In the illustrated specimen, the two “burrows” terminate in large fusiform expansions, unlike anything seen on any of the worm spoor interlacing the matrix of most slabs. Since they appear to come out of the substance of the oral surface, I am prone to consider them as burrows of scavengers which burrowed down through the buried organism and into the matrix below, perhaps to rest contractedly in the swellings now shown at the end of the mines.

A great many accessory markings occur around, upon, and through the molds, but can most readily be identified as various spoor of crawling things, probably “worms” in the main. They seem to have been made both in air, before burial of the organisms, and by mining and ingesting the matrix material after burial. Some of these are shown on Plate 4, figure 6.

Natural casts of Kirklandia.—The three natural casts discovered by Mr. Watkins were the most important new addition to knowledge of Kirklandia beyond the data contained in the original suite of specimens. The casts were picked up as loose cobbles and show signs of erosion. They are calcareous clay fillings of natural molds, apparently. As we see them now they are stained limonitic yellow from the weathering of laccings of pyrite. One of the nodules (Plate 5, fig. 3) is much more rotund and inflated than any of the previously discovered material, whereas the other two casts compare favorably
with the mold material. One specimen, Plate 5, figure 2, seems to preserve in pyrite a circular collar about the slightly elevated apertural knob (Cc). The oral surfaces are much more crushed than in any of the molds and are further altered through erosion. Some of the pyrite strands seem to follow the courses of burrows such as characterize the molds. Both exteriorly and internally (Plate 5, fig. 5) the casts recall Walcott's (1896, 1898) famous "cobble stones" (*Laetita* and *Brooksella*) of the Cambrian Conasauga shale (Coosa formation, *appendix*). However, as for the Cretaceous specimens, I see nothing in the internal motting to suggest a replacement of the original substance of the organism. Concentric and differential chemical weathering will adequately explain such color features.

**Occurrence.**—The molds are known only from the type locality, two miles west of Roanoke, Denton County, Texas. The horizon lies in the Pawpaw formation (Adkins, 1918) of the upper Washita division of the Lower Cretaceous (Comanchian). The three natural casts came from "an old brick-pit at Gainesville, Texas" (W. T. Watkins, letter, June, 1944). The Gainesville site lies in the Washita group, but there is some doubt as to the precise horizon. Neither of the sites is discussed in Winton's (1925) report on the Geology of Denton County. Adkins (1918) considered the Gainesville clay pit as upper Washita (Denton) in age, whereas Bybee and Bullard (1927) in their "Geology of Cooke County" describe the site as Weno. There is such a close faciologic similarity between the three Washita members that detailed regional studies are necessary finally to solve the problem. Mr. Watkins (letter, September, 1944) revisited the Gainesville pit to secure more *Kirklandia* casts and determine the age, if possible. He reports "I've made two trips into this hole, without scouting the adjacent country. On my recent trip I collected fossils from the heavy ledges at the top, but failed to find the fossil. *Kingena wacoensis* (Roemer) that marks the Main Street Limestones immediately above the Pawpaw, nor (did I find) the *Turrilites* that marks the Weno clay in this region. But I still don't think it is Denton." Possibly the occurrence of *Kirklandia* may prove of value in determining the age of the Gainesville clay.

**Environment.**—The molds are known only from sandstone talus, or loose rubble along the Pawpaw outcrop. From the appearance of the slabs, the molds are restricted to a narrow, cross-bedded sandstone zone in the midst of shaly or tough clay beds. The sandstone is a grayish to limonitic brown micaceous rock. Considerable pyrite seems to characterize the unweathered rock, but the principal cement is calcium carbonate. Adkins (1918, p. 26) described the Weno and Pawpaw formations as follows:

The Weno and Pawpaw formations are marked by striking lithologic changes which produce along their outcrops localized lithological regions each with a characteristic fauna. The Pawpaw formation, and to a lesser extent the Weno, passes from north to south along its outcrop through a "typical" series of lithological facies—sand-clay marl-limestone, which aside from various complicating factors of deposition is usually taken to represent a progressive series of marine facies from near-shore to off-shore conditions. Likewise the problem of localized faunas is vividly impressed upon one by the situation of the Pawpaw clay (as also in

*While this paper was in press, several additional natural casts from the same brick pit were secured (October, 1944) by Mr. Watkins, thus indicating prospects for future discoveries in this site.*
the Weno), where within a few miles one finds largely disappears and an equally rich and varied, but different one occupies its stratigraphic position . . .

The Denton County area was cited by Adkins (1918, p. 27) as characterized by the “clay with sandy layers” aspect of the Pawpaw. This facies lie thought to represent the bathyal facies of marine deposition,—unless he intended his “bathyal” notation to refer only to the “marl with sandy layers” category in his list. Everything about the specimens at hand suggests alignment with the neritic zone, and probably an inter-tidal setting.

The under surfaces of the imprint layer carry casts of “fucoids” of the worm burrow and swash-mark sort, and seemingly indicate a clay or shale material (none of which has been seen by the writer). The sandy layer itself is richly tunnelled and the bedding planes grooved by veriform burrows and trails. The molds seem to indicate quick burial and subsequent visitation by scavenging invertebrates. The crusted and shrivelled surface of the molds, especially of the side uppermost in the bed, resembles the surfaces of stranded jellyfish on the seacoast. I have seen such “mummies” along the New England coast in midsummer (see also Walcott, 1898; Kieslinger, 1930A). The disks are most commonly preserved with the inferior (oral) side up, perhaps due to the buoyancy of the various pouchees. The environment in Denton County both looks and reads very much like Walcott’s (1898) description of the Cono-sauga (Coosa) shale setting of his Cambrian Problematica, Laotira and Brook-sella.

Several specimens of the gigantic foraminifer, Nodosaria texana, have been noted on the mold slabs. Two specimens are illustrated on Plate 3, figure 1; Plate 2, figures 7, 8. According to the various students of the Texas Cretaceous, these are especially common constituents of the Weno and Pawpaw formations. Their sporadic presence has very little ecologic significance.

The only other life evidence in my hands, in association with the specimens of Kirklandia, aside from the veriform spoor (Plate 4, fig. 6), is what appears to be a single footprint (Plate 5, fig. 6) of a horseshoe crab (Xiphosura). It resembles the impression of a limulid endognath (simple chelate foot) of the sort known since Devonian times. Comparable material, both fossil and Recent, is shown in various papers by the writer (see Caster, 1944, for the bibliography). This type of imprint can be made readily on wet muddy sand in air (Caster, 1938).

Types.—Holotype: United States National Museum, No. 136131 (A); paratypes: Idem, Nos. 136131 (B, C); University of Cincinnati Museum, Nos. 22979 (1, 2, 4); Princeton University Museum, Nos. A-793, 794; 10 unnum-bered specimens from the original collection of Forrest Kirkland, on deposit at the University of Cincinnati Museum; 2 specimens from the F. V. Studer collection, Pan-Handle Plains Museum, West Texas State Teachers College; 3 specimens from the collection of the Bureau of Economic Geology, University of Texas; 2 molds from the collection of Mr. Wm. T. Watkins, San Antonio, Texas; 2 molds from the collection of Mr. Thos. D. Copeland, Dallas, Texas; 3 natural casts from the collection of Mr. Wm. T. Watkins, presumably
the same species. Elastotypes (latex casts) of all topotype material: University of Cincinnati Museum, Nos. 22979 (1a-).

DISCUSSION

Both Recent and fossil materials appear to offer valid comparisons with Kirklandia. In seeking an answer to the question: What kind of an organism was Kirklandia?—the Recent materials offer best evidence. Without exception, the fossil company belongs to the limbo of Problematica, the biological affinities of which are always under shadow of doubt. If, however, we can establish through neontologic comparisons the systematic nature of Kirklandia, it may through inference redeem certain of the problematical fossils.

Neontologic comparisons.—Algae, sponges, coelenterates, and echinoderms produce fossils or Recent lobate bodies or structures which must be considered when confronted with new and aberrant fossils of the Kirklandia sort. Any of them could have produced the soft and yielding bodies. However, the occasionally four-part radially symmetrical disk, together with the evidence (albeit scantly) of a wide and thin peripheral field which was concentrically rugose, and the central quadrate or polygonal zone so analogous to a stomad-eum and manubrium, plus radial canal-like structures emanating therefrom, seem by a compounding of evidence convincingly to bespeak the coelenterates. Differentiation into an umbrella and subumbrella surface, tough, yet yielding jelly and, curiously, the enormous potential for variability, likewise best fit the coelenterate and medusa pattern.

Of considerable importance in this primary connexion is the similarity between the Cretaceous fossils and the imprints made to-day by stranded jellyfish- es, (Caster, 1912, p. 107, f.u.). When washed shore and left stranded at low-tide in midsummer Aurelia and other meduse quickly dry on the surface and become crisply crusted above. Shrinkage tends to “cramp” (Kieslinger, 1939) the subsurface features, i.e., dehydration of the aqueous jelly brings out in surface relief embedded structures, which in life would hardly be discernible, except by transparency, on the exterior. While the upper surface is hardened, thus inhibiting dehydration, the surface in contact with the beach remains soft and often turgid as in life. Depending on the texture of the strand, the imprint made by the under surface may be faithful or indistinct. The incoming tide often picks up the partially embedded jellies and carries them further ashore, and occasionally turns them over to embed them again at turn of tide with the erstwhile downside up. In the case of the Cretaceous fossils we deal exclusively with buried meduse, many of which were apparently interred oral side up.

Walcott (1898) and Kieslinger (1930A) have very fully considered the possibilities of burying organisms, so highly comprised of water, with any expectation of their remaining intact long enough for the surrounding matrix to

5 Plaster replicas of the original molds can be furnished from these latex casts.
harden or the gelatinous substance to be replaced by chemicals in solution. However, only the former condition, simple burial and matrix solidification, seems to pertain to the present material;—as a matter of fact, the evidence for histometabasic exchange of minerals for mesoglea is very unconvincing in Walcott's Cambrian "cobbles". The calcium carbonate cement of the Pawpaw sandstone suggests rapid hardening of the matrix material, compatible with the nature of the organisms to be preserved. This does not require extraordinary rapidity of solidification, however, for firm jellies can be dug out of the tidal sands today, buried to some inches depth and apparently for much longer time than the tidal periodicity. Everything points to exceptionally tough and firm jelly in the Cretaceous fossils, thus lending greater verisimilitude to the argument.

It is significant that the best preserved molds of Kirklandia show a four-part radial symmetry. How much deviation there may be from this plan the small number of specimens and their fragmental and distorted nature makes it difficult to ascertain. No perfect individuals are known. It does seem, however, that a considerable variation from the basic, and perhaps archetypical, four-part plan occurs. Whether this exceeds the deviation in modern jellyfish, where as high as 20% (Kiesinger, 1930) are atypical, is yet to be discovered. Six-part symmetry is common among modern medusae, and odd-number symmetries frequently result from incomplete fission or vagarious nonfission of radial elements. The mere existence of odd-numbered radial symmetry in fossils must not rule out the Coelenterata in considering assignment of Problematica (for contrary opinion, see Ruedemann, 1934, pp. 28, 29 in his evaluation of Dactylocoelites). The important consideration is the existence occasionally at least of the basic four-part scheme so inherently cnidarian.

But why battle windmills? Probably nobody will seriously doubt the medusa interpretation of Kirklandia. The real question becomes: What sort of medusa was it? Acaleph plans are manifold. But their distinguishing features are of an embryological or histological sort which usually do not lend themselves to fossilization. The paleontologist barely hopes ever to find in the rocks a velum or velarium, distinguish the absence or presence of gastric filaments, or differentiate ectodermal vs. endodermal gonads, let alone see details of the highly significant marginal bodies of the umbrella, or define the character of the tentaculocysts, if present. This does not mean that the quest is hopeless. But it does mean that for paleontological purposes other characteristics than those elected by neontologists for their systematics must be sought, or certain characters reevaluated. Furthermore we must constantly remind ourselves that systematics are human fabrications, and that to most of man's rules nature offers exceptions.

When confronted with the choice of hydromedusa versus scyphomedusa, we center on the most obvious trait applicable to our materials: position of gonads. On the assumption that the pendulous sacs (GgP) of Kirklandia are sexual, there seems to be no alternative to considering them internal expansions of the radial canals and therefore with access to the exterior via the stomach (or esophagus)
and the stomadenum. This is a basic scyphozoan feature (e.g., Parker and Haswell, 1940; Hyman, 1940) in distinction from the hydromeduse which usually emit the sex products directly to the exterior. Further study brings out the fact, however, that scyphozooid internal sex ducts occur in certain hydromeduse. Moreover, eight gonad sacs (instead of four), everted (instead of inverted) and radially disposed upon (instead of between) the canals, and lying upon a similarly pouched stomach which is fed by a simple, armless mouth, belong in the Hydrozoa. The family Ptychogasteridae of the Trachylina has a most similar arrangement. It is characterized by eight gonad pouches which connect by a broad fissure with the lumen of the radial canals, thus discharging the sex products into the gastric chamber or oesophagus in a scyphozoan manner (Haeckel, 1883, p. 13).

Most Hydrozoa are tiny, soft-bodied meduses, and their chances of fossilization are almost nil. From this generalization has come the current tendency among paleontologists, such as Haentzschel (1937) and Kieslinger (1939A), to rule out the Hydrozoa from consideration when confronted with medusoid Problematica. Even the oldest known medusoids are being currently identified as members of the most specialized branches of the Scyphozoa. This tendency will be further considered under the head of paleontologic comparisons, below, but in the present connection it is significant that certain of the Trachylina are in every physical sense as available for fossilization as any Scyphozoa—and possibly more so! There is the added philosophical advantage that the hypogenic Trachylina embrace some of the most archaic living medusae. As Parker and Haswell, (1940, p. 147) and other zoologists point out, the Narcomeduse (a division of the Trachylina) have an especially tough and resistant (fibrous) jelly in contrast to other hydromeduse. Several of the living Trachymedusae grow to a diameter of four inches (100 mm.). The modern marine environmental range of the order is from the surface to very great depths, polar to tropic seas, and to extreme depths of benthonic water. In fact, the one freshwater meduse (Crasspedacusta) of fame belongs to the Trachylina. All of these factors of the Trachylina morphology and environment should make them among the more likely medusid subjects for fossilization. Consequently the current paleontological prejudice against all hydromedusae seems poorly justified.

Now let us turn to more particular comparisons, in the same sequence of details as was used in the species analysis. The single central quadrate or polygonal orifice, if stomadenum it be, is a not too common feature of mature medusae, especially in the Scyphozoa. Simple, cruciform or “iron-cross”-shape mouths are frequently developed among the trachylide hydromedusae and occasionally in the Semeostomeae (Discomedusae). In a few immature rhizostomes an open, cross-shape mouth exists during the growth of the polystomatous arms (biogenetic rehearsal). A simple circular or quadrate mouth is a medusid rarity; especially so is a nonpedunculate mouth and one without manubrial folds. Thus

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Caster, 1940, p. 13.

This trait, together with paleontologic similarities, and the influence of the trend in modern paleontology to enhance hydromedus possibilities of fossilization, led the writer orally to present a preliminary study of the Cretaceous fossils (Denison University meeting of the Ohio Academy of Science, 1942) as rhizostome Scyphozoa.
we see the condition of our fossils is not commonplace, and when we find an analogous condition in modern forms it may have considerable significance. The most telling single species sharing attributes with *Kirklandia* is *Ptychogastria antarctica* (see Pectis Haeckel, 1883, pls. 5, 6, p. 14). The more salient compar-

![Diagram of *Ptychogastria antarctica*](image)
probably also *Kirklandia*, is more like certain of the Narcomedusae. The absence of perradial manubrial (oral) folds (arms) is especially trachylinoid.

Under the head of reevaluated morphologic traits comes the tiny cone (*Cc*) emergent from the orifice of *Kirklandia*. It is perfectly duplicated in *P. antarctica* and so far as known is therein unique among living medusae. As a curiosity it has almost escaped mention in medusology. The cone is formed by the gelatinous umbrella projecting into the center of the stomach and oesophagus so as to cause the aboral gastric wall conically to emerge from the mouth when the manubrium is retracted. The mouth and oesophagus thus resemble an inverted funnel. No doubt in life the cone acted as an equalizing distributor of food drawn by suction into the gastric pouches and radial canals. The fossils show no evidence of the adradial funnels (buccal mesenteries) (*Cf*) of the Recent form.

As was indicated in the description, no brief is held for the shadowy structures labelled *Bp* (buccal pouches) in text figure 6. There is this to be said for them that they were noted before such structures were known by the writer to exist among the medusae. It is also some comfort to find that the very family otherwise most favored by these comparisons also possesses *bursa buccales*. Such evaginate structures are, however, of sporadic occurrence in both branches of the medusae, and occur most frequently in the Scyphozoa. In the Trachymedusae the pouches seem to be a specific character and eight buccal pouches are perhaps commoner than 16. Whether or not these structures "prove up" in *Kirklandia*, they in no way materially influence the current hypothesis.

The "tubular" canals (*Ggc*) of the fossils are the same in position and relation to mouth and manubrium as the descending canals (*Ggc*) of the Trachymedusae (*Ptychogastria*, text figure 5). Again we are confronted with a character uncommon among the acalephs. In the Scyphozoa the radial canals are so deeply invested in jelly and so flabby and flattened as hardly to invite fossilization, even by "cramping".

Likewise in *Ptychogastria* and allies the radial canals expand at some distance from the manubrium into swollen stomach pouches, often quite irregular (figure 5), upon which out-pocketed genital sacs are produced in the same manner as in *Kirklandia*. Gastric sacs are no rarity among both medusa lines. Ancillary genital pouches are another matter and are apparently confined to the psychoastrid trachyelines.

The paired depression (*Pd*) which many of the fossil genital sacs carry are suggestive of the gonads which lie within modern genital expansions. In the Ptychogastriidae stout mesogonia or genital mesenteries (*Mg*) externally anchor the genital sacs to the cœlumbrellar surface and internally separate the gonads within the genital pouch. No evidence of external mesogonia is known in *Kirklandia*, but the narrow carina between the two depressions may reflect its posi-
tion inside the genital sac. At any rate, the gonads in the fossil presumably number 16, thus paralleling the Recent species. Possibly this condition was sometimes carried to the unusual extreme of creating a separate pouch for each gonad, thus explaining the state seen in Plate 3, figure 2, where there appears to be a pair of pendant sacs on each insert petal.

In plan, therefore, the fossil and the genus Ptychogastria are quite similar. In details, other than those mentioned, there are notable differences. First, the gastric disk of the Recent genus (and family) is not toughly and thickly invested with jelly as the fossil must have been. Second, the areas between the gastric pouches are broad, and in no sense sulci as they appear in the fossils. Third, the gastric and genital pouches in the Recent form are quite irregular and may even be multicamerate or labyrinthine which is in marked contrast to the simplicity of the fossils. Fourth, location, and (fifth), in fact a true disk are unknown in the Recent forms. Herein lie the chief bases for a distinct family and possibly even a distinct order within the Trachylina for Kirklandia. There are certain features of Kirklandia which recall the Narcomedusa as well as the Trachymedusa.

The longitudinal sections across the gastric lobes (text figure 5) seem to indicate that Kirklandia had a moderate to large gastric cavity (depending of course on the unknown thickness of the tough investing jelly). In inferred shape it is apparently similar to some of the Narcomedusa. The aboral concavity of the central disk, shown so well in the natural casts, is likewise suggestive. (See for example, Polycolpa, Parker and Haswell, 1940, p. 148, fig. 117). In other respects, such as the coronal tentacles, Kirklandia fails notably to parallel the narcomedusids, unless by chance the basic four exsert lobes might by some far chance represent the anchorage of the roots of the tentacles upon the disk. Why such anchorage should be reflected on the oral surface, as the insert lobes are, would be a real difficulty. Much more probable is the chance that the narcomedusids have some bearing through areas lying outside the main disk (e. g., one such structure may appear at the top of Plate 2, fig. 5) so poorly known as to escape description previously, but possibly analogous, if not homologous, to the four so-called genital plates of jurassic Rhizostomites, considered later. Here again, for Kirklandia at least, such external areas are too poorly known to make their mention more than intuitive.

The meaning of the exsert lobes, so long as structures in any sense comparable have never been described for Recent medusa, is yet to seek. They may be swollen centripetal canals leading inwardly from an unknown circular canal. They may be mere thickenings of the disk wall between the gastric pouches, or they may have internal radial connection with the esophagus but are in that case anomalously deficient in gonads. But all of these are sheerest guesses. The exsert lobes must rate as a primary trait of the new family.

The supplementary structures, shown on Plate 4, figures 1-4, carry tiny clusters of nodules much resembling urticating nodes of medusa. Associated with them seem to be other nodes having a concave outer surface. Together the pic-
ture seems most to resemble the umbrella margin of certain of the Trachymeduse. Comparable structures are sketched in text figure 6, E. Perhaps the most significant feature of these cnidarioid structures is the circle of 8-9 columns shown on Plate 4, figure 4. If these pertain to our specimens, as they probably do, they may represent peripheral expansions of the characteristic marginal location of the Trachymeduse. It is not unreasonable that the suggestions of nettle clusters such as occur on the margin of Ptychogastria (fig. 6) were expanded into pendant stinging tentacles in certain related forms. Deep invaginations of the umbrella characterize many, if not most, Trachylina. Until we can establish the attachment of these nodose structures to our disks, however, the conservative course, shown by the restoration on text figure 4, is the safer one.

We should also in passing consider the possibility that these columns are rhizostomatous mouth-arms, and that the European students of Jurassic (Solnhofen) meduse (Rhizostomites) have been right in assuming, utterly without evidence, that peripheral polystomatous arms were somehow attached at the margin of lobate disks somewhat analogous (if not homologous) to ours. The present structures seem to be too short, much too firm, too little varied, and too lacking in ramifications, not to mention multiple mouths, very conveniently or convincingly to fit the diaphanous rhizostome pattern. Moreover Kirklandia’s functional central mouth with evidence of a manubrium, etc., would seemingly offer strong opposition to the idea that it represents so advanced a rhizostome condition as marginal arms would imply. For such well-developed arms we would expect firm attachments on the disk margin. Their complete absence suggests that the nodose structures pertained instead to the peripheral field-margin, the perimeter of which has not thus far been seen.

To be sure, the mere absence of arm scars shouldn’t deter us as paleontologists from making Kirklandia a rhizostomatous Scyphozoan if we choose. Rhizostomites has never yielded arms or scars of arms either. Moreover, the precise pattern of sulcation seen on the aboral surface of the Kirklandia disk has often been offered as incontestible evidence of the rhizostome alliance. In order thus to translate our material we would have to interpret (as is customary among rhizostome students) the sulcations as the healed furrows made by the growing together of the extended corners of the cruciform scyphozoan mouth. At the end of each furrow there should be found (but never is found in the fossils) an arm scar or fragment. Thus the aboral disks of Kirklandia are similar to the supposed oral disks of Rhizostomites (see Plate 5, fig. 4). The trouble lies in our knowing too much about Kirklandia: the oral surface with a central, functional, and unique mouth is preserved. European colleagues might do well to institute a search for impressions similar to our oral surface in their great store of Rhizostomites material, (and, as we will see, below, such material has in all probability already been described but not correlated with the famous medusa).

If the sulcations of Kirklandia were not developed on both surfaces of the disks, and if they were irregular instead of clean-cut, and if no central mouth with a manubrium about it were present, then the rhizostome argument might prevail. But these conditions have never been met in full by any fossils.
The planate and concentrically rugose zone lying outside the *Kirklandia* disks is similar to the impression made by the cramped ring-muscles of a medusa subumbrella. This is the likely explanation especially when the peripheral zone is adnate to the rim of the disk. In other specimens where the zone is free, there is no proving that it is not part of a velum, since well-developed pendant vela are present in the Trachymedusa.

In summary then, we find that a survey of existing jellyfish shows greatest resemblances to our fossils to lie in the radicle of the psychogastriid Trachymedusa. Similarities in plan are close enough to offer strong inference of subclass (Trachylina) alliance. Differences in detail make assignment to order (Trachymedusæ vs. Narcomedusæ) less certain. There seems here to be rather a possibility of mixed attributes plus certain new traits, such as the heavily invested, lobate disk, requiring for the fossils a separate order. Assuredly, there is every justification in view of these differences in proposing the new family Kirklandiidae as we have done. Certain of the fossil Problematica discussed under the next heading may be assignable to the new family, or at least to the new order when it is proposed.

*Paleontologic comparisons.*—Many medusoid fossils have been described, but it is doubtful if a single one has been definitively identified as to systematic position. These constitute our Problematica par excellence. We must not hope therefore for light from this quarter upon the biologic alignment of *Kirklandia*. Instead, the exceptional details preserved on the new fossil may help in a better understanding of somewhat analogous Problematica,—all of which have been interpreted quite differently from the present fossils. We are very fortunate in having two modern papers by Dr. Alois Kieslinger in which knowledge of the fossil medusoids is systematized. From his excellent Scyphozoa chapter in Schindewolf's (1930) "Handbuch der Paläontologie" and the bibliographic references in his previous (1924) "Medusae Fossiles" in "Fossilium Catalogus" the following Problematica have been selected for similarities of one sort or another to *Kirklandia*. All of these medusoids are lobate, and all appear to be coelenterates.

*Doctyloides asteroides* (Fitch, 1850), Hall, 1886. Lower Cambrian, Vermont.


*M. princeps* (Torell, 1876). *Idem.*

*M. radiata* (Linnaeus, 1871). *Idem.*

*Palaosemecostoma geryonides* (von Huene, 1901), Rüger-Haas, 1925. Middle Jurassic, Germany.
*"Problematische Form" Ulrich, 1893. Devonian, Icla shale, Bolivia.

*Medusina liasia* Küger-Haas, 1925. Middle Jurassic (Liassic G), Württemburg, Germany.

*Medusina (Craspedonites) deperdita* (Beyrich, 1849), Haeckel, 1886. Upper Jurassic, Solnhofen shale, Bavaria.

*Acraspidites antiquus* (Haeckel, 1866). *Idem.*


*Peytoia nathorsti* Walcott, 1911. Middle Cambrian, Burgess shale, British Columbia.

*Lorenzina (Bassiania) moriae* (Renz, 1925) Kieslinger, 1939. Upper Cretaceous, Greece.

*Lorenzina (Hollites) zitteli* (Maas, 1902), Kieslinger, 1939. Upper Cretaceous, Moravia.

*Rhizostomites admirandus* Haeckel, 1866. Upper Jurassic, Solnhofen shale, Bavaria.

(Rhizostomites lithographicus Haeckel, 1886). *Idem.*

(Hexarhizites insignis Haeckel, 1870). *Idem.*


Those forms preceded by an asterisk (*) are in Kieslinger’s (1939A) list of Lucertae Sedis of probable scyphozoan (if medusan) affinity. All other forms have been variously assigned within the Scyphozoa by Kieslinger and his predecessors. The species listed in parentheses are referred by Kieslinger under synonymy of the first species listed above without parentheses. We will consider these species in the order of listing.

As I indicated in the preface, similarities to Walcott’s (1896, 1898) Cambrian “cobbles” first attracted me to the Cretaceous imprints. In reality, I was impressed by the similarity between a symmetrical lobate impression of the Upper Cambrian of Wyoming, which I (Caster, 1932) inferred to be referable to Walcott’s Alabama “genera” and the Cretaceous imprints. As the photographs show, the natural casts are especially reminiscent of Brooksella and Laetia. Any comparisons are based on the assumption that Walcott’s specimens are natural casts (or perhaps as he thought replacements) of the organisms, and not concretionary caricatures, as so many of his cretaceous specimens suggest. The range of morphologic variation in the Cambrian material far surpasses the Cretaceous, and is perhaps somewhat concealed by Walcott’s two arbitrary form genera where apparently only one such genus or a welter of “genera” would suffice. As for Walcott’s hypothetical interior structures, they are far from established; likewise his whole argument on molecular replacement of mesogloeae. Nothing which Walcott shows by way of substantiation but what could apparently have been caused by concentric and differential chemical weathering of an occasional nodule. There is no gainsaying, however, the remarkable similarities that exist between some of Walcott’s transverse sections and the Vermont Dactylolidites asteroides.
Brooksella embraces the less variable Coosa material and, therefore, the forms most like Kirklandia. The most symmetrical specimens are swollen disks proportionally quite like the Cretaceous natural casts. Radial sulci divide both surfaces of the disks into swollen pouches, with deep, melon-like peripheral grooves. Some of the Cambrian specimens are very simply lobed (e.g., Walcott, 1898, pl. 1, figs. 1, 2). Others, such as his plate 1, figures 3, 3a. show supplementary, incomplete lobes in the main sectors radiating from the central zone toward the periphery. These Walcott calls canals or arm lobes. They occur on either or both surfaces of Walcott’s specimens. Several of Walcott’s specimens (for example, pl. 1, figs. 1, 2, 3) show a deep central concavity. This he thinks is a relic mouth structure. In many of Walcott’s specimens deep dimples are invaginated in the ends of the lobes, thus fortifying his idea that they were originally radial canals or arm canals. Unfortunately we know these structures only from drawings. Walcott worked with such a plethora of material (over 10000 specimens) and all of it so extraordinarily variable, that almost any preconceived pattern of variation ought to have turned up. Some of his supposed tube openings lie in such a position that they recall the Pit, perhaps gonadal, structures of Kirklandia.

Although I am inclined to the belief that Walcott’s material is ctenedentate, and medusid, I cannot see in it any verification of his rhizostome hypothesis, and I think Kieslinger (1939, ) is on pretty thin ground even to impugn them the possibility of being exceedingly primitive rhizostomes. On the other hand, I am not sure they belong to any existing group of acalps. Any similarities to Kirklandia, and there are several striking specimen similarities, I am inclined to call fortuitous. However, I see no insuperable reason why such a form as Kirklandia might not readily have “crystallized” out of the mutative Cambrian “cobbles”. “Order out of chaos” does seem to apply in certain groups of organisms, and to none better than the still highly variable jellyfish, both craspedote and acraspedote. Perhaps a separate class of medusa, which we might call the Protomedusace (first), would best accommodate Walcott’s protomedus horde.

Dactyloidites ascroboites (Fitch, 1850) is probably of the same fabric as Walcott’s forms, and would seem to have the same bearing (if any) as they upon Kirklandia. It seems to be a gastric filling and apparently shows radial canals and swollen stomach lobes. Ruedemann (1931) thinks another explanation for these Problematica is to be sought.

Spatamopsis costata Torell (1870) (Medusina costata auct.) is a curiously
lobate medusoid from the Lower Cambrian of Sweden and Estland which is probably not assignable to coelenterate class either. It is a pyramidal and narrowly radially costate fossil. Walcott (1868) and Kieslinger (1938A) supplement the original illustrations. *Spatangopsis costata* carries from 4-6 radii. No pouches or lobes are known. Kieslinger (1939A) identifies this as the internal gastric mold of the form described by Torell one page earlier (1870) as *Protolyellia princeps* and in 1871 redescribed by Linmarsson as *Astylagnosta radiata*. If Kieslinger is correct, and there seems to be no reason to doubt him, this Swedish fossil has no bearing on *Kirklandia*, for the “species” based on the umbrellar portions show a large number of moniliform radii on the subumbrella (?) (Nathorst) and according to Kieslinger, on the aboral umbrella also. The so-called umbrellar portions are preserved as doughnutlike rings in the center of which the gastric fillings have been seen, although originally found separately. The features as presented by Kieslinger are anomalous, for the umbrellar portions are reminiscent of the equatorial (Leptomedusae) (except for the duplication of the beaded feature in both disks) whereas the gastric mold, with a cruciform mouth and swollen stomach, resembles the Scyphozoa (intermediate between the Semecostome and the Coronata, Kieslinger thinks). Considering this conflict of evidence, we cannot even admit the Swedish fossils as craspedotes at this time. They are, however, no better craspedotes, and again intimate the possibility of early coelenterate classes and orders very different from those now living. There are no tangible features in common between Walcott’s Cambrian “cobbles” and the Swedish fossils.

The Paleozoic and Mesozoic group of Problematica which Kieslinger (1939A) sets aside as the “form-group of *Paleosemecostoma geryonides*” (probable Scyphozoa) contains some of the most telling similarities to *Kirklandia*. All are small wheels, 3-6 cm. in diameter, divided by incised radii into pillowy sectors grossly analogous to *Kirklandia*. Most, if not all, show a circular central area, sometimes sharply defined by a ring-sulcus. A few have accessory aboral pillows on the main sectors, thus closely simulating *Kirklandia*. There are great differences within the group, however, and from *Kirklandia*. Most notable over-all distinction lies in the absence of extant lobes of the disks and no evidence of a polygonal or quadrat central zone. Almost all other features of *Kirklandia* are duplicated within the group as a whole.

anteceplent form genera. It is proposed that the first species to be considered by Walcott, *Spatangopsis (Medusea) costata* (Torell) be considered the genotype. This is, however the monotypic genotype of Torell’s *Spatangopsis* (1870). Furthermore, the second species considered by Walcott after his proposal, *Protolyellia (Medusea) princeps* Torell (1870), Kieslinger (1938A) says positively is the umbrellar cast of the same medusa of which *Spatangopsis* is the gastric mold. *Protolyellia*, of which *P. princeps* is the monotypical genotype, has one page priority over *Spatangopsis*. Hence *Medusa* Walcott (1898) equals *Protolyellia* Torell (1870). Due to the very peculiar morphology of Torell’s genus it must for the present be restricted to the genotype and its synonym *Spatangopsis costata*. Probably more is lost than gained by such a suggestion as Walcott had in mind, anyway, and the passing of *Medusa* is a good thing. Individual form genera tailored to the peculiarities of Problematica are to be preferred to all-embracing “genera” which imply a greater degree of relationship than is known.
Oldest problematicum of the group is an unnamed petallate disk (cast) from the Devonian 1ca shale of Bolivia (Ulrich, 1893) which Kieslinger (1939A) re-illustrates. It is 33-34 mm. in diameter and is symmetrically and regularly divided into 12 sectors. The center is elevated into a tiny mound on which the sectors lose their identity. An irregular central depression occupies the position of a central mouth. Since it has neither a manubrial zone nor any signs of ancillary genital lobes or exsert petals, there are no close grounds for comparison with Kirklandia.

The English Gothlandian radially grooved disks named Actinophyllum plicatum by Phillips and Salter (1848) and reconsidered by Straw (1926) carry 32 sectors, or thereabout, and may have a central orifice. Like Ulrich’s problematicum, they are only remotely to be compared with the present fossils.

Peytoia nathorsti Walcott (1911) from the famous Burgess Pass Middle Cambrian also has 32 sectors, but they are divided into quadrants of seven each with four somewhat larger and radially longer inserts between the quadrants. The center of Peytoia is more ragged and less circular than subquadrature, in further contradiction from the Bolivian cast. The general unlikeliness of Peytoia to Kirklandia is patent.

Kieslinger did not include the last two forms, above, in his “form-group”, although they share the same general plan, except for a greater number of sectors. In the case of Peytoia everyone who has discussed it has considered it to be a true jellyfish. Ruedemann (1934, p. 30), for example, says, “. . . Peytoia nathorstii (pl. 11, figs. 1, 2) described by the same author from the Middle Cambrian Burgess shale is an undoubted Scyphomedusa”. Walcott calls it a medusa and makes no further interpretation, aside from comparing it superficially with the Swedish Medusina costata (see above), which he previously (1898) had accepted as a Scyphozoa. There are no significant resemblances, and even if there were, we have already seen that they would not necessarily spell Scyphozoa. For the moment it is apparently safe only to interpret the Burgess specimen as a medusa, class undetermined. The similarities are fully as much with the Hydromedusa as with the Scyphozoa. Mainly we need more knowledge of the extremely rare Peytoia.

Von Huene’s (1901) lobate medusoid, Palaeoseaeostoma geryonides, from the Alpha and Beta Dogger of South Germany is a perplexing fossil. Eleven or twelve pillowy sectors sharply defined by deep narrow furrows lead to a circular depressed central (mouth?) area. Around the circular mouth (?) rises a sharp narrow collar. The floor of the mouth (?) depression seems almost always to be floored by a lowly convex surface. The lobation extends around the rounded sides of the disk and on the aboral side there is said to be a central hollow stem some 1-2 cm. in length. No exsert sectors are known, and homologies of neither the quadrate zone nor the genital sacs in Kirklandia are known. What similarities exist are apparently accidental. Kieslinger does not attempt to place P. geryonides in the scheme of coelenterate classification, aside from his general assumption that it is a scyphozoan. In evaluating this form and also the following Medusina liasica, it might be well, as Von Huene (1901) inferred, to keep in mind
the stolonal larvae of such modern Narcomedusae as Cunecenthia kollickeri (see, for example, Mayer, 1910, vol. 2, pl. 54, fig. 8). The shape, modus vivendi and proportions of this modern medusa are certainly intimate of relationship.

Medusina lassica Rüger-Haas (1925) of the German Gamma Lias is too poorly known for more than cursory comparisons. It is a large form, 6.5 mm. in diameter, and shows 10 pillowy sectors of the P. geryonides sort which nearly attain the middle. If at all comparable with Kirklandia it would be with the aboral surface of the disk. Apparently only one surface is known in the Lias form.

Deyrich's (1839) Acalephus deperditus was the first medusa to be named from the Solnhofener Hattenkalle of Bavaria. Reference to Walcott's (1898) and Brandt's (1871) illustrations of C. deperditus shows a medusoid rosette of eight moderately distended sectorial pillows or pouches adhate to a central ring zone in the center of which is found a large circular depression. Brandt showed that the radial sulci separating the pouches do not reach the central depression as Haeckel had previously thought. These disks are quite similar in superficial aspect to Kirklandia but differ in the absence of any exsert disk lobes, a circular rather than a quadrante central area, and in the absence of analogues of the Kirklandia genital sacs. The sulci between the eight petals of the Jurassic fossil are somewhat broader than they are in Kirklandia.

Although placed in the form-group of P. geryonides by Kieslinger (1939A), the general pattern of C. deperditus is much more comparable to certain of the Trachythemusae, as Haeckel (1865) thought, than to the presently constituted Scyphozoa. The evidence of a simple pouched stomach and large central, circular opening fit the Trachymenidae as Haeckel first believed. How to make them approach the aequorids, as now conceived, with their large number of simple radial canals along which the gonads are distributed, the unpouched stomach, etc., Brandt (1871) failed to show. The large round mouth or gastric aperture is especially important in distinguishing between the Trachynemidae and the Psychogastriidae in the Trachyuemusae. Hallicretus racovitza (Maas) of the trachy- 

2 Since the name Acalepha was proposed by Eschscholtz (1829) for the entire medusoid colorate part of Lamarck's Brandtia, it has never been available for generic usage. For Beyrich's "pouched medusa" Haeckel (1866) proposed the genus Trachy- 

nemita. (1800) was a substitute name proposed when he changed his interpretation of the fossils and is, of course, a synonym of Trachy- 

nemida. (1871) studies of C. deperditus led him to make comparisons with the lentomedusid family Aequoridae rather than the Trachymenidae (Trachythemusae) toward which Haeckel (1860) had pointed. The basis for this change of view is not clear, but apparently Haeckel didn't choose to delate the matter and abandoned both his committal names for this species in favor of the noncommital Medusites in his 1880 list of world fossil medusae.

10 Never having been confronted by the clear-cut evidence in Kirklandia that the swollen sectorial lobes (and genital pouches of that genus) are expansions of the radial canals, and not interradial zones, Brandt (1871), Haeckel, and many others since, correlated the sulci with the canals. This misconception is at the base of much of the confusion which these early students (and some recent ones as well) bequeathed us. Thus Haeckel (1856) imagined "spindle-shape" sex bodies along the sulci of Acalepha deperditus which Brandt subsequently disproved, the while clinging to the bin of radial sulci. It would probably be a safe rule henceforth to assume, subject to disproof, that the lobes of all Kirklandia-like Problemata are radial and the sulci or furrows are interradial.
which the gonads are developed. The absence of oral peduncle and lips (oral folds) also fits the Jurassic fossils, in accordance with Haeckel's perspicacious original views.

Acraspidites antiquus (Haeckel, 1866), also from the Plattenkalke, shows a double series of eight swollen sectorial sacs. These are at least schematically analogous to the gastric and gonadic pouches of Kirklandia. The central circular area of A. antiquus is somewhat larger proportionately than in the associated Craspedonites deperditus, and the ancillary (gonadic?) pouches are a new feature in A. antiquus. Beyond the disk there are two concentric zones of ring-muscle imprints. The chief differences from Kirklandia are the large and circular central area of A. antiquus, its complete absence of manubrial structures, contiguity of its inner circle of pouches, complete lack of tubular canals, and,—possibly most significant,—lack of exert lobes.

These differences from Kirklandia seem to be well within the possibilities of the Trachymedusa. Much though we must respect the genius of Haeckel, it seems unfortunate that he placed A. antiquus and Craspedonites deperditus so far apart in classification. I fail to see any virtue in comparing A. antiquus with the Pelagide of the Discomedusae (Semaestomeae), at least as that family is understood to-day, (Mayer, 1910, vol. 2, p. 359). Kieslinger's inclusion of both these species in the P. gyrogyodes form-group intimates closer alignment of the two forms, even though neither seems to show the true jellyfish features which he implies for the entire group. It is probably safe to predict that future study will unite A. antiquus and C. deperditus as a single species. From similarities to the general scheme of Kirklandia, it is possible that A. antiquus represents oral imprints of a medusa the aboral gastric surface of which is imprinted as C. deperditus. The two forms bear to each other the same relationship as the two sides of the Kirklandia disk. Both forms are easily fitted into the Trachymedusa, family Trachymedidae. To be sure, none of the modern species within this family (at least as known to me) develop genital outpouches on the gastric (radial) canals. However, the gonads are so situated on the canals as conveniently to stimulate such growth, as it is assumed they did in Kirklandia, and as they do in the Physogastriidae.

Of less direct, demonstrable bearing, but of great interest, is the Solnhofen Jurassic medusa, Medusina bicincta (Haeckel, 1869), referred by Kieslinger (1930A) to a group of "medusae of uncertain affinity". This form is characterized by an "iron-cross" pouch structure in the center of which apparently occurs a circular depressed (mouth?) area. Alternating with the four "iron-cross" pouches which attain the central area are four somewhat broader, and apparently non-pouched, exert "quadrants". This is a very small disk, and contrary to Haeckel's (1866) and Ammon's (1886) opinion, it may be an early stage (or ephelic ancestral relic contemporary) of C. deperditus. It may also shed some light on the origin of the lobation in the whole Trachymedusa line, and possibly even account for the basically four exert lobes in Kirklandia. All this is speculation, of course, but it might be supposed that in youth and ancestry Kirklandia

11 They apparently thought of it as an acoelopedont, probably related to Acraspidites; in 1869, however, Haeckel pointed out supposed similarities to Aculepea deperdit.
began with four radial canals leading centrifugally from the center gastric area. These developed into the four basic gastric lobes in accordance with familiar traits. Subsequently, in customary medusa manner, each primordial canal split into two; this was probably a distal split which progressively migrated centripetally until the stomadeal area was attained and the system of eight discrete canals of average adulthood formed. The original nonpouched exserts remained exsert, but were forced by inflation and investiture of the radial elements into smaller centrifugal space than was theirs originally. Supplementary exsert lobes might be developed either by a sexpartite variant, or irregularly by expansion of a secondarily interradial element. Walcott (1898, pl. 45, fig. 2) illustrates *M. bicinta*. Like the other two members of the Solnhofen triad, the safest assignment of this form seems to me to lie with the Trachymedusae, and possibly in the Trachynemidae.

We now pass to comparisons with forms assigned with fewer reservations by Kieslinger (1939A), and most of his predecessors in the study of fossil medusa, to definite lines within the Scyphozoa. *Basseaia morea* Renz (1925) of the Upper Cretaceous of the West Peloponnesus exhibits a double circlet of 22 bulbous sacs arranged in concentric circles. What these may be and whether they are connected, and if radial or interradial, is not known or determinable from the material thus far discovered. The inner circlet of bulbous sacs is reminiscent of our Cretaceous fossils, but in the greater number of elements in each circlet and absence of definite lobes or canals we find insuperable differences. Kieslinger's reference of *Bassseaia* to the Atollides is a hazard worth making.

*Atollites zitteli* Maas (1902) occurs in the lower chalk of the Carpathian Wernsdorfer Schichten (Mähren und Schlesien). It comprises scalloped disks with 17 or 18 pouched petals, some of which seem to be without central connection and thus resemble the exsert lobes of *Kirklandia*. The greatest inflation of the sectors occurs in the peripheral half. The central half of the disk is a flattish depressed zone across which elevated tubules (as in *Kirklandia*) connect the swollen petals with the central opening. There appear to be a few swollen petals, perhaps analogous to the exsert ones in our fossils, which have no tube connection. A narrow circular zone surrounds a tiny central aperture. A few petals seem to show minuscule swellings just peripheral of the canal junction. From this it is obvious that a large community of gross characteristics link *Atollites* and *Kirklandia*. This Carpathian genus is unique among comparative materials in showing tubular canals leading from the orifice area to the expanded lobes, thus once again demonstrating the radial instead of interradial position of the expanded portions. It is seriously to be doubted if *Atollites* is related to the Recent genus *Atolla* or the Atollideae. Such assignment entails the assumption that the *Atollites* lobation is equivalent to the marginal lappets of the Coronata. This is most risky when we see such clear-cut evidence in *Atollites zitteli* of gastric connection of the lobes via the tubular canals. The plan is better suited to the trachymedusoids herein espoused. This argument seems likewise to apply to *Atollites minor* Maas a consociate of *A. zitteli*. Both may eventually find their niche in the same order as *Kirklandia*. 
Kieslinger places Bassenia and Atollites as subgenera of Gabelli’s (1906) Eocene genus Lorenzinia, typically of the Apennines (L. apenninica Gabelli, genotype). Truth is, Gabelli’s forms are too problematical to make such assignment more than speculative. He dealt with concentric circlets of fusiform or ovoid imprints, apparently without any good evidence of animal or vegetable origin, let alone cedenterate proof. They **might** be atollids, or a dozen other radial organisms. *Atollites zitteli* is especially infelicitously submerged in this form-genus, with which it shares virtually nothing but radial symmetry and a possibility of similar lobation. No comparison between *Kirklandia* and *Lorenzinia*, s.s., seems profitable.

Figure 7.—Composite representation of *Rhizostomites admiranda* Haeckel of the Solnhofen Upper Jurassic of Bavaria. Sm, centric (aboral) crossing of the primary sulci; S, excent lobe; *L*—*L*—, margin of inflated part of gastric disk; D, shadowy imprints on a single specimen; *Pn*—*Pn*—, marginal lappet; *Pr*—*Pr*—, aboral gastric zone; *Pq*—*Pq*—, periphract of gastric surface; *Pr*—*Pr*—, peronal canal position; *Pr*—*Pr*—, position of personal notch; *Pr*—*Pr*—, ring muscles; *Sm*—*Sm*—, smooth zone between central and peripheral umbrellas; *S*—*S*—, primary sulcus; *S*—*S*— , secondary sulcus; *S*—*S*—, centrifugal extension of secondary sulcus; *Te*—*Te*—, primary tentaculocyst position; *Te*—*Te*—, secondary tentaculocyst position; *Te*—*Te*—, possibly teatqual body upon aboral gastric surface; *Te*—*Te*—, possibly zone of muscular adhesion lateral to tentacle root on aboral gastric surface; *Vm* umbrelle (peripheral zone). Drawn from United States National Museum specimen, No. 35778 (hypotype) and Walcott (1898), Brandt (1871), Ammon (1886), and Kieslinger (1930A).
Our final comparison offers both greatest prospects and gravest difficulties,—though possibly more of the latter are scriptural than morphologic. No fossil jellyfish can compare with *Rhizostomites admirandus* from the Solnhofen deposits either in perfection of preservation or ubiquity of discussion. Apparently nobody has ever doubted Haeckel’s (1866) original assignment, as the name implies, to the rhizomatous Scyphozoa. Yet to the central area of this jellyfish our new material bears such important similarity as to make it incumbent upon us to reconcile, if possible, the ideological differences between the two. But first, a résumé of the Jurassic fossil. In addition to the various original sources, Walcott, (1888) and the two 1939 papers by Kieslinger, should be consulted. The work of the latter has greatly clarified our knowledge of the jellyfish by an ecological approach which has resulted in a healthy reduction in number of genera and species of Solnhofen medusae.

As shown by the species of medusoids in parentheses under *Rhizostomites admirandus* in the foregoing list, Kieslinger’s synonymy includes three supposed genera and four species of Jurassic forms. The last three forms of preservation do not especially concern us, since they are of no direct bearing on *Kirklandia*. Nor will we attempt to appraise Kieslinger’s arguments for including them under *Rhizostomites*. *Hexarihizites insignis* Haeckel (1871) has been considered, without dissenting vote, a six-part variant of *Rhizostomites admirandus* ever since Ammon’s (1886) revealing study. There seems to be no doubt that Haeckel (1866) was correct in reevaluating his (1866) *Rhizostomites lithographicus* as a preservational phase of the central region of *R. admirandus*. All subsequent students of the Jurassic medusa have agreed.

The features of *R. admirandus* are shown in outline by text figure 7 which is taken from a photograph furnished by Dr. R. S. Bassler of a specimen in the U. S. National Museum collection. This specimen was also illustrated by Walcott (1888, pl. 41) in his great monograph of “Fossil Medusae”. Marginal features are taken from studies by Brandt (1871).

*Rhizostomites* reached gigantic proportions for fossil medusae; specimens in the Solnhofen deposits attain 40 cm. in diameter. The central disk area of typical forms (including *R. lithographicus*) is characterized by four deep sharp primary sulci (*S*) which cross at the center. About halfway to the perimeter of the main disk these bifurcate into secondary sulci (*S*₂). The areas between the sulci are moderately inflated into four insert (*I*) and four evert (*E*) lobes. Lying outside the main, inflated disk are four subtrigonal areas (*Tn. Tum*) with a middle elevated, ovately fusiform area radially dividing the trigonal region. These triangles lie within a less inflated, but weakly sulcate eight-lobed continuation of the main central disk. The periphery of this area is cleanly defined (*Pag*) into four broad scallops which center on the triangular areas. Peripherad of the boundary is a “smooth zone” (*Sm*), so-called because it does not show the concentric markings (*Rm*) so characteristic of the peripheral area. Brandt (1871) illustrates the perimeter of the disk with tiny lappets (*Lp*) which are apparently separated into 16 marginal groupings, in some of which the roots of tentacular
(or tentaculocyst) structures are present, and in others, absent \((T_{c1}, T_{c2}, Prn)\).

The hypothesis of rhizostomatous alignment has been so thoroughly and so often presented in the past that we need only touch the high points here. It has been assumed by all that in these typical \(R.\) admirandus we deal with oral imprints of a rhizostome oral disk; that the sulci are the beaded mouth grooves and that the eight grooves lead to arm pillars somewhere out near the periphery of the disk (Brandt) or even near the perimeter of the bell (Kieslinger, after Maas, 1902*). Of the remnants of such arms, or any signs of such structures, there is not a smid of published evidence, apparently, and herein lies the chief difficulty in matching the fossils with any known Rhizostomeae. The four trigonal areas have been likened to the four subgenital pouches of the Scyphozoa, and the elevated central portion of these areas has been interpreted as an opercular cover to the subgenital pit. Brandt (1871) and Walcott (1898, copying Brandt) give a restoration of \(Rhizostomites\) in accordance with the rhizostomatous theory, quite gratuitously restoring arms at the termini of the sulci. This classical interpretation has much to recommend it, but certain similarities to \(Kirklandia\) suggest an alternative hypothesis.

The sharp, rather than the expected zigzagging ("sewed"), course of the sulci, the absence of any vestige of bona fide oral structures, and the anomalous trigonal areas, raise doubts. On the aboral surface of \(Kirklandia\) disks almost precisely the same sort of loculation and sulcation, including the central crossing of the primary sulci, apparently exists (Plate 5, fig. 4); insert and exsert lobes, of which we have made so much, occur here in certainty for the first time. To be sure, the number of lobes in the Jurassic specimens is smaller, and the symmetry more regular (not forgetting \(Hexarhizites\), of course).

A specimen of \(Rhizostomites\) admirandus illustrated by Ammon (1886) and copied by Kieslinger (1939A, fig. 22) is unique among illustrations of the species in showing a circle of shallow excavations (in the mold) \((Gn)\) in the same position as the genital pouches of \(Kirklandia\). The shallowness suggests a sagging of the aboral gastric wall into the gastric chamber which thus permitted the swollen gonadic pouches or external gonads to stand out in aboral relief. How to account for these unique structures in \(Rhizostomites\) is almost impossible if the sulci are oral and radial and the four trigonal areas are subgenital камер. However, we cannot stress the shadowy structures too strongly from this very imperfect intimation.

\(Kirklandia\) demonstrates the fossil existence of toughly invested gastric disks, with melonoid lobation due to interradial sulci. The central disk of \(Rhizostomites\) in several respects recalls the aboral surface of the \(Kirklandia\) disk. Now can we find in the Hydromedusae class any analogues for the new features exhibited by \(Rhizostomites\)? The answer seems to lie in the Narcomedusae, or at least seems as potentially to lie there as it does in the Rhizostomeae. These potentials are illustrated by text figure 8.
Figure 8.—Semidiagrammatic radial sections through Recent Narcomedusae. Showing potentiality of these Hydrozoa to account for certain features of *Rhizostomites admirans* and possibly of *Kirklandia texana*. Of especial significance is the contact of the tentacle roots (*Trc*) with the umbral gastric wall, thus perhaps accounting for the four (or more) so-called genital coverplates in the Jurassic genus. Note also the pendant gastro-genital sacs in figure A. *A. Pegantha pantheon* Haeckel. B. *Cunarcha aginoides* Haeckel. C. *Polycolpa forskali*; Haeckel. Ac. auditory club of tentaculocyst; *Cc*—coronal (tentacular) groove of umbrella; *Gc*—central stomach; *Gpp*—gastro-genital sac of *Pegantha*; *Gn*—gonads; *Gu*—umbral wall of central stomach; *Gv*—subumbral wall of stomach; *M*—circular mouth of *Pegantha* and *Polycolpa*; *Mn*—manubrium; *Oo*—ototorm of tentaculocyst; *Op*—peduncle of auditory club; *Pu*—peronal canal in *Cunarcha*; *Pc*—peripheral umbral jelly; *Sue*—subumbral epithelium; *Tc*—tentaculocyst; *Tn*—coronal tentacle (many in *Pegantha* and *Polycolpa*; four in *Cunarcha*); *Tr*—root of coronal tentacle; *Trc*—contact area of tentacle root with umbral gastric wall; *Us*—umbral epithelium; *Us*—gelatinous substance of umbrella; *Us*—urticating swelling at base of tentacle. From Haeckel (1883).

In such forms as *Cunarcha* and *Polycolpa*, illustrated in figure 8, we have four (*Cunarcha*) or more (*Polycolpa*) powerful coronal tentacles emerging through the umbrall jelly on the tentacular furrow (*Gc*). Their roots (*Tr*) are deeply buried in the umbrall jelly (*Us*) and lie in contact with the umbrall wall of the central stomach (*Gu*) or the peripheral extension thereof. It is conceivable (but unproved from modern writings) that this impingement of the tentacular root
upon the umbral wall of the stomach is now occasionally, or has been in the past, recorded by a cicatrice or at least depressed zone. The suggestion arises that herein may lie the explanation of the four trigonal areas in Rhizostomites. If in an archaic narcomedusid the umbraller jelly (above the coronal groove) were to be destroyed soon after death and stranded jellies, without tentacles, were to be imbedded aboral side down, imprints much like those of Rhizostomites might result, providing of course, that these jellies possessed tough and sulcate gastric disks of the *Kirklandia* sort. All other features of the Jurassic peripheral jelly would fit most conveniently into the pattern of this hypothesis, including the marginal fractionation into the lippets (shown by Brandt, 1871), and the well-known concentric muscle zone. The "smooth zone" nearest the central sulcate disk might correspond to the cleavage plane between the main mass of aboral jelly and the peripheral jelly (Pu) at the coronal furrow. The "smoothness" might be attributable to absence of the strong circular muscles which characterize the peripheral zone.

According to this hypothesis, then, European colleagues should institute a search among their large collections of Jurassic acrolephs for true oral surface imprints or casts. These should show either a quadrate or circular mouth in a disk characterized by insert, and probably exert, lobes separated by deep sulci of the same general sort already known. Gonads or sex sacs may or may not be visible, but if so, should lie upon the sectorial expansions, either interiorly or exteriorly. Almost exactly the required forms, albeit of smaller size and possibly without gonadic pouches, are already known at Solnhofen in the various lobate Problematica such as *Medusina* (Craspedonites) *deperdita* (Beyrich), *Acraspedites antiquus* (Haeckel) and *Medusina bicinctus* (Haeckel),—the latter perhaps even fulfilling the gonad requirements as well. All of these show some evidence of a circular aperture, and the same basic sort of quadrirpartite loration as *Rhizostomites*. They are quite probably immature phases of the famous fossil, and seem to substantiate the new hydromedusa hypothesis.

If the present postulate is right, then apparently, contrary to the opinion of Kieslinger (1909A), the laterally crushed imprint from the Solnhofen beds known as *Leptobrachites trionobrachius* Haeckel (1869) is not a synonym of *Rhizostomites admirandus*. The evidence for Kieslinger's view is most hazy, since the *Leptobrachites* disk is not known. Moreover, *Leptobrachites* shows pendant scyphozoan arms which could not be attached to the known surfaces of *Rhizostomites* and would be equally incompatible with a hydromedusa oral surface.

Whether we have achieved the desired reconciliation or not is a moot question, but there are assuredly as many arguments in favor of considering *Rhizostomites admirandus*, *s. s.*, to be a hydromedusa as a scyphozoan, and a trachylina as a rhizostomiid. Of all Problematica, this European Jurassic form seems quite

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12 We must recall also that ever since the studies of Mann (1902) medusologists have recognized that *Rhizostomites* can enter the ranks of the Rhizostomea only by drastic dispensation. As Kieslinger (1903A, following Mann, 1902) points out, the while considering it a primitive rhizostome, *Rhizostomites* probably carried marginal, instead of central moutharms (as pure guess) and was further anomalous in having undoubted marginal tentacles. This organizational scheme would appear to render the rhizostome argument imponderable.
probably to lie closest to our new Cretaceous forms from Texas. In its simpler organization, i.e., fewer lobes, it would adequately fulfill the ancestral position. As an aboral imprint only, however, we know too little about critical structures to venture congeneric or even confamilous assignment. If the circular mouth of *Medusina desperita* and analogous consociates belongs to *Rhizostomites*, they probably are a distinct family line. Until we know of trigonal (tentacle?) scars in *Kirklandia* we must not consider alignment with the cororate Narcomedusae for it. Gastric pouching and internal gonads of the *Kirklandia* sort better fit the trachymedusid Psychogastriidae, as we have urged for many a page.

We must be ready to meet the possibility that this jumbling of modern ordinal characteristics had no such significance in Jurassic and Cretaceous times; that a Mesozoic ancestral stock merged these features in an order now wholly extinct, and whose attributes exist today only in fractionated dissipation.

**CONCLUSION**

From this survey of Recent and fossil analogues it seems probable that *Kirklandia* represents external likenesses of a medusa gastric disk, which was possibly toughened by thick investiture of a fibrous mesoglea; that the closest living relatives are probably the Trachylina, to both existing orders of which *Kirklandia* shows important similarities; and that this mingling of Recent traits, plus others either idiosyncratic or shared only with fossils, will probably require a distinct order of extinct trachylines for their accommodation.

The morphologic details of *Kirklandia* are shared by several Problematica so similar as to suggest organic relationship; thus intimating that the unnamed order was of some size and of considerable geologic range.

The doubts which *Kirklandia* raises concerning *Rhizostomites* pervades the whole structure of paleomedusology. It would be fatuous to suppose that the Scyphozoa were not an ancient group of coelenterates, but it is equally unwarranted to believe that they alone held the potentiality for fossilization. By this study we would focus attention on the equal availability of the phylogenetically older trachylines. Many of our leading students of present day medusae have vigorously insisted (e.g., G. Stainsky as quoted by Bassler, 1941) that most so-called fossil jellyfish are not assignable to either of the discomedusan lines (Semanostomeae and Rhizostomeae). The other scyphozoan orders have seldom been called upon to admit fossils. Paleontologists would do well utterly to exhaust the possibilities of the Hydromeduse when working with Paleozoic medusoid Problematica. The greatest surprise of this study has been the evidence which suggests that these simple acanthoids were probably the dominant "jellyfish" as late as the Jurassic and Cretaceous periods.
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PLATES

PLATE I (VOL. PL. 16)
EXPLANATION OF PLATE I (16)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-6. <em>Kirklandia texana</em> Caster, n. gen., n. sp.</td>
<td>7</td>
</tr>
</tbody>
</table>

Lower Cretaceous (Pawpaw formation), Denton County, Texas.

Figure 1. Rubber cast of holotype natural mold. Oral surface; note polygonal manubrial area, 8-lobe symmetry, and suggestions of paired gonadic imprints (*Pd*) on the genital saes (*Gsp*). Mold, U. S. National Museum, No. 136131A; rubber cast, University of Cincinnati Museum, No. 22979-7a; ×1.

Figure 2. Rubber cast of paratype mold. Oral surface; note 7-lobe symmetry and evidence of shrinkage on the surface of the genital saes. Original in the F. V. Studer Collection, West Texas State Teachers College; rubber cast, University of Cincinnati Museum, No. 22979-5a; ×1.

Figure 3. Natural mold, reversed lighting; oral surface showing unusual trilobate condition of several sectors. Kirkland Collection, University of Cincinnati Museum; ×1/2.

Figure 4. Rubber cast of paratype natural molds; oral surfaces of three growth stages. Note variation in shape and degree of pendency of the genital saes and in the number and nature of the lobation from specimen to specimen. Mold, U. S. National Museum, No. 136131B; rubber cast, University of Cincinnati Museum, No. 22979-6a; ×1.

Figure 5. Rubber cast of paratype natural mold; oral surface, illustrating variation in shape of genital pouches and nature of manubrial features. Emergent central plug (*Cc*) well defined (hollow in life?). Note suggestions of ovate structures around the cone (*Bp*). Kirkland Collection, University of Cincinnati Museum; ×1.

Figure 6. Rubber cast of paratype natural mold; oral surface exhibiting two pendant structures or worm spoor emergent from the central zone. Note the absence or poor development of the genital saes. Kirkland Collection, University of Cincinnati Museum; rubber mold, *idem*, No. 22979-13a; ×2/3.

All symbols explained in text figures 1-4.
PLATE II (VOL. PL. 17)
EXPLANATION OF PLATE II (17)

Figure 1-6. *Kirklandia texana* Caster, n. gen., n. sp.

1. Lower Cretaceous (Parapaw formation), Denton County, Texas.

Figure 1. Paratype natural mold. Oral surface showing only faint traces of genital pouches (*Gp*), but a striking record of the paired impressions (*Pd*) (gonads *) and the intervening ciliated area. Kirkland Collection, University of Cincinnati Museum; X1.

Figure 2. Rubber cast from paratype natural mold. Sole lateral record in the topotype suite; shows the aboral duplication of the oral salivary area and the entrance of the gastric wall by the undug oral funnel (*Ar*). Note the record of the radial canals (*Rc*) on the replaced mound. Mold, University of Cincinnati Museum, No. 29979-4; X1. (rubber cast): X1.

Figure 5. Rubber cast from paratype natural mold. Oral surface showing 7 gastric and genital lobes; genital sacs pedunculate; except gastric lobes not developed; Kirkland Collection, University of Cincinnati Museum, No. 29979-5e (rubber cast); X1.

Figure 4. Rubber cast from paratype natural mold. Oral surface showing 10 or 11 genital pouches and an intimation of stomodal structures. Kirkland Collection, University of Cincinnati Museum, No. 29979-5d (rubber cast); X1.

Figure 5. Rubber cast of paratype natural mold. Oral surface showing a 7-part disk; centrifugally pendulant genital sacs bearing paired gonad imprints; insert and exsert gastric lobes; mouth and radial-canal features. Shrinkage marks well developed on lobe margins; structure at extreme top of picture problematical; in mold seems perhaps to be connected with an aboral tentacular arm. Princeton University Museum, No. A751; rubber cast, University of Cincinnati Museum, No. 29979-11b; X1.

Figure 6. Enlargement of the central area of figure 5 to show radial details.

Figure 7-8. *Nodolithus* cf. *texana*. Enlargement of the two foraminifers shown on the periphery of figure 1, Plate 5.

All symbols explained in text figures 1-4.
PLATE III (VOL. PL. 18)
EXPLANATION OF PLATE III (18)

1-6. *Kirklandia texana* Caster, n. gen., n. sp. Lower Cretaceous (Pawpaw formation), Denton County, Texas.

**Figure 1.** Paratype natural mold. Oral surface showing 12-14 peripheral lobes; 8-9 lobes appear to be insert and carry gonadic pouches. Note two *Nodosaria* on the matrix margin of the disk (see Plate 2, figs. 7, 8). Private collection of Thomas D. Copeland, Dallas, Texas; X.1. Kirkland Collection, University of Cincinnati Museum; X.1.

**Figure 2.** Paratype natural mold. Oral surface showing various split lobes and fused genital sacs. Note faint evidence of lobate structures *Bp* around the central zone. Kirkland Collection, University of Cincinnati Museum; X.1.

**Figure 3.** Rubber cast of paratype natural mold. Oral surface of aberrant individual showing evidence of sporadic radial splitting; 12 genital sacs—all much shriveled. University of Cincinnati Museum, No. 22979-1, la; (rubber cast); X.1.

**Figure 4.** Rubber cast of paratype natural mold. Oral surface showing 7 genital sacs, only 5 of which are well developed; note fusion of gastric lobes at periphery. Texas Christian University Collection; rubber cast, University of Cincinnati Museum, No. 22979-10a, X.1.

**Figure 5.** Rubber cast of paratype mold. Oral surface of a somewhat amorphous individual with large, sessile genital pouches and polygonal oral features. University of Cincinnati Museum, No. 22979-2, 2a; (rubber cast); X.1.

**Figure 6.** Enlargement of central area of figure 5.

All symbols explained in text figures 1-4.
PLATE IV (VOL. PL. 19)
EXPLANATION OF PLATE IV (39)

Figure

1-5.7. *Kirklandia terana* Caster, n. gen., n. sp.

Lower Cretaceous (Pawpaw formation), Denton County, Texas.

Figure 1. Rubber cast of paratype slab showing disposition of accessory structures over and around the lobate impressions. See figures 2 and 3 for enlargements. U. S. National Museum, No. 136131-2; rubber cast, University of Cincinnati Museum, No. 22979-H4a; ×1.

Figures 2, 3. Enlargements of portions of figure 1 to illustrate the nodose character of the accessory structures; possibly nettle organs.

Figure 4. Slab from original locality showing ovoid disposition of 8-9 columns of nodose structures (surfacially similar to figures 2, 3). Suggests tentacular function of these possibly urticaceous structures in life. Collection of Fred T. Mosley, Dallas, Texas; ×1.

Figure 5. Portion of a disk periphery showing shrunken margin and suggestion of its continuation into a fragile peripheral region. Same slab as partially illustrated in figure 1; ×1.

Figure 6. Under surface of a slab bearing *Kirklandia* imprints showing sandstone filling of various invertebrate spoor originally made in the clay underlying the jellyfish layer. Bureau of Economic Geology Collection, University of Texas; ×1.

Figure 7. Natural oral mold of *Kirklandia* showing 9 lobes, two of which appear to be split from an originally 7-lobed state. Collection of W. T. Watkins, San Antonio, Texas; ×1.
EXPLANATION OF PLATE V (20)

1-5. Kirklandia texana Caster, n. gen., n. sp. Page 7


Figure 1. Aboral view of a cast showing sulci, swollen margin, and central elevated area (compare with figure 2, Plate 2); X1.

Figure 2. Oral surface of figure 1. Note circular central area which consists of an emergent central plug with a circular planate collar around it; plug and collar preserved in pyrite. The irregular darker bands from the center toward the left also preserved in pyrite, (compare with structures shown in figure 6, Plate 1) and resembling worm burrows; X1.

Figure 3. Lateral view of figures 1, 2, showing the hollow inlaid nature of the casts and their characteristic distended margin which is in contrast to the shrunk aspect of this zone in the topotype material; X1.

Figure 4. Aboral surface of another natural cast showing the bilobate pattern of primary sulci and central shallow concavity of the undeformed disk; approx. X4/5.

Figure 5. Polished section near middle of a natural cast fragment showing profile and a suggestion of the concentric weathering of the margin and differential chemical weathering of pyritic calcareous nodule. White and gray areas are pyrite; black streaks are shrinkage crevasses in the residual clay cast; X1.

Figure 6. Deeply imprinted spoor associated with original molus of Kirklandia. Form very similar to the tracks made by the simple, chelate feet of modern Limulus; X1.
PALAEONTOGRAPHICA AMERICANA

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PALÆONTOLOGICAL RESEARCH INSTITUTION
Ithaca, N. Y.
NO. 19, OBSERVATIONS ON GASTROPOD PROTOCONCHS

By

Burnett Smith

September 11, 1945

Paleontological Research Institution
Ithaca, New York, U. S. A.
## CONTENTS

<table>
<thead>
<tr>
<th>Introduction</th>
<th>Acknowledgments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 5</td>
<td>Page 5</td>
</tr>
</tbody>
</table>

**Part I.—Review of selections from the literature**

<table>
<thead>
<tr>
<th>Terminology</th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 6</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>The term protoconch</th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 7</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Protoconch redefined</th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 9</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Protoconch of gastropods</th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 9</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Value of the protoconch in classification</th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 9</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Different types of protoconch</th>
</tr>
</thead>
<tbody>
<tr>
<td>Differences in size</td>
</tr>
<tr>
<td>Page 12</td>
</tr>
</tbody>
</table>

| Differences in composition |
| Differences in shape        |
| Page 12                     |

<table>
<thead>
<tr>
<th>Protoconch uniformity and variation in natural groups</th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 13</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Genera with relatively uniform protoconchs</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Fusinus</em></td>
</tr>
<tr>
<td>Page 13</td>
</tr>
</tbody>
</table>

| _Busycon_                                  |
| Page 14                                   |

<table>
<thead>
<tr>
<th>Different types of protoconch within the genus or natural group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 15</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Protoconch differences in the round-whorled species of <em>Ficus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 17</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Protoconch differences in <em>Conus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 18</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Protoconch differences in <em>Athleta</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 18</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Protoconch differences in <em>Eucithara</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 19</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Protoconch differences in <em>Colus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 19</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Different types of protoconch within the species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 20</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Partial summary</th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 22</td>
</tr>
</tbody>
</table>

**Part II.—Some protoconchs in _Busycon, Fasciolaria_, and _Plicifusus_**

<table>
<thead>
<tr>
<th>Method of whorl counting</th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 22</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>The protoconch of <em>Busycon</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 23</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Protoconch in <em>Busycon contrarium</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 24</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Protoconch in <em>Busycon cf. fusiforme</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 26</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Protoconch in <em>Busycon coronatum or B. rugosum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 27</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Protoconch in <em>Busycon incile</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 27</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Protoconch in <em>Busycon pyrum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 27</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Protoconch in <em>Busycon excavatum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 28</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Protoconch in <em>Busycon cf. excavatum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 28</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Interpretations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 29</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>The protoconch of <em>Fasciolaria</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 30</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Protoconch in <em>Fasciolaria apicina</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 31</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Protoconch in <em>Fasciolaria tulipa</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 32</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Protoconch in <em>Fasciolaria papillosa</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 33</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Interpretations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Page 34</td>
</tr>
<tr>
<td>The protoconch of <em>Plicijusus</em></td>
</tr>
<tr>
<td>Protoconch in <em>Plicijusus kroyeri</em></td>
</tr>
<tr>
<td>Interpretations</td>
</tr>
<tr>
<td>Obscure markings on the protoconch</td>
</tr>
<tr>
<td>Summary of Part II</td>
</tr>
<tr>
<td><em>Busycen</em></td>
</tr>
<tr>
<td><em>Fasciolaria</em></td>
</tr>
<tr>
<td><em>Plicijusus</em></td>
</tr>
<tr>
<td>Bibliography—Parts I and II</td>
</tr>
<tr>
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OBSERVATIONS ON GASTROPOD PROTOCONCHS

By

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INTRODUCTION

The purpose of the present study of gastropod protoconchs is twofold, namely, (1) to review selections from the literature, mostly publications appearing since 1885, and (2) to make available somewhat disconnected notes accumulated by the writer for a number of years.

It is well known that many gastropod shells exhibit several distinct stages of individual growth (ontogenetic stages). That these stages may give some information on the race history or phylogeny of a shell is probably accepted by most students of the Gastropoda. However, there seem to be wide differences of opinion on the degree to which ontogeny reveals phylogeny. In any case it is highly advisable to study the ontogenetic stage or stages shown by the gastropod protoconch and to make any necessary comparisons with the earlier stages of the conch. Regardless of the possible value of young stages in theoretical biology it is believed that the practical importance of identifying immature shells will be recognized by all.

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Drawings have been favored for the purpose of illustrating the protoconch. In spite of possible idealizing on the part of the artist and in spite of possible distortions and exaggerations it is believed that the drawing elucidates the protoconch much better than does the photograph.
PART I.—REVIEW OF SELECTIONS FROM THE LITERATURE

TERMINOLOGY

A number of terms are in current use for young stages of the gastropod shell. The attempt is often made to correlate these terms with certain periods of the life history such as embryonic, larval, youthful, or again, terms may be employed merely in a descriptive sense. The same term may be used in different ways by different authors—even in different ways by the same author in a single publication. A few examples of inconsistencies will now be given.

In the beautiful illustrations of Gastropoda collected by the Challenger the term “apex” is used in the plate explanations in such a way as to include some whorls with adult characters. The text, on the other hand, seems to restrict “apex” to those early whorls, smooth or sculptured, which differ markedly from the later whorls with adult features (Watson, 1886, pl. 11, figs. 3e, 8e, pp. 182, 185). The present writer considers that the text should govern in this case and that it represents the intent of the author of the Challenger report.

Dall (1890, pp. 66, 67) speaks of “larval specimens” ready to emerge from the capsule (egg capsule). In a later paragraph occur the words “nucleus of larval shell” presumably as synonymous terms. Somewhat farther along in discussing the “bulbous nucleus” the following is found—“Still another important step is taken when the larval shell becomes larger, bulbous or subspherical, one-sided and inflated. The number of whorls is less and the nucleus is generally slightly larger than the next succeeding whorl.” From this latter quotation one may draw the inference that the “nucleus” is now part of the larval shell and that the terms “nucleus” and “larval shell” are no longer synonymous as at first indicated. Still a third conception of the term “nucleus” is given in Dall’s discussion of the “horny protoconch”—“In the typical form the larva is clothed with a cuticular or horny protoconch, probably similar in form to that which when shelly results in the ‘bulbous nucleus’ of the other line of descent. Later on, but while still in the ovicapsule, the deposition of limy matter begins as a slender cone or elevated point along the line of the axis of the protoconch, and as the larva grows the posterior part of the mantle secretes a shelly dome. Being thus cut off from the horny protoconch, the latter falls in shreds and is lost. The nucleus of the larva, still in the ovicapsule, then presents a slightly irregular dome, with a slender point rising from the apical part (Pl. 6, fig. 5).” If one consults this figure it is found to be of a “Larval shell taken from the ovicapsule of the recent Scaphella magellanica Sby., showing calcarella;” etc. “Nucleus” is therefore used by Dall in three different senses.

In 1897 George F. Harris (1897, p. 97, pl. IV, figs. 8a, 8b) states in his text that the protoconch of Voluitilites antiscalaris M'Coy consists of 1 1/2 smooth rounded turns. However, his figure of the protoconch of this species shows more than the smooth stage and includes one whorl showing two different types of sculpture. It is probably safe to assume that the text should rule in this case and that the intent was to exclude the sculptured whorl from the protoconch.

In 1902 Smith (1902, p. 505) uses the term protoconch without defining it while Grabau (1902, p. 918) writes as follows:
"The Protoconch of Gastropods.—The apical whorl of a gastropod shell has come to be generally known as the protoconch, though this term has been pre-occupied for the corresponding apex of cephalopod shells. The protoconch of gastropods is essentially different from that of cephalopods in that it is (at least in the majority of types) twisted into one or more coils of a spiral nature, whereas that of cephalopods, so far as known, is a mere swollen bulb." Note contradiction between a protoconch which is an "apical whorl" and a protoconch "twisted into one or more coils of a spiral nature," etc.

In 1907 Smith (1907a, p. 194) uses the term "apex" to cover from one to several whorls but also uses it in the sense of initial whorl (1907a, p. 194: 1907b, pp. 235, 236).

A search through the literature would probably reveal many other inconsistencies in usage but the above will suffice to illustrate the point.

In modern practice there seems to be a rough equivalency between "protoconch" and "nucleus." The term "apex" is less easy to fix but it makes an approach to, or may even agree in meaning with, "protoconch" and "nucleus." The term "apical whorls" is used in this paper in a descriptive sense and may include not only the protoconch but some of the early conch volutions.

THE TERM PROTOCONCH

Hyatt (1880, p. 399) attributes the term protoconch to Owen and later (p. 401) he speaks of "the protoconch of—veligers of Gasteropoda, etc." Grabau (1902, p. 918) points out that the term was applied first to the young cephalopod shell. Later it was put into use in describing the shells of gastropod veligers and a varying number of the early whorls of any well-preserved gastropod shell.

George F. Harris (1897, p. X) following Hyatt, together with Buckman and Bather, considers that the individual history from ovum to the acquisition of class characters is assignable to the embryonic stage. He adds: "In the fossil state we can only have left for investigation the hard part of the organism, which in the case of the Gasteropoda is here called the Protoconch, and in the Lamellibranchiata the Prodissococonch." This correlates the protoconch with an ontogenetic stage, the embryonic, but it does not tell one how to distinguish the protoconch from post-protoconch (conch) whorls. Harris, however, clarifies this difficulty in part by saying that "in the case of shells that are quite smooth it is hard to say where the protoconch ends and the brephic stage begins; but in very many instances a characteristic varix is present, denoting the termination of the former." The meaning is hardly clear but the varix would appear to be excluded from the protoconch (see also Harris, 1897, p. XIV).

The term "protoconch" occurs frequently in the writings of Grabau and a few of his observations will be briefly noted. He remarks (1902, p. 918), "It is not always possible to determine the precise line of demarcation between protoconch and conch, since in a large proportion of types the two grade into each other imperceptibly." This, however, is not always so for "In certain types
(Buccinum, etc.) a line and a slight change in the growth of the shell indicate the place where we may most reasonably make the separation between protoconch and conch. In a number of cases (Fusus, Hemifusus, certain Murexes, etc.) the end of the protoconch is strongly marked by the existence of a pronounced varix and an abrupt change of ornamentation (Fig. 5). In the majority of cases, however, no such definite line of demarcation exists.” The figure 5 is of the Recent Hemifusus colosseus Lam. showing “protoconch with riblets in the last portion, and the abruptly beginning, accelerated conch with the shoulder developed at the beginning.” This figure (5) shows no true varix.

In discussing the protoconch of the genus commonly known as Fusus (Fusinus Rafinesque, see Woodring, 1928, p. 250) Grabau (1904, p. 9) writes as follows:

“The protoconch generally ends abruptly with a varix, which sometimes is a riblet scarcely more prominent than the other riblets on the protoconch, or again is a strong rounded vertical ridge, two or three times the width of the normal riblets of the protoconch. The ornamentation of the nepionic shell begins abruptly, commonly in the form of spirals and rounded vertical ribs.” It is obvious that here Grabau intends to include the above mentioned varix in the protoconch.

Kesteven (1905a, p. 326) notes that the protoconch may be formed during one or all of four early growth stages. He continues: “An ideal protoconch would, in my conception be composed of—(1) the plug of the primitive shell-gland, (2) a portion formed by the veliger, (3) a portion formed during the nepionic stage, and finally (4) a portion formed during early neanic stages.” Kesteven regards the term “protoconch” as a “redundant misnomer” but justifies its retention in the following words: “The term has been in the past, and is here, used to designate those few apical whorls which differ markedly either in contour or sculpture, or both, from the succeeding structure, which latter I have, for want of a better term, designated ‘adult structure.’ In the above sense the term ‘protoconch’ is certainly useful,” etc. This last is a definition of the term protoconch on a utility basis.

Kesteven (1905b, p. 184) notes that the protoconch, as almost universally interpreted, “consists of an indefinite number of the apical whorls of a Gastropod shell, irrespective of whether these apical whorls are the first shell or not.” The discussion of the term protoconch is then continued by Kesteven in the following words: “Moreover the term is a useful one; it is here used in the above broad sense, namely, to include those apical whorls, disregarding their age, which by smoothness, distinctiveness or size are differentiated from the succeeding whorls, and thereby indicate that at their conclusion the mollusc entered upon a new and important ontogenetic phase—such, for example, as the change from veliger to sedentary life, or the emergence from the egg capsule.”

Woodring (1928, p. 4) in his conception of the gastropod protoconch approaches closely that of Kesteven. His paragraph on the subject is as follows:

“The term ‘nucleus’ used in the description of the gastropods refers to the part of the shell from the apex to the beginning of adult sculpture or to a change in the texture or color of the shell when sculpture is absent. It embraces the whorls formed in the egg case, called ‘embryonic’ whorls by some writers, and
also the 'neptic' whorl, or part of a whorl, intervening between the 'embryonic' and adult whorls. 'Nucleus' is an unsatisfactory term and it has been used by some writers to refer only to the apical whorl. 'Protoconch' is a more satisfactory term and its use in nautiloids and ammonoids seems to be no valid objection to its use in gastropods also. 'Nucleus' or 'nuclear whorls' is adopted because 'post-nuclear' is a convenient term for the remaining whorls. 'Post-protoconch' is unwieldy and 'conch', the corresponding term in nautiloid and ammonoid terminology, is objectionable when applied to gastropods."

PROTOCONCH REDEFINED

The definitions of Kesteven (1905a, p. 326; 1905b, p. 184) can be applied equally well to fossils or to Recent shells which are complete but whose history is unknown. In the present paper Kesteven's definitions are adopted with some slight modification as follows:

PROTOCONCH OF GASTROPODS

The term protoconch is here used to designate those apical whorls of the gastropod shell, usually few in number, which differ in contour, or sculpture, or attitude from the succeeding and more or less adult whorls. These later or succeeding whorls have been usually called conch whorls and will be so designated in this paper.

It is fully realized that this conception of the term protoconch may meet the disapproval of the embryologist and student of life history. When, however, this life history is unknown or, at best, inferred, tangible criteria appear to be desirable.

VALUE OF THE PROTOCONCH IN CLASSIFICATION

The value of the gastropod protoconch as a means of classification has been much debated. Two quite different views have been expressed on this question. According to one the protoconch is an important factor, perhaps the most important factor, in determining the relationships of the gastropod shell. The other view denies this either wholly or in part.

Examples of the former of these conflicting opinions will now be given.

Grabau (1902, p. 922) makes the following statement: "Thus, while the initial whorl of the protoconch does not differ widely, except in size, in the majority of gastropods, indicating the characters of the more distal radicle of the class,—i.e., the nautiloid ancestor,—the whole character of the protoconch must be considered in the determination of the more immediate relationships. Therefore, I believe it is not too much to say that the protoconchs of all the species within a given genus should agree as to their essential characteristics, and that no species can be considered congeneric in which the protoconchs show a radical difference." The same author two years later (Grabau, 1904, pp. 1, 2) says that—"In determining genetic boundaries, the most important shell feature is the protoconch. The genus should represent a phyletic series, in which all the members (species and varieties) are descended from each other or from a common ancestor within the genus." In this 1904 paper Grabau gives excellent evidence to show that the protoconch is quite uniform within the genus *Fusinus* ("*Fusus"*). This, however, does not prove that it is uniform in every genus.
Iredale (1911, pp. 320, 321) argues for the value of the gastropod "apex" in
generic assignment and endorses Grabau's views of 1902 concerning the value
of the protoconch in classification. Iredale apparently uses "apex" and "proto-
conch" as synonymous terms.

The value of the gastropod protoconch in classification is further maintained
by Grabau (1912, pp. 762, 763) in the following statement.

"On the hypothesis defended by Boettger, Cossmann, and others that the proto-
conch is variable even within the genus to the extent that an entirely different
type of protoconch may be developed, it is absolutely incomprehensible why the
Fusus type of protoconch should be maintained in its essential unity in a variety
of related genera, and be replaced by a wholly different type in some supposed
species of Fusus itself." Examples of such supposed species are then mentioned.

Grabau's next paragraph (1912, p. 763) will now be quoted,

"The foregoing considerations lead to the inevitable conclusion that the proto-
conch of Gastropods has a very important phylogenetic significance, in that it pre-
serves intact inherited characteristics, instead of being merely a product of local
environmental conditions. The gastropod protoconch is therefore a true guide to
phylectic relationship, and it becomes invaluable for the determination of the larger
taxonomic divisions. It follows, as a natural corollary, that smaller divisions,
such as genera, must have all their species agree in the type of protoconch, and
that in consequence the protoconch becomes the primary guide in the determina-
tion of genera, and, conversely, no genus can have species with different types of
protoconch, although variation within the type may be considerable. The proto-
conch is often more reliable than the adult shell characters, as illustrated by the
so-called Eocene fusoid shells above referred to."

A much more recent advocacy of the value of the gastropod protoconch in
classification has been put forward by Finlay (1931, p. 9) who says "it would be
aburd to say that all species which agreed in type of apex were congeneric. But
I would definitely say that species which do not agree in type of apex cannot be
congeneric." The same author (1931, p. 19) further says "I am fully satisfied, in
spite of what several authors have written, that the protoconch is one of the most
valuable criteria for systematic classification. Not only have I never found it
to vary from type in a homogeneous genus, but I have also found it so generally
constant that in my opinion considerable importance must be placed on it in de-
termining lineage relationships."

Some of the arguments in favor of a high classificatory value for the gastropod
protoconch have now been given and it is therefore in order to review some of the
opinions which deny this value either wholly or in part.

An early, if somewhat guarded, challenge is to be found in the writings of
Kesteven (1905a, pp. 333, 334) who says:

"Really critical differences between two protoconchs would be—(1) two abso-
lutely different types of sculpture, which were not merely the first appearance
of the adult sculpture, whether accompanied or not by differences of contour; (2)
the presence in one and absence from the other of some such bizarre feature as the
situation and claw-like processes of Purpura protoconchs; and (3) a completely
different axis of coiling in the two, as between Triphora and Turbonilla. Such,
however, will most probably be found to be correlated with differences, of equal
or greater importance, in shell or anatomy.

"The conclusions of this section are that the protoconch is to be used in con-
junction with other features, and that only where the other features, anatomic or
coneological, are negative or unknown is it to be used in deciding a systematic
position or generic segregation. It will often be found useful as an indicator of
deep seated differential characters otherwise unsuspected."

Cossmann (1906, p. 225) reviews and criticizes Grabau's Fusus (Fusinus)
paper of 1904 and says:

"L'introduction de ce Mémoire pose d'abord en principe que la protoconque d'un
Gastropode est le critérium le plus sûr pour l'étude phylogénétique des Génres
d'une même Famille: deux espèces de Gastropodes, dit-il, dans lesquelles les
caractères adultes sont semblables, tandis que leurs caractères primitifs sont
dissimilés, sont moins voisines que deux autres coquilles dont les proto-
conques sont identiques, tandis que leurs derniers tours différent.

"Cette assertion peut être très juste dans quelques cas particuliers; mais si
l'on en fait, comme l'a essayé M. Grabau le pivot de toute une classification, on
arrive à des résultats inadmissibles, comme cela se produit toutes les fois qu'un
auteur n'a qu'un seul criterium comme objectif. Ainsi, dans les cas des Fusites,
cette théorie exclusive amène M. Grabau à négliger complétement les
caractères de l'ouverture, essentiels cependant chez un Gastropode!"

Smith (1907a, p. 194) came to the conclusion that the importance of the "proto-
conch" as a means of generic discrimination had been greatly exaggerated. The
same author (1907b, p. 219) after a study of some Recent and fossil Pyrulas
(Ficus) agrees in substance with Kesteven (1905a, p. 334). A further study of
Athleta (Smith, 1907b, p. 242) leads to a somewhat similar result and quite at
variance with the view expressed by Grabau (1902, p. 922) that "the smaller
the taxonomic group, the more nearly identical must be the earlier stages, since in
a small group the members have not become widely separated from their common
ancestor."

Kesteven (1912, p. 59) in a later paper reaffirms his earlier views in the follow-
ing words:

"If it be found that any given feature has been so little affected by the phy-
logenetic history of the organisms possessing it, that it fails to show modifications
corresponding to the major groups into which those organisms are divisible; and
if, further, it be shown that this character is plastic to its environment, that feature
is surely hardly trustworthy as a guide to the division of the major into minor
groups. Such a feature as this is the Gastropod Protoconch." The same author
discusses the Sinusigera apex on a later page (1912, p. 63) and says of it: "Here
then is an exceedingly characteristic Protoconch, such as one was justified in ex-
pecting to prove taxonomically significant, but not only is it not present in all the
members of any one genus, but occurs sporadically in at least four genera dis-
tributed over three families, one of which falls within the Tacnioglossa, and two in
the *Rachiglossa*, and of these latter one belongs to the subdivision *Glossophora* and one to the *Aglossa*.

"It may be used neither to correlate nor to segregate."

Strong argument against the value of the gastropod protoconch in classification is contained in one of Dall's later papers (Dall, 1924, p. 178). He says:

"In common with most students of the mollusca for some years I have regarded the nucleus characters as more or less indicative of genetic affinity, but recently having had to work over large numbers of deep water species, especially toxoglossate forms, and to utilize Hedley's fine monograph of the Australian Turridae, I have found this view to involve so many apparently preposterous combinations of unlike things and separation of similar things, that I have come to the conclusion that this view cannot be maintained."

**DIFFERENT TYPES OF PROTOCONCH**

What constitutes a "type" of protoconch must now be considered and also what constitutes a difference—essential, radical, or otherwise. Kesteven's conception of "critical differences" in protoconchs (Kesteven, 1905a, pp. 333, 334) has already been quoted in this paper. In brief his critical differences are in sculpture, in presence or absence of bizarre features, and in axis of coiling. These differences are important and others can be safely added. In fact the present writer feels that almost any differences among protoconchs should be regarded as essential. This will be more fully discussed under the variations found in genera or other natural groups.

**DIFFERENCES IN SIZE**

This has been regarded as generally not constituting a radical difference (Iredale, 1911, p. 321). However, any marked difference in size, let us say an increase in size, is usually brought about by enlargement of the initial whorl or by increase in the number of whorls. In either case shape and proportions are decidedly affected and the type of protoconch is changed. Should both of the above factors operate the resulting differences would be more marked still.

**DIFFERENCES IN COMPOSITION**

Some protoconchs are wholly or predominately shelly or calcareous throughout. Others have an early portion which is horny and usually lost and a later portion which is shelly and capped by a more or less pointed septum which separated the horny from the calcareous part (Dall, 1889, pp. 452, 453; 1890, pp. 67, 68).

**DIFFERENCES IN SHAPE**

Dall (1890, pp. 66, 67) discusses "several forms of the shelly nucleus" in the volutes. He recognizes a Trochiform Nucleus, a Planorboid Nucleus, a Pupiform Nucleus, a Bulbous Nucleus, and a Melo Nucleus among the shelly protoconchs. In the volutes possessed of an early horny portion of the protoconch Dall (1890,
recognized a Caricella Nucleus, a Scaphella Nucleus, and a Cymba Nucleus. These three terms Caricella, Scaphella, and Cymba are descriptive only of the calcareous or shelly portion of the protoconch and indicate its appearance after the horny portion has been shed.

In a much later paper Dall (1924, pp. 178, 179) adds other types of nucleus to those he had already named. They are the Sinusigera Nucleus, Tonna Nucleus, and Triton Nucleus apparently all uncalcified.

A still later grouping of gastropod protoconchs has been made by Finlay (1931, pp. 8, 9). His first kind is not named but it seems to correspond approximately to Dall's Tonna Nucleus. His second group is not named but is stated to be polygyrate and turbinate. Finlay's third and fourth groups are stated to be paucispiral. One he calls Scaphellloid and gives as an example the apex of *Voluta junonia*. It therefore becomes a synonym for Dall's Scaphella Nucleus. Finlay calls his last group "fusid" and it is presumably an approximation to the *Fusinus* ("*Fusus*") type of protoconch described by Grabau (1904, pp. 8, 9).

**PROTOCONCH UNIFORMITY AND VARIATION IN NATURAL GROUPS**

Baker (1897, pp. 685, 686) recognized many years ago that the "apex" in some genera is characterized by uniformity, in other genera by variation. He wrote: "There are some 15,000 species of gastropodous mollusks of which but a few hundred have been examined for the apex, so that much work must be done before conclusions can be made. In some groups the apex variation seems to be of specific value (Oliva, Voluta) while in others almost no variation exists (Natica, Litorina, Neritina)."

**GENERA WITH RELATIVELY UNIFORM PROTOCONCHS**

Genera and perhaps larger groups may show species with relatively uniform protoconchs. Whether or not this is the prevailing condition for most natural groups of gastropods the writer is not prepared to say but probably many such cases could be found if a detailed study were undertaken. For present purposes, however, it is believed sufficient to call attention to two good examples of relative protoconch uniformity within the genus.

**FUSINUS**

Grabau (1904, pp. 8, 9) presents strong evidence in favor of a general uniformity of protoconch characters throughout the genus *Fusinus*. Under the heading "The Protoconch of Fusus" he says:

"The protoconch generally consists of one and a half volutions, but may be somewhat shorter or longer. . . . . . The first whorl is smooth, obliquely erect, and rather prominent, the apical end convex and large. The diameter just below the apex is but slightly less than that at the end of the first volution. The enlargement of the remaining portion of the protoconch is also very slight, the shell thus having the appearance of having a swollen or apical whorl. The last half of the protoconch is marked by fine vertical riblets, which are either closely crowded or separated by interspaces having from two to three times the width of the riblets."
The same writer (Grabau, 1904, pl. XVII, fig. 1 and p. 21) figures the protoconch and early conch whorls of *Fusus turriculus* Kiener and says: "The protoconch of this species represents the typical *Fusus* protoconch. The whole protoconch comprises about one and one half volutions, of which the first is smooth, and the other half furnished with faint crowded, vertical ribs, which become stronger towards the end. A strong, smooth varix marks the end of the protoconch."

Grabau (1904, p. 25) describes the protoconch of *Fusinus colus* (Lin né) in the following words:

"The protoconch of this species has been observed in only one specimen, all the others being imperfect. In that specimen it partakes of the brown color of the other apical whorls, but is perfectly smooth for the first volution. The remaining half volution of the protoconch is ornamented by fine smooth vertical ribs, about fifteen in number. The protoconch ends abruptly with a strong varix."

*Fusinus colus* is the genotype of *Fusinus* and the characteristics of its protoconch must therefore furnish the standard of comparison for the protoconchs of other species of the genus.

The uniformity of the *Fusinus* protoconch is, however, relative and not absolute for differences have been shown to exist in the protoconchs of *Fusinus bifrons* (Sturany) and *F. paucicostata* (Sturany) (Sturany, 1904, pp. 220, 221, pl. 1, figs. 1a, 2a, 3a, 3b, 4a, 4b, 4c).

Grabau (1907, p. 625) meets this difficulty in the following words:

"Referring again to the Red Sea shells cited by Sturany, . . . . . . . we note on reference to Sturany's illustrations that the difference between the protoconchs of *F. bifrons*, and *F. paucicostata* is one of degree and not of kind. Both protoconchs are of the same type, the true *Fusus* type; but that of *F. paucicostata* has a somewhat larger initial whorl. This species is a highly accelerated type, as compared with *F. bifrons*, and hence it is not surprising to find the protoconch partaking of this acceleration. Besides the initial larger whorl, the number of whorls appears to be less than in *F. bifrons* where 1½ smooth volutions, followed by a delicately ribbed portion constitute the protoconch."

**BUSYCONS**

One may infer from Dall's observations (Dall, 1918, pp. 207, 208) that differences exist among the larval Busycons of the egg capsule. The works of Mansfield (1937, p. 119) and of Gardner (1944, pp. 449-458) indicate that there is some variation in the *Busycon* protoconch. However, the genus in general seems to present a rather uniform series of protoconchs. The smooth and rounded stage is usually restricted to the first three-quarters of whorl 1. More rarely it occupies the entire whorl. The next stage is sculptured and persists for about a quarter of a whorl. It starts with simple axial ribs alone or with ribs and spirals on a rounded whorl and this part of the stage may be the correlate of the riblet stage of the *Fusinus* protoconch. The remainder of this first sculptured stage in *Busycon* seems to be usually, if not always, transitional into the noded and angulated stage of the conch. As a rule in *Busycon* end of protoconch and beginning of conch cannot be determined exactly. Possible exceptions to this condition will be noted on a later page.
Having given these examples of relative uniformity in the protoconchs of natural groups it is now proposed to inquire into cases in which this uniformity is not present.

**DIFFERENT TYPES OF PROTOCONCH WITHIN THE GENUS OR NATURAL GROUP**

In taking up this subject one is immediately confronted with two difficulties. What constitutes a difference in protoconch type? What constitutes a genus? There is, of course, no perfect answer to either question but the attempt will now be made to reach at least an approximation to a logical treatment of the subject.

Considering the first difficulty the present writer believes that a good case has been made for uniformity of protoconch characters in *Fusinus*. However, as already noted, this uniformity is relative and not absolute. The following quotation (Grabau, 1907, p. 630) will bring out this point:

"Finally I may again call attention to the fact that I have described in detail the variation in the protoconchs of *Fusus* and that I have readily admitted the possibility of the existence of larger and smaller initial whorls, of an increase or decrease in the number of whorls in the protoconch, and of the variation in the number of riblets on the protoconch. In fact I have illustrated such variations but I am not ready to admit that there is ever a difference of type in the protoconch in what can otherwise be referred to the same genus."

Difference in size of initial whorl, variation in number of whorls, and variation in number of riblets are therefore not considered by Grabau as falling within differences in the type of protoconch. For the convenience of other workers it is much to be regretted that this author did not follow his statement on these points with a list of those differences which he regarded as constituting differences in type for a protoconch. If size, whorl number, and sculpture are unimportant features it seems that one may well ask what are important features? The answer can perhaps be found in some of Grabau's illustrations. Three examples will suffice. *Fusus meyeri* Aldrich was made by Grabau the type of a new genus—*Fusolatirus* (Grabau, 1904, pp. 80-82, fig. 4; pl. Xvii, fig. 9). The figure 9 of plate XVII shows the "apical whorls" of this species. Probably three of these whorls should be assigned to the protoconch and two of them to the conch. The protoconch whorls show the smooth and curved-rib stages and are quite different in proportions, number, and sculpture from those of the protoconch of *Fusinus* (cf. Grabau, 1904, pl. XVII, fig. 1). Other protoconchs quite different from the *Fusinus* type are those of *Larvifusus trabecatus* Conrad and *Latirofusus? interstitialis* (Heilprin) (Grabau, 1904, pl. XVII, figs. 7, 8).

The present writer has already stated the belief that almost any difference between protoconchs is an essential one. However, it is not claimed that all differences are of equal value. Slight differences in the sizes of initial whorls may perhaps be of little importance but such are none the less worth recording. Small differences in the number of smooth whorls may be in the same category and perhaps also differences in the number of riblets or curved ribs. On the other hand, the following differences can hardly be dismissed as unimportant: (1) very minute as against very large initial whorls, (2) a smooth stage of one whorl as against a smooth stage of two, three, or four whorls, (3) marked differences
in the length of the riblet or curved-rib stage, (4) differences in proportion of
the length of the smooth and sculptured stages, (5) differences in sculpture, (6)
differences in shape or contour, (7) differences in attitude, (8) differences in
the axis of coiling, (9) differences in the direction of coiling, (10) presence or
absence of marginal situations, (11) differences in composition with or without
resulting differences in shape due to loss of horny portion.

In connection with this last item (11) it may be said that the calcareous cast
or filling of a horny protoconch (not the calcified axis) is treated as a protoconch,
or as part of the protoconch, for it gives not only interior size and shape but also
shows the number of whorls as well as did the shell which it filled.

The next question is what constitutes a genus or natural group of genera? An
answer on this point can never be final. Many "genera" are rather surely poly-
phyletic and are not natural groups. On the other hand, there are genera or sec-
tions of genera and groups of genera which seem to be natural groups. At least
on a balancing of probabilities such would seem to be the case. Two outstand-
ing examples falling under this second category are furnished by that section
of the genus Ficus with rounded whorls and long anterior canal and the genus
Conus, or, if one prefers, the cones as a group.

It may always be argued that each of these genera, sections, or groups merely
represents an assemblage of unrelated species, more or less alike in adult shell
characters, but of various lines of descent. Such an argument can never be whol-
ly-disproved. When different types of protoconch are found in such an assemblage
one school of workers holds that on this account the group should be divided
into distinct genera or even larger units.

The present writer believes that in very homogeneous and restricted groups
the adult shell characters should govern in making a decision but it must be
stressed that this applies only to groups in which the homogeneity is obvious.

The problem is aptly summed up by Dall. A quotation from his paper (Dall,
1924, p. 178) has already been given under the discussion of the value of the
protoconch in classification. This particular quotation need not be repeated in
full here. It is sufficient to say that Dall considers dependence on the nucleus
(protoconch) for determining genetic affinity results in "many apparently pre-
puseterous combinations of unlike things and separation of similar things," etc. On
another later page (Dall, 1924, p. 180) the same author says further:

"When two marine forms of similar anatomical structure exhibit different
nuclei, I conclude that the adaptive modification is not of serious value in classi-
fication, and in most cases should not be considered as of more than sectional
or subgeneric importance. The parallel occurrence of similar nuclei in widely
different groups of families is obviously no indication of genetic affinity."

Kesteven (1902, p. 459, figs., pl. XVII) appears to be the first author to
culphasize protoconch differences within a genus (Lottorium) but earlier and more
or less incidental mention of such differences can be found (Jeffreys, 1867, pp.
333, 335, 338; Baker, 1897, pp. 683, 686).

The present writer proposes to give a few published examples of protoconch
differences within the genus or natural group.
There are but 18 species and subspecies of *Ficus* known in the Recent fauna (Clench, 1942). The Recent and fossil species of *Ficus* with rounded whorls constitute a small and homogeneous group. The adjective "homogeneous" might still be used if the angulated Eocene species were included. However, it is deemed best to exclude these in order to deal with a group whose monophyletic nature seems beyond doubt. Certainly the burden of proof rests with any one who contends that the similarities in the adult shells of the rounded species of *Ficus* are the result of parallelism. The group is so uniform in adult shell characters and so different from any other genus that the probabilities for homogeneity are overwhelming. It is realized that these arguments will probably prove insufficient to convince the believer in protoconch infallibility but in any case the protoconch differences within the group will now be taken up.

In the genus *Ficus*, as here restricted, the term protoconch should probably be applied only to the first or smooth and rounded stage. The sculptured stage of spirals and axial ribs, cancelled or reticulated stage, is assigned to the conch. It has been shown (Smith, 1907b) that protoconchs in the eastern American members of this group may run from about three whorls in the Vicksburg *Ficus mississippiensis* Conrad (Pl. 1, fig. 4) down to about one whorl in the Recent *F. papyratus* (Say) (Pl. 1, fig. 1). The three-whorled condition is believed to be the more primitive. In general the pre-Pliocene species show protoconchs of 1½ or more whorls, though one species exhibits a protoconch of but one whorl. Pliocene individuals of *Ficus papyratus* show slightly more than one whorl for the protoconch (Pl. 1, fig. 2). Reduction in number of whorls usually goes hand in hand with increase in the size of the initial whorl. The largest initial whorls may be tilted. For Recent Indo-Pacific species the protoconchs examined run from two whorls down to half a whorl in length. However, the protoconchs of from 1 2/3 to two whorls seem to be the prevalent ones in this region (Pl. 1, figs. 6-8). It is of interest to note that most Recent Indo-Pacific protoconchs are very like most Atlantic and Caribbean Eocene, Oligocene, and Miocene protoconchs (Pl. 1, figs. 3-8).

It may be argued that these protoconch variations in the round-whorled species of *Ficus* represent differences of degree but not of kind. However, the difference between a protoconch with three whorls and another with one whorl can hardly be dismissed so lightly. When such reduction in number of whorls is accompanied by increase in the size of the initial whorl and perhaps by tilting there seems little justification for regarding the differences as unimportant.

It is possible that some *Ficus* "protoconchs" are in reality calcareous casts or fillings of originally horny structures. Even if this be so, the present writer does not consider that the proof of protoconch differences within the group is negatived thereby in any way. As already stated such casts show differences in size and shape of protoconch interiors as well as differences in the number of whorls.
If it is acknowledged that Conus is a genus one must at the same time admit that it is a very large genus. Ficus is insignificant by comparison. Conus is rather surely less homogeneous than Ficus but the naturalness of the group can hardly be questioned. If Conus is more extensive than the ordinary genus the fact still remains that the group cannot be pictured as other than an assemblage of closely related forms. Minor differences in shell characters do, of course, occur but in general the shells of the numerous species of Conus are so remarkably alike and so different from anything else that genetic affinity becomes a virtually certain matter.

That there is not a little variation in the Conus protoconch was demonstrated long ago by George F. Harris (1897, pl. 2, figs. 2a, 2b, 3a, 3b, 3c, 3d, 3e, 2f, 3b, 4a, 4b, 5a, 6a, 6b, 7a, 7b, 8a, 8b, 9a, 9b). His figures show that in the protoconchs of eight species of Conus there is present much more difference than uniformity. There are variations of shape, size, size of initial whorl, number of smooth whorls, and attitude.

Several different types of apex have been found in Recent and late Tertiary cones from the southeastern United States (Smith, 1931, pp. 270-288, figs.). The protoconch is here treated as part of the “apex” and to it are now assigned the smooth and rounded stage and the curved-rib stage. The latter stage is absent in Conus vaccamawensis Smith (Pl. 1, fig. 9) but present in C. floridanus Gabb (Pl. 1, fig. 10), C. stearnsii Conrad (Pl. 1, fig. 11), and, in a modified form, in C. diluvianus Green (Pl. 1, figs. 12, 13). The smooth stage may run from about one to 1 1/4 whorls in Conus floridanus, somewhat over one to perhaps nearly 1 1/2 whorls in C. stearnsii. The very tip of the protoconch was not found in C. diluvianus and C. vaccamawensis. However, the protoconch in the former probably had three smooth whorls to which must be added a riblet or curved-rib stage of about 1 1/4 whorls. In C. vaccamawensis the smooth stage is still longer. It cannot have less than three and may run as high as 4 3/4 whorls. For this small number of species then there are found in the protoconch differences in size, differences in shape, differences in number of smooth whorls, and presence or absence of a curved-rib stage. The protoconch of the sinistral Conus adversarius Conrad (Pl. 1, figs. 14-16) has from 1 1/4 to 1 1/2 smooth and rounded whorls (Smith, 1930, pp. 659-663, figs.). The curved-rib stage has not been found in this species.

Two types of protoconch have been found in American species of the genus Athleta (Smith, 1906, figs. 4, 7, and tables; 1907c, figs. 1, 3, 4, 5, and tables). The more primitive type has from two to three smooth and rounded whorls followed by a curved-rib stage of from 1/4 to 1/2 whorl. The initial whorl is quite small. This primitive type of protoconch characterizes the races of Athleta petrosa (Conrad) occurring in the Eocene of Greggs Landing, Bells Landing,
Woods Bluff (Pl. 1, fig. 17), and Claiborne in Alabama. It is also found in
specimens from Jackson, Mississippi, (Pl. 1, fig. 18) and from localities in
Texas and Louisiana (Pl. 1, fig. 19). The other type of *Athleta* protoconch
has a much larger initial whorl, a smooth and rounded stage of one or slightly
over one whorl, and a condensed curved-rib stage in which the ribs are much
less curved than usual or even straight. This type of protoconch is found in
*Athleta clavi* Smith from St. Maurice, Louisiana, and in *A. sayana* (Conrad)
from Claiborne, Alabama (Pl. 1, figs. 20-22). The latter species, though con-
generic with *A. petrosa*, differs from it in adult characters. The adult *A. clavi*,
on the other hand, is so like the adult *A. petrosa* that one may argue specific
identity for the two. In such a case the peculiar protoconch features of *A.
clavi* become varietal or even individual characteristics.

**Protocohn Differences in Euclitara**

Figures given by Hedley (1922, pl. XLVI, figs. 54, 55, 56, 57, 55, 56) show
that there is great type variation in the protoconchs of Australian Turridae.
However, the turrids are a large group and are perhaps, to a certain degree,
polyphyletic. The same can hardly be said of all genera in the family. One
genus, Euclitara, will suffice as an illustration. *Euclitara alacris* Hedley is
shown with a protoconch different from that of *E. arenivaga* Hedley and mark-
edly different from the protoconch of *E. miriamica* Hedley. Judging by the
figures *E. phyllidis* Hedley differs decidedly from *E. miriamica*. The latter ap-
ppears to have a protoconch of several whorls while *E. phyllidis* seems to have
a protoconch of but one large whorl. Comparison of the figures of the adult
shells in these four species indicates that the first two are congeneric and that
all four may be reasonably placed in the same genus or natural group.

**Protocohn Differences in Colus**

Jeffreys (1869, vol. V, pl. 80, figs. 1-3) figures adult shells and apices of three
species of *Colus*. They are *Colus islandicus* (Gmelin), *C. gracilis* (da Costa),
and *C. propinquus* Alder. The figures of the adult shells indicate strongly
that the three species are congeneric. Furthermore the odontophores of *Colus
islandicus*, *C. gracilis*, and *C. propinquus* are similar (Jeffreys, 1867, vol. IV,
p. 344). On the other hand, the figures of the apices show a very large, “swol-
len” and tilted, initial whorl in *Colus islandicus*, a moderately large but not
bizarre initial whorl in *C. gracilis*, and a small and normal initial whorl in *C.
propinquus*. The interesting nature of such differences did not escape Jeffreys
for he says of *Colus islandicus* “apex stiliform, and exhibiting a prominent bulb-
ous point, which is broader than the first regular whorl”: etc., (1867, vol.
IV, p. 332). Of *C. gracilis* he says “apex irregularly mammiform, and twisted
in front. but not prominent or forming a bulbous point as in the last species”: etc. (1867, vol. IV, p. 335). For *C. propinquus* we have “apex blunt, but regu-
larly spiral and compressed, never mammiform or distorted”: etc. (Jeffreys,
1867, vol. IV, p. 338). It is believed that these protoconch differences consti-
tute specific features but the problem is somewhat complicated by evidence
(Thorson, 1935, pp. 13-17, figs. 6-8) that there is much individual variation in
the protoconch of *Colus islandicus*. 

239  **Gastropod Protoconchs: Burnett Smith**
DIFFERENT TYPES OF PROTOCONCH WITHIN THE SPECIES

The problems are now, in many ways, like those encountered in dealing with the genus. When so doing, the present writer discussed different types of protoconchs and the opinions there expressed need not be repeated. One can, however, call attention again to the possible interpretation of *Athleta clayi* Smith as a variety of *Athleta petrosa* (Conrad) or even as an individual variant of that species. If either interpretation were adopted the *A. clayi* type of protoconch would furnish an example of protoconch variation within the species *A. petrosa* (Pl. 1, figs. 19-21). As with the genus, the problem of what constitutes a species can never be finally settled. This is particularly true for fossils and for Recent forms with unknown life history. On the other hand, when the life history is known the matter may be much simplified. For instance, larvae from the same egg capsule, group of capsules, or from capsules of the same kind have a virtually certain specific identity. Some quotations and references bearing on this will now be given.

Dall (1890, p. 66) makes the following statement:

"In general, the advance in biologic rank of any group in process of evolution is marked, if by any change in the larval conditions, by a decrease in the number of embryos and an increase in size of the individual larve. In *Purpura* and *Buccinum* it has been shown that a diminution of the total number is caused by the cannibalism of certain inmates of the same capsule which devour their mates, consequently through this extra diet becoming larger and more sturdy than the embryos less unscrupulous, but which may also chance to survive. At all events, great disparity may be observed in the size and development of larval specimens contained in a single capsule and ready to emerge, not only in the above-mentioned genera, but more markedly in *Chrysodomus* and *Volutopsis," etc.

Many years later the same author (Dall, 1918, pp. 207, 208) says:

"The nuclei or larval shells of species belonging to *Chrysodomus* and its allies present several distinct types and numerous mutations.

"In many cases, as in *Buccinum* and *Busycon*, it was shown many years ago by Lovén and others that a single ovicapule contains a number of ova fertile and unfertile. The unfertile eggs serve as food for the larvae developed from the fertile ones and there is a certain amount of competition between the larvae in the capsule which results in the most vigorous larvae getting more food and making a larger growth than the more weakly coinhabitants of the capsule. Thus at the time of leaving the capsule and coming into the outer world, it sometimes happens that there will be perceptible differences between the individuals issuing from a single capsule, not only in actual size but in the length of the coil of whorls and the size and compactness of the larval apex,"

On an earlier page the present writer has expressed the opinion that there is a general protoconch uniformity among the species of *Busycon*. However, it appears from Dall's statement that this uniformity does not always extend to the inhabitants of a single capsule.
A further observation by Dall in the same paper (p. 208) is: “I have found cases where from the same bunch of capsules one might select bulbous turbinoid, or laxly coiled nuclei.”

Thorson (1935, pp. 7-13, fig. 2) gives some results of studies on the larvae (“embryos”) and egg capsules of a species which he designates as *Siphon curatus* (Jeffr.). After calling attention to the relative uniformity of size and whorl number for individuals of *Buccinum undatum* as they emerge from the capsule the same author writes as follows: “In *Sipho* conditions are different. When two embryos are found in the same egg-capsule, they are as a rule of equal size. In a single case, however, ( . . . . . . .), the two embryos in one egg-capsule were of very different sizes: The developmental stage of the embryo of *Sipho* when it leaves the capsule—in contrast to *Buccinum*—varies greatly, which is but natural when it is considered that one or two embryos can develop in one egg-capsule.” He further says: “It will be seen that examples of capsules with both one and two embryos are almost equally common in the small and the big capsules. This naturally implies that in a capsule with two embryos each of them receives only half the amount of nourishment that is at the disposal of a solitary embryo in a capsule of the same size. Now, the available material showed that in egg-capsules of the same size the embryos ready to hatch were always bigger in capsules containing one than in those with two embryos. Hence it appears that the embryos have no definite time of development in the capsules nor do they emerge at a certain stage, but they remain in the capsule as long as the latter contains any nourishment for them. How long the development will take seems to be determined at a very early stage, since the formation of liver and shell does not seem to begin until all the nurse eggs of the capsule have been absorbed in the intestine of the embryo. If, therefore, the amount of nourishment available for the individual embryo is considerable, and the embryo does not begin to differentiate liver and shell until it has absorbed all this nourishment—that is, after it has reached a rather large size—the number of embryonic whorls will of course be much larger in such embryos than in embryos which have had to compete hard for their nourishment.” Thorson notes further that “embryos of this species” have “always commenced the formation of the final, sculptured, shell before leaving the egg-capsule.” The term “embryonic whorls” he applies to the smooth and unsculptured whorls. The sculpture in *Siphon curatus* may begin at the end of two smooth whorls when the nourishment is used up at this stage but, on the other hand, a solitary “embryo” in a capsule, having no competitors, may not use up its nourishment until it has grown to large size and it may have somewhat over three smooth whorls.

A still more convincing demonstration of protoconch differences within a species is given by Thorson (1935, pp. 13-17, figs. 6-8) for the form which he designates as *Siphon islandicus* (Chemn.). Under the name *Colus islandicus* (Gmelin) (Dall, 1918, pp. 216, 217; Johnson, 1934, p. 124) this species has been considered in discussing protoconch differences within the genus *Colus*. Thorson’s figures (Thorson, 1935, figs. 7A, 7D, 7E, 7F) show clearly the dif-
ferences in size and whorl number to be found in the larval shells from egg capsules. The biggest of these shells, a "solitary" in its capsule, had a length of 8.5 mm. and "showed three and a half whorls, a little more than half a whorl with sculpture." Judging from some of the figures, this sculpture may begin at the end of whorl two or perhaps earlier. The "embryos of one and the same egg-capsule" are often of very different sizes, though in other cases they "seem to be of equal size." Shells of different sizes within a single capsule are figured (Thorson, 1935, fig. 6) and give further confirmation, were any needed, of the statements in the text.

In making specific determinations of the larvae of the two species just reviewed Thorson compared the specimens from egg capsules with apices attached to more or less adult shells. The present writer believes that there can be no reasonable doubt that Thorson was describing protoconch differences within a species in each case. His figures give impressive testimony that these differences were considerable both in degree and in kind.

PARTIAL SUMMARY

The writer has now given a brief review of selections from the literature and has discussed the terminology and some of the more fundamental aspects of the gastropod protoconch, its value or its lack of value in classification, some of its different types, and some of its variations within such natural groups as genera and species. No claim can be made that the subject has been treated exhaustively. The matter so far put forward is in the nature of an introduction to that which follows. The opinion is here expressed that the time has not yet come when a broad philosophy can be built upon the gastropod protoconch. Good evidence has been presented to show that its characters are relatively uniform in some natural groups (Fusinus, Busycon) but equally good evidence has been advanced to show that in other natural groups its characters may vary widely (Ficus, Conus, Athleta, Eucithara, Colus, Sipho curtus, Colus islandicus). In any case the more facts accumulated the nearer to a solution may be the philosophical problems. From the practical standpoint in paleontology the specific identity of any protoconch or other small shell becomes of possible value as a clue to the presence of some important index fossil in a small sample.

It is now proposed to give short descriptions of a number of available protoconchs. Some of these apparently have not as yet been figured and others have not been adequately figured.

PART II.—SOME PROTOCONCHS IN BUSYCON, FASCIOLARIA, AND PLICIFUSUS

METHOD OF WHORL COUNTING

Before taking up the protoconch and its relations with the early conch in any of these forms it is necessary to explain the method of whorl counting used in this paper. A symmetrically coiled larval stage has been recognized in the Gastropoda (Cunningham, 1910, pp. 506, 507; Swinnerton, 1923, pp. 228, 229, fig. 160 after Robert and Pelseneer). In it the shell may be imagined as provided with an umbilicus on the right side and another on the left. With the
subsequent initiation of unsymmetrical coiling one umbilicus becomes conspicuous in apical view, the other, if still retained, in basal view. The expression "apical umbilicus" is here used for an umbilicus well displayed in apical view, the term "basal umbilicus" for an umbilicus conspicuous in basal view. These two terms are used purely in a descriptive sense and carry no implications that the apical or basal umbilicus in a dextral shell is the anatomical equivalent of a corresponding umbilicus in a sinistral shell. Diagram text figure 1 represents the shell in apical view with the apical umbilicus (U) occupying the position as shown. The end of whorl i is arbitrarily fixed at the position of the dotted line V—W. U, V, and W are thus placed in a straight line on the diagram. The shell can be held in such a way that the apical umbilicus occupies a position similar to that of U in the diagram and the end of whorl i as here fixed can be visualized readily on the shell. The ends of whorls 2, 3, 4, etc., can be located on the shell by imagining a line similar to V—W of the diagram projected across these later whorls on the shell. This method of whorl counting does not allow for flexures or angularities at the aperture and is therefore inaccurate to that extent. However, it permits of a rapid whorl count which is approximately correct especially in the earlier whorls of the gastropod shells considered in this paper.

![Diagram Text Figure 1](image)

**Diagram Text Figure 1**

**THEPROTOCONCH OF BUSYCON**

In Recent forms knowledge of the protoconch is usually derived from young individuals which have been removed from the egg capsules. These were known at an early date (Ellis, 1755, pl. XXXIII, figs. a, a¹, a²) but little attention has been paid to them. Apices of the larger specimens of *Busycon* have been similarly neglected. Baker has briefly described and figured the protoconchs of three species of *Busycon*. These are "*Fulgor perversus* Linné," *Busycon canaliculatum* (Linné), and *B. pyrum* (Dillwyn) (Baker, 1897, pp. 693, 694, pl. 19, figs. 27-31). Unfortunately Baker’s figures lack detail and little can be learned from them. Cossmann figures the protoconch of "*Fulgor pyrum* Dillw." (1901, p. 77, fig. 24) but here again the figure is not sufficiently detailed.
Grabau (1903, pp. 516-519, figs. 1, 2, 4; 1912, pp. 754-756, figs. 1-10) figures the protoconch in Recent individuals of *Busycon canaliculatum* (Linné) and describes it in some detail. Shells from the egg capsule of *B. carica* (Gmelin) are also figured with brief description (Grabau, 1903, pp. 516-519, fig. 3). The same author (1903, p. 520) mentions early stages of "Sycotypus pyrus" but presents no figure. In the same paper a sinistral *Busycon* from the egg capsule is figured and referred to "Fulgur perversum" (1903, p. 533, fig. 17). In this paper Grabau gives no figures of the protoconch in fossil examples of the genus *Busycon* but his figures and description of the young stages of Recent *Busycon canaliculatum* furnish points of interest which will now be briefly noted.

According to Grabau (1903, pp. 516, 517) the velum is present on the individual in the egg capsule but "is dropped just before the animal emerges from the capsule, and after the shell is already well developed." At an "early stage the shell is also umbilicated, and since there is no anterior canalicular as yet, this stage has the characteristics of a *Natica* shell." However, a figure published in a later paper (Grabau, 1912, fig. 10) indicates that the anterior canal begins to grow before the basal umbilicus has become completely obscured.

In fossil *Busycon* the protoconch is commonly missing; when present, its preservation is apt to be poor. The well-preserved protoconchs which do occur among the fossils seem to have attracted little attention in the past but recently Gardner (1944, p. 453, pl. 50, figs. 1, 2) has described and given interesting figures of the protoconch in *Busycon montforti* Aldrich from the Alum Bluff group (middle Miocene) of Florida.

As previously noted the protoconch of *Busycon* is relatively uniform throughout the genus. It begins with a smooth and rounded stage usually of about three-quarters of a whorl but sometimes persisting to the end of whorl 1. The smooth and rounded stage is followed by a sculptured stage of about one-quarter of a whorl. This sculpture at first consists of axial ribs or riblets alone or of ribs and spirals on a rounded whorl. There is soon, however, a rather rapid transition into an angulated whorl with "concentration" of the ribs on the angle and their degeneration above and below it. This quarter whorl of youthful sculpture would appear to be largely transitional between the protoconch and the noded and angulated stage of the conch. In most cases one cannot say where protoconch ends and conch begins.

**PROTOCONCH IN BUSYCON CONTRARIUM**

The left-handed or sinistral *Busycons* whose protoconchs are noted in this paper are treated as referable to *Busycon contrarium* (Conrad) (Conrad, 1840, p. 387; 1861, republication of 1893, p. 81, pl. 45, fig. 11). The specific name "contrarium" may eventually become restricted to Miocene and perhaps also to Pliocene forms. However, pending a critical study of all sinistral *Busycons* it is deemed best to employ Conrad’s term for left-handers not assignable to the true *Busycon perversum* (Linné) (Smith, 1939, pp. 23-26, pl. 7, figs. 1, 2).

The type locality for *Busycon contrarium* is at the Natural Well, southwest of Magnolia, Duplin County, North Carolina (Dall and Harris, 1892, pp. 72,
The species is quite abundant in the upper or brownish marl of the Duplin Miocene at this locality. The protoconch is not infrequently present in specimens from the brownish marl but is usually weathered to such an extent that details are obscured. However, this very weathering serves to emphasize an occasional feature not shown by most Busycons. The feature in question is a sharp line, diagonal and sunken, which is seen late in whorl 1 or early in whorl 2. A line much like this marks the end of the protoconch in some gastropods. In the Natural Well specimens under consideration this line in one case seems to precede the earliest sculpture.

Figure 1 of Plate 2 depicts the apical whorls of a Natural Well specimen (Smith Collection, 718, Pal. Research Inst., No. 20054) with a sharp diagonal sunken line in the last quarter of whorl 1. The shell which precedes it is smooth and rounded and rather well preserved. The shell which immediately follows the diagonal line is rounded and probably was ornamented with simple axial ribs. These cannot be certainly recognized here as the shell is weathered considerably. However, axial ribs do show before the whorl becomes angular and they can be seen as the angulation becomes definite at about the end of the first quarter of whorl 2. In this specimen the evidence points to a sudden change in shell growth at the end of a smooth and rounded stage and before the appearance of sculpture. Figure 2 of the same plate represents another individual (Smith Collection, 718, Pal. Research Inst., No. 20055) from the same locality and horizon. Here simple axial ribs or riblets follow the smooth and rounded stage without the interposing of a sharp sunken line. No such line can be identified on this specimen.

The possibility of abrupt protoconch termination in *Busycon contrarium* is again presented by two individuals (Smith Collection, 702, Pal. Research Inst., Nos. 20056, 20057) from the Waccamaw Pliocene of Acme, North Carolina. Figure 3 of Plate 2 shows a sharp angulated sunken line very early in whorl 2. This line occurs after whorl angulation has developed. The line is preceded by faint sculpture and it is followed for a short space by crowded growth lines before the typical noded and angulated stage is established. Figure 4 of the same plate depicts the apical whorls of another individual from the same locality and horizon. Here the sunken line comes very early in whorl 2 and is on an angulated whorl. In this case, however, the line itself is more curved than in the first Acme specimen. It is preceded by definitely curved axial ribs and is soon followed by the noded and angulated stage. This particular sunken line may represent nothing more than an unusually deep depression among a series of axial ribs. On the other hand, this is by no means certain and its possible interpretation as a break in shell growth must not be ignored.

These sharp sunken lines found in examples of *Busycon contrarium* seem to be exceptional features for the species and for the genus *Busycon*.

Although protoconchs in the genus *Busycon* are usually quite uniform in size and shape this uniformity is relative and not absolute. An example of variability within the species is furnished by two individuals (Smith Collection, 702, Pal. Research Inst., Nos. 20057, 20058) of *Busycon contrarium* from the Wacca-
maw Pliocene of Acme, North Carolina. Figure 5 of Plate 2 gives an outline of whorls 1 and 2 in one of these. In this specimen the initial bulb of whorl 1 is normal. Figures 6 and 7 of Plate 2 are outlines representing the early whorls of another Acme individual. Here, however, the initial bulb is not normal but large and discordant.

Figures 8 and 9 of Plate 2 give different views of an immature individual of Busycon contrarium from the Waccamaw Pliocene of Tillys Lake, Horry County, South Carolina (U. S. Nat. Mus. 371028). The apertural view (fig. 8) shows the smooth and rounded stage of the protoconch, the ribbed and spiralled stage late in whorl 1 and early in whorl 2, and the noded and angulated stage above the aperture. The nonapertural view (fig. 9) shows the apical umbilicus and smooth and rounded stage of the protoconch at top and the transition from the ribbed and spiralled stage to the noded and angulated conch stage early in whorl 2.

Figures 10, 11, and 12 of Plate 2 represent a Recent individual of Busycon contrarium taken from the egg capsule (Pal. Research Inst., No. 20935). It was collected (September 2, 1936) by Katherine V. W. Palmer from the ocean beach at Cape Lookout, North Carolina. Figure 10 is an apertural view showing the initial bulb followed by prominent growth lines. Spirals appear on the rounded whorl. The aperture (at about the end of the first quarter of whorl 2) shows the shoulder angulation. Figure 11 represents the same individual turned clockwise slightly. At top is the initial bulb. Rather strong growth lines follow and then spirals appear. Axial ribs and incipient angulation are shown at the right of the figure. The same individual is depicted in nonapertural view by figure 12. Here the initial bulb shows at the top. Below the rounded ribbed stage is seen at the left. Its transition into the noded and angulated stage of the conch is about accomplished by the first quarter of whorl 2 (right of figure).

**PROTOCONCH IN BUSYCON CF. FUSIFORME**

An immature individual probably referable to Busycon jasiforme (Conrad) (Conrad, 1861, republication of 1893, p. 82, pl. 46, fig. 3; Martin, 1904, pp. 178, 179, pl. 45, figs. 2, 3a, 3b) is to be found in the collection of the United States National Museum (U. S. Nat. Mus. 371029). The specimen is from the St. Mary’s Miocene of the St. Mary’s River, Maryland (U. S. G. S. Sta. No. 2252). So far, the writer has seen no adult shells of B. jasiforme with the protoconch intact. The specific identification of the specimen in question is therefore tentative. Figure 13 of Plate 2 depicts this immature individual in apertural view. The smooth and rounded first whorl appears above. Whorl 2 shows the beginning of spirals and axial ribs. Whorl angulation is marked at the aperture. Figure 14 gives the nonapertural view of the same individual. At top is the smooth and rounded stage of whorl 1. Whorl 2 shows at right the transition from ribs and spirals on a rounded whorl into the noded and angulated stage of the conch. This latter stage is well established at center and to left.
Gastropod Protoconchs: Burnett Smith

Protococon in Busycon Coronatum or B. rugosum

Figures 15 and 16 of Plate 2 depict two immature individuals from the St. Mary's Miocene of the St. Mary's River, Maryland (U. S. Nat. Mus. No. 115307, U. S. G. S. Sta. No. 2252). They are believed referable either to Busycon coronatum (Conrad) or to B. rugosum (Conrad) (Conrad, 1861, republication of 1803, pp. 82, 83, pl. 46, figs. 1, 4; Conrad, 1868a, p. 267, pl. 24, figs. 1, 4; Martin, 1904, pp. 180-182, pl. 46, figs. 1a, 1b, 2a, 2b). Figure 15 of a broken immature shell shows the early development of the columnella and the beginning of the sutural channel. Figure 16 is of another individual in nonapertural view. Its general proportions and sculpture indicate that it belongs to the channeled division of Busycon (Sycotypus) (Grabau, 1903, fig. 4) but no attempt is here made to decide whether the specimen should be referred to B. coronatum or to B. rugosum—the two channeled Busycons of the St. Mary's Miocene. The smooth and rounded stage is followed by a very short stage of spirals and axial riblets on a rounded whorl. The noded and angulated stage starts at about the beginning of whorl 2 and can be seen at the left of the figure.

Protococon in Busycon Inzile

Figures 17 and 18 of Plate 2 are of an immature individual from the Yorktown Miocene, near Yorktown, York River, Virginia (Smith Collection, 739, Pal. Research Inst., No. 20059). Shell shape and sculpture indicate that the specimen belongs among the channeled Busycons (Sycotypus) (Grabau, 1903, fig. 4). As Busycon inzile (Conrad) (Conrad, 1868b, pp. 64, 65, pl. 6, fig. 2) appears to be the only channeled Busycon from the Yorktown formation of this locality (Clark and Miller, 1912, p. 168) the immature individual is assigned to that species. Figure 17, the apertural view, shows in whorl 1 the smooth and rounded stage followed by a short stage of weak sculpture consisting of axial riblets and spirals. At slightly over 1½ whorls the aperture is plainly angulated. Figure 18, the nonapertural view, shows the smooth and rounded stage in the upper volution. In the lower volution illustrated (parts of whorls 1 and 2) the transition from the early sculpture to the noded and angulated stage of the conch is seen. This latter stage is definitely established early in whorl 2.

Protococon in Busycon Pyrum

It may eventually become necessary to make a number of species out of the Recent and fossil shells which are usually referred to Busycon pyrum (Dillwyn) (Dillwyn, 1817, vol. 1, p. 485; Dillwyn (Lister), 1823, pl. 877, fig. 1). The term is therefore used broadly here to designate those forms assigned to B. pyrum which have a short spire, long anterior canal, and a not too deep sutural channel. In such a sense the term would include Recent examples (Gardner, 1944, pl. 50, fig. 9), B. pyrum epynotum (Dall) and probably B. pyrum liber-tiensae Mansfield but would not include B. pyrum propiceincte Mansfield (Mansfield, 1930, pl. 8, fig. 6; pl. 10, fig. 3; pl. 9, fig. 5), B. inzile (Conrad) (Conrad, 1868b, pp. 64, 65, pl. 6, fig. 2), and B. excavatum (Conrad) (Conrad, 1840, p. 387; 1861, republication of 1893, p. 82, pl. 45, fig. 12).
Figures 19 and 20 of Plate 2 give different side views of the apical whorls of a Recent individual of *Busycon pyrum* from Sanibel Island, Florida (Pal. Research Inst., No. 20036), collector Katherine V. W. Palmer. Figure 19 shows the smooth and rounded stage followed by early sculpture late in whorl 1. Whorl 2 shows the noded and angulated stage of the conch. Figure 20 is of the same individual turned slightly so as to bring to view the passage from the early sculpture to the noded and angulated stage. The largest volution illustrated (parts of whorls 2 and 3) shows the noded and angulated stage of the conch. Figure 21 gives an outline of another Recent individual of *B. pyrum* collected by Katherine V. W. Palmer at Sanibel Island, Florida (Pal. Research Inst., No. 20037). This outline is introduced for comparison with figure 19. It shows a protoconch with relatively smaller initial bulb.

**PROTOCONCH IN BUSYCOK EXCAVATUM**

Figures 22, 23, and 24 of Plate 2 give different views of the apical whorls of an individual (Smith Collection, 709, Pal. Research Inst., No. 20061) from the Waccamaw Miocene of Aome, North Carolina. It is referred to *Busycon excavatum* (Conrad) (Conrad, 1830, p. 387; 1861, republication of 1857, p. 82, pl. 45, fig. 12; 1868a, p. 267, pl. 23, fig. 6). In figure 22 is seen the noded and angulated stage and the early sculpture of ridlets and spirals in whorl 1. This early sculpture appears first on a rounded whorl but angulation is attained by the end of whorl 1. Whorl 2 shows the noded and angulated stage of the conch. In figure 23 the shell is turned slightly in order to bring to view the passage from the early sculpture into the noded and angulated stage. Largest volution illustrated (parts of whorls 2 and 3) shows the noded and angulated stage of the conch. Figure 24 depicts slightly more than the first two whorls in apical view. Smooth and rounded stage and early sculpture are seen in whorl 1, noded and angulated stage in whorl 2. Beginnings of sutural channel appear toward the end of whorl 2.

**PROTOCONCH IN BUSYCOK CP. EXCAVATUM**

Figures 1, 2, and 3 of Plate 3 give different views of the apical whorls of an immature individual (Smith Collection, 746, Pal. Research Inst., No. 20060) which is probably referable to *Busycon excavatum* (Conrad). It came from the bluish beds below the highly fossiliferous brownish marl at the Natural Well, southwest of Magnolia, Duplin County, North Carolina (Dall and Harris, 1892, pp. 72, 73; Miller, 1912, p. 241). The age is Duplin Miocene. Figure 1 shows the smooth and rounded stage followed by the early sculpture of axial ridlets and spirals late in whorl 1. Whorl 2 shows the noded and angulated stage. In figure 2 the shell is turned slightly to bring out another view of the passage from the early sculpture to the noded and angulated stage. The largest volution illustrated (parts of whorls 2 and 3) shows the noded and angulated stage of the conch. Figure 3 is an apical view of whorl 1 and almost all of whorl 2. Smooth and rounded stage, early sculpture, and noded and angulated stage are shown.

**INTERPRETATIONS**

Protoconch and early conch have now been figured and briefly described or noted in some 15 individuals of *Busycon*. This includes Miocene, Pliocene, and
Recent specimens of *Busycon contrarium*, a Miocene individual probably referable to *B. fusiforme*, two Miocene specimens assignable either to *B. coronatum* or to *B. rugosum*, a Yorktown Miocene example of *B. inculle*, Recent specimens of *B. pyrum*, a Pliocene example of *B. excavatum*, and a Miocene specimen which may be assignable to *B. excavatum*.

In only three of these 15 specimens is there evidence of any abrupt halt or change in shell growth. This evidence is furnished by the sharp sunken line present in one Miocene and two Pliocene examples of *Busycon contrarium* (Pl. 2, figs. 1, 3, 4). In the Miocene specimen the line comes in the later part of whorl 1, apparently preceding all sculpture. The lines in the Pliocene examples are associated with the early sculpture and precede the typical noded and angulated stage. Such irregularity in the position of the lines would seem to rule out their interpretation as protoconch terminations. As already noted these sharp sunken lines appear to be exceptional features in *Busycon contrarium* and in the genus *Busycon*.

Most of the well-preserved specimens of *Busycon*, examined so far, show an unbroken ontogenetic sequence in going from the first or smooth and rounded stage, through the short period of early sculpture, and into the typical noded and angulated stage. The first of these changes cannot be described as abrupt while the second is clearly transitional. The smooth and rounded stage is obviously referable to the protoconch and the typical noded and angulated stage is as surely assignable to the conch. The difficulty then is to properly interpret what comes between these two stages. The first sculpture to appear on the rounded whorl is made up either of axial riblets alone or of these and spirals with the riblets dominant. This earliest sculpture on the rounded whorl is believed assignable to the protoconch and is regarded as the correlate of the riblet stage of *Fusinus* and the curved-rib stage of *Athleta* and other forms. The remainder of the early sculpture in *Busycon* consists of shortening axial riblets which “concentrate” on a developing shoulder angle and this period of growth cannot be placed in either protoconch or conch but must be regarded as a transition from one to the other.

**THE PROTOCONCH OF FASCIOLARIA**

An early comment on the *Fasciolaria* protoconch is to be found in the work of Watson (1886, p. 243). He describes *Fasciolaria rutilla* Watson and adds that the species “is an exceptional form, having the apex of a *Fusus* (a feature shared by *Fasciolaria coronata*, Lam.),” etc.

Dall figures the apical whorls of *Fasciolaria tulipa* (Linnae) and describes and figures those of *F. distans* Lamarck and *F. apicina* Dall (1890, pl. 7, fig. 11, p. 193; pl. 7, figs. 10, 11b). His statement on *F. distans* is as follows:

“In *F. distans* (recent) the nucleus is smaller than the first whorl, smooth, subglobular, and is followed by a nearly smooth half whorl; then the succeeding coils to the number of two are faintly spirally sulcate, with two or three channels behind the periphery and ten or fifteen in front of it. The shell soon becomes perfectly smooth and remains so, except on the canal.” For *F. apicina* the following occurs:
"In *F. apicina* the nucleus is swollen and often larger than the first succeeding whorl. The latter is sculptured with numerous equal, distinct, transverse ribs extending across the whorl and without spiral sculpture. The spirals appear suddenly in the shape of about five strong, flattish, elevated bands, of which the two anterior are shorter than the rest. The transverse ribs become more distant and are visible only as the spirals rise and become swollen in passing over them. There are about ten to the whorl of these waves or ribs; they are strong at the periphery, but do not reach the sutures." It is to be noted that the word "ribs" of this quotation is used by Dall for conch features later than the early sculpture for which the terms "riblet" and "curved-rib" have been used in this paper. The apical whorls of a form referred to *Fasciolaria apicina* will be discussed beyond.

Baker has given brief descriptions of the early whorls in *Fasciolaria* which he assigns to the species "*tulipa*", "*distans*", and "*gigantea*"; he also figures the last of these (Baker, 1897, p. 293, pl. 19, figs. 25, 26). These figures of early whorls and young shell are in outline only.

Grabau figures the young shell in a form referred with some doubt to "*Fasciolaria gigantea*" (Grabau, 1903, pp. 535-536, figs. 18d, 19). Grabau’s figure 19 is of a young shell taken from the egg capsule. He also says of this shell: "In *Fasciolaria gigantea* ribs appear first (Fig. 19), the spirals afterwards." The same writer (Grabau, 1912, p. 756) states that the initial whorl in "*Fasciolaria gigantea*" has a diameter of 2.35 mm.

Strebel figures the protoconch in *Fasciolaria tulipa* (Linne), *F. distans* Lamarck, *F. papillosa* Sowerby, *F. salmo* Wood, *F. aurantiaca* Lamarck, *F. acutispira* Strebel, *F. heynemani* Dunker, *F. dunkeri* Strebel, *F. filamentosus* Martini, *F. filamentosus globulosa* Dunker, *F. trapezium* (Linne), *F. lignaria* (Linne), and *F. coronata* Lamarck (Strebel, 1911, pl. 1, figs. 1a, 1b, 1c, 6; pl. 2, fig. 8a; pl. 3, fig. 16; pl. 5, figs. 23a, 26, 28a, 28b; pl. 6, figs. 32a, 33a; pl. 7, figs. 37, 38a; pl. 9, fig. 40; pl. 10, figs. 50, 50a). In this work he discusses some 32 forms. To have 13 of these with protoconch intact seems remarkable regardless of whether or not the entire 32 are congeneric. All of Strebel's protoconch figures depict the smooth and rounded stage. In six figures an early sculpture (riblet stage, curved-rib stage) is definitely shown preceding the more or less adult features of the conch. These six figures represent the five species *Fasciolaria tulipa*, *F. distans*, *F. salmo*, *F. acutispira*, and *F. heynemani*. The whorls of the protoconch appear to be large and few in number in *F. salmo*. On the other hand the protoconch whorls appear to be small in *F. acutispira* and the smooth and rounded stage have unusual length. Strebel's figures also picture variations in the relative size and attitude of the initial whorl. On the whole his illustrations indicate that rigid uniformity is not present in the early whorls of all the species included in the genus *Fasciolaria*.

Woodring (1928, pp. 255, 256) discusses the early whorls of *Fasciolaria semistratata leura* Woodring from the Bowden formation (middle Miocene) of Jamaica. He says: "Nucleus consisting of about one and a half whorls, the first whorl cap-shaped and forming a broad blunt apex, the last half whorl bearing obscure spiral threads and very obscure axial wrinkles. . . . . . . . . . . . First few
post-nuclear whorls bearing a broad thread at suture and obscure finer threads over remainder of whorl, and also very obscure axial undulations.” Woodring, in comparing his subspecies with the Recent F. tulipa (Linne), says: “It also has a stouter nucleus, and the axial sculpture on the latter part of the last nuclear whorl is much fainter. Likewise the suggestion of axial nodes is stronger on the first post-nuclear whorls of living specimens.”

Gardner (1944, p. 443, pl. 49, figs. 5, 6) describes and figures the apical whorls of Fasciolaria kindlei Maury from the Alum Bluff group (middle Miocene) of Florida. She writes: “The nucleus is large and obtuse and performs approximately two revolutions. The initial turn is smooth, rather strongly inflated, and partially immersed. The first half of the second revolution is moderately inflated mediadly and smooth. Axial sculpture is introduced within the final half turn in the form of 4 to 8 axial costae, which are uniform in elevation between the sutures and become increasingly broader toward the close of the protoconch. The beginning of the conch is indicated by the introduction of the postnuclear axial sculpture and by the gradual initiation of the spirals; the spiral that later crowns the periphery, the primary in front of it, and a single shoulder spiral appear at the beginning of the conch.” Gardner’s figures both show the smooth and rounded stage and the conch sculpture. Her figure 3 shows also the early sculpture of riblets (curved-rib stage) and the apparently abrupt start of conch features.

Figures published by Strebel and by Gardner prove the presence of a smooth and rounded stage and of a stage of early sculpture (riblet stage, curved-rib stage) in the apical whorls of Fasciolaria tulipa, F. distans, F. salmo, F. acutispira, F. keynemannii, and F. kindlei. These two stages are assigned to the protoconch by Gardner (1944, p. 443) and are so interpreted in this paper.

Although protoconch differences in Fasciolaria may not be so wide as in some other genera, there are nevertheless quite appreciable variations, individual and specific. Attention will now be called to some of these.

Protoconch in Fasciolaria apicina

In the Waccamaw Pliocene of Acme, North Carolina, there is a form which is believed to be referable to Fasciolaria apicina Dall (Dall, 1890, pp. 102, 103, pl. 7, fig. 11b). This species was originally described from the Caloosahatchee Pliocene of Florida but it has since been reported from the Waccamaw Pliocene of the Carolinas (Dall, 1892, p. 212; Miller, 1912, p. 256). The Acme specimens agree fairly well with Dall’s figure and also with his description except that they lack the “internal presutural elevated rib.” It is believed that the absence of this feature in the Acme specimens hardly justifies their removal from F. apicina. Five ontogenetic stages are indicated for the adult Acme individual. These are, first, a smooth and rounded stage of about 1½ whorls followed by an axial riblet stage of slightly over 1½ whorls; these two stages being assigned to the protoconch. Early in whorl 2 begins a gently angulated stage with spirals and axial undulations or ribs. The latter soon weaken with “concentration” of nodes at the shoulder angle. The nodes themselves then weaken and the shoulder angle disappears. This more or less angulated stage is believed to be the correlate of the noded and angulated stage of Busycon. Following this angulated stage
is a fourth with spirals on a rounded whorl which may persist for perhaps one
volution. The fifth and last stage is rounded and without sculpture except for
weak spirals on the anterior canal. Spiral color markings, however, are present
in this last ontogenetic stage.

Two individuals from the Waccamaw Pliocene of Acme, North Carolina, are
illustrated on Plate 3, figures 4-10. They are assigned to *Fasciolaria apicina* Dall
though it may eventually be necessary to provide them with a subspecific designa-
tion. The smaller specimen (Smith Collection, 699, Pal. Research Inst., No.
20062) has a small and normal initial bulb and never attains the fifth or final
ontogenetic stage of the species. Figure 4 gives this individual in nonapertural
view and shows successively the smooth and rounded stage and axial riblet stage
of the protoconch, the angulated stage of early conch life, and the succeeding stage
of spirals on a rounded whorl. Figure 5 is a side view of whorls 1 and 2 of the
same individual and depicts the smooth and rounded stage followed by the riblet
stage in whorl 1 and the angulated stage in whorl 2. Figure 6 is another side
view showing whorl 1 and approximately the first quarter of whorl 2. Figure 7
is an apical view of somewhat more than the first two whorls of the same individ-
ual. It shows the relatively small initial bulb, the first two ontogenetic stages,
and a part of the third. The larger individual (Smith Collection, 699, Pal. Re-
search Inst., No. 20063) is noteworthy in having a very large initial bulb. Figure
8 is a side view of whorls 1 and 2 and depicts the smooth and rounded stage and
the riblet stage of the protoconch in whorl 1 and the angulated stage of the conch
in whorl 2. Figure 9 is another side view showing smooth and rounded stage, the
end of the riblet stage, and its passage into the angulated stage of the conch. The
last is shown with the sculpture’s “ruggedness” somewhat exaggerated. Figure
10 displays an apical view of slightly more than the first two whorls of the same in-
dividual. The very large initial bulb is brought out and the first three ontogenetic
stages are shown.

The two individuals just discussed are from the same locality and horizon
and are rather clearly to be included in the same species. The protoconch differ-
ences are therefore interpreted as individual variations probably comparable in a
general way to those observed by Thorson (1935, pp. 7-17, figs. 2, 6-8) in Arctic
gastropods.

**PROTOCONCH IN FASCIOLARIA TULIPA**

Mention has already been made of published figures of the protoconch and
other apical portions of this species (Dall, 1890, pl. 7, fig. 11; Strebel, 1911, pl. 1,
figs. 1a, 1b). An immature Recent specimen referable to *Fasciolaria tulipa*
(Linné) is introduced on Plate 3, figures 11-13 for comparison with the young
stages of *F. apicina*. The specimen in question (Smith Collection, 1071, Pal. Re-
search Inst., No. 20064) was collected by Anastasia Beatty on the west coast of
Florida. Figure 11 gives the individual in nonapertural view and shows the
smooth and rounded stage and the riblet (curved-rib) stage of the protoconch.
followed by the conch stage of spirals on a rounded whorl. The angulated stage seen in *F. apicina* is here omitted except for some faint vestiges of axial undulations early in whorl 2. Figure 12 depicts whorls 1 and 2 of the same individual. Whorl 1 shows the smooth and rounded stage and the riblet (curved-rib) stage of the protoconch, whorl 2 the conch stage of spirals on a rounded whorl. Figure 13 represents very slightly more than the first two whorls of this individual in apical view. The smooth and rounded stage of the protoconch occupies a little more than 1/2 whorl while the riblet (curved-rib) stage of the protoconch is a little less than 1/2 whorl. Whorl 2 is mostly characterized by the conch stage of spirals on a rounded whorl with indications of vestigial axial undulations in the first 1/3 of the whorl.

In the distribution of its protoconch stages this individual of *Fasciolaria tulipa* is very like the specimens of *F. apicina* from Acme, North Carolina. In the virtual suppression of the first or angulated stage of the conch *F. tulipa* is quite different from *F. apicina* in which this stage, though short, is well marked. Both species have the next conch stage of spirals on a rounded whorl but in *F. apicina* this is short while in *F. tulipa* it is more persistent. The last and longest stage in *F. apicina* is rounded and smooth and without sculpture except for weak spirals on the anterior canal. This last stage in its typical form is apparently never attained by *F. tulipa*.

**Protoconch in Fasciolaria papillosa**

As already noted the protoconch of *Fasciolaria papillosa* Sowerby has been figured by Strebel (1911, pl. 2, fig. 8a). His figure shows a large and prominent initial whorl which displays the smooth and rounded stage of the protoconch. This is followed by three conch volutions characterized by the angulated stage. The intervening stage of early sculpture (riblet stage) is, however, not illustrated. On Plate 3, figures 14-16 the apical whorls of a Recent individual of this species are depicted in different views. The specimen here illustrated (Smith Collection, 1970, Pal. Research Inst., No. 20691) was collected by Anastasia Beatty on the west coast of Florida. Its initial whorl is less prominent than the initial whorl of the subject of Strebel's figure. Figure 14 is a side view of whorls 1 and 2 and part of whorl 3 in this west Florida specimen. At top the smooth and rounded stage is followed by the first part of the riblet stage, here without spirals. At bottom is the angulated stage of the conch with its axial undulations crossed by spirals. Figure 15 is another side view, the specimen being turned in such a way that the late riblet stage, with faint spirals between its axials, can be seen. The change from the riblet stage of the protoconch to the angulated stage of the conch follows. Here the spirals cross the axial undulations. Figure 16 is an apical view of slightly more than the first two whorls. The smooth and rounded stage is seen occupying all of whorl 1. This is followed early in whorl 2 by the riblet stage of the protoconch which persists to about the middle of the whorl. Toward the end of this stage faint spirals appear between the axial riblets. The remainder of whorl 2 is characterized by the angulated stage of the conch with its axial undulations crossed by spirals.
INTERPRETATIONS

As already stated protoconch differences observed in *Fasciolaria apicina* are believed to represent individual variations. A like interpretation will probably cover the discrepancy in size of initial whorl noted in *F. papillosa*. There appear to be, however, other protoconch differences in *Fasciolaria* which characterize species and groups of species. The protoconch of one whorl or slightly over divided rather evenly between the smooth and rounded stage and the riblet (curved-rib) stage is known to be present in *F. tulipa*, *F. apicina* and the Miocene *F. rhomboidea* Rogers (Rogers, 1884, p. 672, pl. 5, fig. 3). Judging from Strebel's figures (1911, pl. 1, figs. 43, 6) this condition probably prevails in *F. cistans* as well. Contrasted with the type of protoconch just noted is that found in *F. papillosa*. Here the smooth and rounded stage occupies all of whorl 1 and may go a short distance into whorl 2. This is followed by half a whorl or less of the riblet stage to complete the protoconch. It would appear from Gardner's description and figures (Gardner, 1914, p. 543, pl. 49, figs. 5, 6) of the early whorls of *F. kiideli* that the conditions there approach those encountered in *F. papillosa*. The evidence, so far, indicates that there are two kinds of protoconch variation in *Fasciolaria*, one individual, the other to be regarded as specific.

THE PROTOCONCH OF *PLICIFUSUS*

No general statement can be made for the protoconch characters in the species, closely related on the one hand, heterogeneous on the other, which have been placed in this genus. However, a form believed to be referable to the genotype (Dall, 1902, p. 523) has furnished protoconchs and two of these will now be considered.

PROTOCONCH IN *PLICIFUSUS* KNOWN

The early whorls of this species have been described and figured by Friele (1882, pp. 5, 10, 17, pl. 2, figs. 12-13) and by Thorson (1925, pp. 19, 20, fig. 13). These figures, however, lack detail and do not bring out some of the interesting features of shell growth. An adult individual of the species apparently goes through four ontogenetic stages. There is first a smooth and rounded stage occupying about one whorl which is followed by about ½ whorl of weak early sculpture. These two stages are assigned to the protoconch. Conch sculpture begins abruptly as far as known and consists of axial undulations and fine spirals. This third stage persists for several volutions. Toward the end of shell growth a relatively short fourth stage is reached. In this last stage the axial undulations become vestigial or absent but the fine spirals still remain on the body of the whorl. Anteriorly the spirals become much coarser though they diminish in strength somewhat on the siphonal fasciole proper where they may also be more or less obscured by growth lines. In all of the ontogenetic stages the whorls are rounded and without any true angulation.

Figures 17-22 of Plate 3 show the apical whorls of two individuals that are believed referable to *Plieifusus kroeyeri* (Möller) (Tryon, 1881, pp. 130, 205, pl. 53, figs. 333-335; Harmer, 1914, pp. 128, 149, pl. 15, fig. 5). Figures 17-19 give
three different views of the apical whorls of one of these individuals (Smith Collection, 999, Pal. Research Inst., No. 20664). Its initial bulb is of relatively small size. The specimen came from the Quaternary deposits of the Petite Rivière-du-Loup, Province of Quebec, Canada. It is probably post-Glacial in age. Figure 17 shows the smooth and rounded first whorl of normal proportions and the weak protoconch sculpture of faint ribletlike growth lines. These start at about the beginning of whorl 2. The largest volute illustrated (parts of whorls 2 and 3) shows the conch stage of axial undulations crossed by fine spirals. In figure 18 the specimen is turned in such a way that the later protoconch sculpture and sharp end of protoconch can be seen. The later protoconch sculpture is made up of faint ribletlike growth lines now straight and diagonal in position. The sharp end of the protoconch might be regarded as the last of these growth lines. The conch sculpture begins abruptly and is seen in the rest of whorl 2 and in whorl 3. Figure 19 gives the apical view of slightly more than the first two whorls. Figures 20-22 give three different views of the other individual referred to Plicifusus kroyeri (Smith Collection, 1121, Pal. Research Inst., No. 20667). It has a large and tilted initial bulb. This specimen came from the Quaternary deposits of the Rivière-du-Sud, near St. François Montmagny, Province of Quebec, Canada. It is probably post-Glacial in age. Figure 20 depicts the smooth and rounded stage followed by weak protoconch sculpture of growth lines and faint spirals. The protoconch sculpture starts at about the beginning of whorl 2. The largest volute illustrated (parts of whorls 2 and 3) shows the conch stage of axial undulations crossed by fine spirals. Figure 21 is of the same individual turned in such a way that the later protoconch sculpture and end of protoconch can be seen. The conch sculpture of axial undulations and fine spirals begins abruptly. The first two or three undulations are diagonal and roughly parallel the protoconch growth lines and termination. After these early undulations in whorl 2, the conch sculpture is of the normal kind in the remainder of this whorl and in whorl 3. Figure 22 shows the first two whorls and about 1/4 of whorl 3 in apical view.

**INTERPRETATIONS**

The examples of Plicifusus kroyeri just discussed were derived from terraces bordering the Petite Rivière-du-Loup and the Rivière-du-Sud respectively. In neither case was the specimen obtained in place but in each case the landslide which brought the fossils to light could only have come from terrace material. Whitcomb and Richards (1937, pp. 252, 253) report glacial till overlying late glacial clays at “Rivière du Loup.” The Petite Rivière-du-Loup landslide locality did not yield a section but the terrace surface, intact and displaced, did not suggest glacial till. The Rivière-du-Sud terrace has an altitude of about 125 feet (Orleans Sheet); the Petite Rivière-du-Loup terrace is probably lower. A meager section near the top of the Rivière-du-Sud terrace showed a coarse layer overlying the fine-grained marine deposit and underlying fine material passing into soil. This coarse layer was quite thin, rather surely stratified, and not at all like glacial till. It is interpreted as representing a transient fluviatile episode
preceding the erosion of the material constituting the present terrace. It is believed that at each locality the fossils came from a deposit not overlain by till and to that extent post-Glacial. These geological data are given in order to clarify the statement that the specimens are probably post-Glacial in age.

The protoconch differences seen in these two individuals of *Plicifusus kroyeri* may, of course, be racial and related to bathymetric, geographic, or geologic factors. Without a large set of well-preserved protoconchs from each locality the question of racial differences must remain an open one. However, in the absence of evidence to the contrary, it is believed that individual variation furnishes the more probable explanation and that the differences in these two protoconchs are comparable in a general way to those observed by Thorson (1935, pp. 7-17, figs. 2, 6-8) in other gastropods of Arctic environment.

**OBSOLETE MARKINGS ON THE PROTOCONCH**

Throughout the present paper the first ontogenetic stage of the protoconch has been called either “smooth and rounded” or more simply “smooth.” Apparently the term “rounded” can always be used appropriately but “smooth,” though applicable in the great majority of cases, is, in rare instances, subject to qualification. Transverse, oblique, and slightly curved or bent wrinkles have been observed on the otherwise smooth stage of a Waccamaw Pliocene specimen (Smith Collection, 699, Pal. Research Inst., No. 20062) of *Fasciolaria apicina* Dall and also in a Recent specimen (Smith Collection, 1071, Pal. Research Inst., No. 20064) of *F. tulipa* (Linné). In the former (diagram text figure 2) the curve or bend is convex to the left and is seen in the region of the apical umbilicus. In the latter species (diagram text figure 3) the curve is convex to the right and is seen just above the suture of contact below. The origin of these wrinkles is unknown but in each case a shrinking or withdrawing visceral mass might cause the surface of the protoconch to wrinkle if its material were sufficiently plastic. The specimen of *F. apicina* is from Acme, North Carolina, and has been illustrated in figures 4-7 of
Plate 3. The specimen of *F. tulipa* is from the west coast of Florida. It has been illustrated by figures 11-13 of Plate 3. The wrinkles just considered must not be confused with the riblets or curved ribs which are found later in the protoconch.

The Quaternary individual (Smith Collection, 999, Pal. Research Inst., No. 20066) of *Plicifusus kröyeri* (Möller) from the Petite Rivière-du-Loup (Pl. 3, figs. 17-19) exhibits an abundance of obscure markings of a different nature. These are faint and very closely spaced spirals (diagram text figure 4) on the otherwise smooth portion of the protoconch in whorl 1. They may represent incipient sculpture produced by the mantle or they may be features roughly comparable to the radiating lines noted by Grabau (1902, p. 925, fig. 8; 1903, p. 517) in the early transparent hyaline shell of *Busycon conicum*.

![Diagram Text Figure 4](image)

**SUMMARY OF PART II BUSYCON**

The protoconch has been described and figured in *Busycon contrarium*, *B. cf. fusiforme*, *B. coronatum* or *B. rugosum*, *B. incile*, *B. pyrum*, *B. excavatum*, and *B. cf. excavatum*. In these forms the protoconch is relatively uniform in its characters. Evidence at hand indicates that in the genus *Busycon* there is usually a transition from the late protoconch sculpture into the noded and angulated stage of the conch.

**Fasciolaria**

For *Fasciolaria apicina* individual variation in the protoconch has been described and two different protoconch types have been figured. In their protoconchs *F. apicina* and *F. tulipa* are much alike but they both differ from *F. papillosa* with its relatively long smooth and rounded stage and less typical riblet stage. Protoconch variations in *Fasciolaria* are therefore of two kinds—individual and specific. In the Fasciolarias studied the change from protoconch to conch would appear to be much more rapid than in *Busycon*.

**Plicifusus**

Two types of protoconch have been described and figured for *Plicifusus kröyeri*. Their differences are believed to represent probable individual variation. In the specimens of *P. kröyeri* discussed the change from protoconch to conch is an abrupt one.
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PLATES

PLATE I (VOL. PL. 21)

14,15. *Conus adversarius* Conrad

(14) Nonapertural view of young individual of two whorls. Smooth stage (protoconch) occupies about 1 1/2 whorls. This is followed by the noded and angulated stage of the conch. Length dimension about 2.6 mm. (15) Apertural view of same individual. Outer lip of aperture shown restored. Acad. Nat. Sci. Philadelphia, No. 4662. Miocene (Duplin). From the upper or brownish marl at the Natural Well, southwest of Magnolia, Duplin Co., N. C.

16. *Conus adversarius* Conrad

Apical whorls. Smooth stage (protoconch) occupies about 1 1/2 whorls. Growth lines but no true curved ribs occur late in the protoconch. Protoconch is followed abruptly by the noded and angulated stage of the conch. Diameter of whorl 3 is about 1.9 mm. U. S. Nat. Mus., No. 16457. U. S. Geol. Surv. locality, No. 3399. Pliocene (Caloosahatchee). Shell Creek, Fla.

Figures 9-16, drawings by Ethel Ostrander Smith

17. *Athleta petrosa* (Conrad)

Apical whorls. Smooth stage (protoconch) of about 3 whorls followed by the curved-rib stage (protoconch) of 1/2 whorl or less. Conch ornamentation begins in the next to the last whorl illustrated. Length, 1.5 mm. Specimen, Acad. Nat. Sci. Philadelphia. Eocene. Woods Bluff, Ala.

18. *Athleta petrosa* (Conrad)

Apical whorls. Smooth stage (protoconch) of about 2 whorls followed by the curved-rib stage (protoconch) of about 1 1/2 whorls. Conch sculpture shown in last whorl illustrated. Length, 1.3 mm. Specimen, Acad. Nat. Sci. Philadelphia. Eocene. Jackson, Miss.

19. *Athleta petrosa* (Conrad)

Apical whorls. Smooth stage (protoconch) of somewhat over 2 whorls followed by the curved-rib stage (protoconch) of about 1 1/4 whorls. Largest illustrated whorl shows curved-rib stage at right, conch sculpture at left. Length about .75 mm. Specimen, Acad. Nat. Sci. Philadelphia. Eocene. St. Maurice, La.

20. *Athleta clayi* Smith


21. *Athleta clayi* Smith


22. *Athleta cyanus* (Conrad)


Figures 17-22, drawings by Helen Winchester
EXPLANATION OF PLATE I (21)

1. *Ficus papyratia* (Say)*  ........................................... 17
   Apical whorls. Smooth stage (protoconch) occupies about one whorl.
   Greatest diameter, 3.2 mm. Specimen, Acad. Nat. Sci. Philadelphia. Re-

2. *Ficus papyratia* (Say) ........................................... 17
   Apical whorls. Smooth stage (protoconch) occupies slightly more than 
   one whorl. Greatest diameter, 3.2 mm. Specimen, Acad. Nat. Sci. Phila-

3. *Ficus papyratia* (Smith) ......................................... 17
   Apical whorls. Smooth stage (protoconch) occupies about 1 3/4 whors.
   Greatest diameter, 3 mm. Specimen, Acad. Nat. Sci. Philadelphia. Mis-
   sissippi. Bowden, Ifamien.

4. *Ficus mississippicus* Conrad ..................................... 17
   Apical whorls. Smooth stage (protoconch) occupies slightly more than 3
   whorls. Greatest diameter, 3.5 mm. Specimen, Acad. Nat. Sci. Philadel-
   phia. Oligocene. Vicksburg, Miss.

5. *Ficus filia* Meyer .................................................. 17
   Apical whorls. Smooth stage (protoconch) occupies almost 2 1/2
   whorls. Greatest diameter, 3.5 mm. Specimen, Acad. Nat. Sci. Philadel-
   phia. Eocene. Jackson, Miss.

6. *Ficus acuminata* (Wood) ......................................... 17
   Apical whorls. Smooth stage (protoconch) occupies almost 2 whorls.
   Greatest diameter, 2.8 mm. Specimen, Acad. Nat. Sci. Philadelphia. Re-
   cent. Acapulco.

7. *Ficus dussuaniri* Valenci ........................................ 17
   Apical whorls. Smooth stage (protoconch) occupies slightly more than
   1 1/2 whorls. Greatest diameter, 3 mm. Specimen, Acad. Nat. Sci. Phila-
   delphia. Recent. Guiana.

8. *Ficus ficus* (Gmelin) ............................................ 17
   Apical whorls. Smooth stage (protoconch) occupies about 1 2/3 whorls.
   Greatest diameter, 2.6 mm. Specimen, Acad. Nat. Sci. Philadelphia. Re-
   cent. East Indies.

Figures 1-8, drawings by Helen Winchester

9. *Conus waccamawensis* Smith .................................... 18
   Apical whorls. Smooth stage (protoconch) estimated at about 4
   whorls. In the largest illustrated voluiton the diameter at shoulder angle
   measures about 3.5 mm. Acad. Nat. Sci. Philadelphia, No. 5722. Plio-
   cene (Waccamaw). Nixon’s Landing, Waccamaw River, S. C.

10. *Conus floridanus* Gabb  ........................................ 18
    Apical whorls. Smooth stage of about 1 1/4 whors is followed by a
    curved-rib stage of about 1 1/4 whorl. Coach follows curved-rib stage.
    In the largest illustrated voluiton the diameter at shoulder angle mea-
    34535. Recent. Oyster Bar, Pine Key, west coast of Florida.

11. *Conus stearnsii* Conrad ......................................... 18
    Apical whorls. Smooth stage of somewhat over one whorl is followed by
    a curved-rib stage of about 1 1/4 whorl. Coach follows curved-rib stage.
    In the largest illustrated voluiton the diameter at shoulder angle mea-
    34535. Recent. Oyster Bar, Pine Key, west coast of Florida.

12,13. *Conus dilatatus* Green ....................................... 18
    (12) Apical whorls. Smooth stage, estimated at 3 whorls, is followed
    by an equivalent of the curved-rib stage of about 1 1/4 whorl. In the larg-
    est illustrated voluiton the diameter at shoulder angle measures about
    2 mm. (13) The same individual turned counter clockwise about 1/4
    Mary’s River, Md.

*Inadvertently printed *Ficus* op. 17 as of masculine gender. 
(Continued on previous page)
PLATE II (VOL. PL. 22)

17,18. *Busycon incile* (Conrad) .................................................. 27

Immature individual of slightly over 1 1/2 whorls having a long
dimension of about 4 1/2 mm. (17) Apertural view. (18) Nonapertural
Coll., No. 739. P.R.I., No. 20059.

19-21. *Busycon pyrum* (Dillwyn) ................................................... 28

(19) (20) Side views of the apical whorls of the same individual
(P.R.I., No. 20036). In figure 19 whorl 2 has a right-left diameter of
about 3 mm. at the shoulder angle. In figure 20 the largest volut
illustrated (parts of whorls 2 and 3) has a right-left diameter of about
4 mm. at the shoulder angle. (21) Outline of another individual
(P.R.I. No. 20037) having a protoconch with relatively smaller initial
bulb. Lower volut (whorl 2) has a right-left diameter of about 3
mm. at the shoulder angle. Recent. Sanibel Island, Fla. P. R. I.
Nos. 20036, 20037.

22-24. *Busycon excavatum* (Conrad) ............................................. 28

(22) (23) Side views of the apical whorls of the same individual. In
figure 22 whorl 2 has a right-left diameter of slightly over 3 mm. at the
shoulder angle. In figure 23 the largest volut illustrated (parts of
whorls 2 and 3) has a right-left diameter of about 4 mm. at the shoulder
angle. (24) Apical view of slightly more than the first two whorls of the
same individual. Diameter at end of whorl 2 is slightly over 3 mm. Plioc
20061.

Figures of plate 2, drawings by Ethel Ostrander Smith.
EXPLANATION OF PLATE II (22)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Basycn contrarium (Conrad)</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Apical whorls. Sharp diagonal line shown late in whorl 1. Largest volution illustrated (parts of whorls 2 and 3) shows early conch sculpture and has a left-right diameter of about 4 mm. at the shoulder angle. Miocene (Duplin). Natural Well, southwest of Magnolia, Duplin Co., N. C. Upper or brownish marl at this locality. Smith Coll. No. 718. P. R. I., No. 20054.</td>
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<tr>
<td>2.</td>
<td>Another individual from the same locality and horizon. In this specimen no sharp line is recognizable. Long dimension about 6 mm. Smith Coll. No. 718. P. R. I., No. 20055.</td>
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</tr>
<tr>
<td>4.</td>
<td>(4) Apical whorls of another individual. The sharp line comes very early in whorl 2 but in this case the line is more curved. Largest volution illustrated shows early conch sculpture and has a left-right diameter of about 4 mm. at the shoulder angle. (5) Outline of whorls 1 and 2 of same individual turned about 1/2 whorl. Whorl 2 in this position has a left-right diameter of about 5 mm. at the shoulder angle. Pliocene (Waccamaw). Acme, N. C. Smith Coll., No. 702. P. R. I., No. 20055.</td>
<td></td>
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<tr>
<td>5.</td>
<td>(6) Outline of whorl 1 and part of whorl 2 in another individual. In this specimen the initial bulb is large and discordant. Larger volution (parts of whorls 1 and 2) is about 2 1/2 mm. from left to right. Compare with figure 4. (7) Outline of whorls 1 and 2 of same individual turned about 1/2 whorl. Whorl 2 in this position measures about 3 mm. from left to right. Compare with figure 5. Pliocene (Waccamaw). Acme, N. C. Smith Coll., No. 702. P. R. I., No. 20055.</td>
<td></td>
</tr>
</tbody>
</table>

(Continued on previous page)
PLATE III (VOL. PL. 23)

20-22. *Plicatus kroyeri* (Möller) .................................................. 34-35

Three views of an individual with large and tilted initial bulb. (20)
Side view of whorls 1 and 2 and part of 3. The largest volutions illustrated (parts of whorls 2 and 3) has a right-left diameter of about 4 mm.
(21) Another side view but with specimen turned clockwise almost 1 2
whorl. Largest volutions figured has a right-left diameter of about 5 mm.
(22) Apical view of somewhat more than the first two whorls. Maxi-
num diameter of whorl 2 is about 3 mm. Quaternary. Rivière-du-Sud,
near St. François Montmagny, Province of Quebec, Canada. Smith Coll.

Figures of Plate 3, drawings by Ethel Ostrander Smith
EXPLANATION OF PLATE III (23)

Figure

1-3. Busycon cf. excavatum (Conrad) ........................................... 28

(1) (2) Side views of the apical whorls of an immature individual of
about 2.5-4 mm. Right view in figure 1, view 2 has a right-left diameter
of about 3 mm. at the shoulder angle. In figure 2 the largest whorls
illustrated (parts of whorls 2 and 3) has a right-left diameter of about
4 mm. at the shoulder angle. (3) Apical view of whorl 1 and almost
all of whorl 2 in the same individual. Diameter toward end of whorl
is about 3 mm. Mississippian (Duquesne). Natural Well, southwest of Magna-
linia, Duplin Co., N. C. Lower or bluish bed at this locality. Smith
Coll., No. 744. P.R.I., No. 20060.

4-7. Fasciolariia apicina Dall ..................................................... 32

Young individual of about 1, 1/4 whorls having a long dimension of
about 15 mm. Initial bulb small. (4) Nonapertural view. (5) Side
view of whorls 1 and 2. The part of whorl 2 shown has a diameter of
about 1, 1/4 mm. (6) Side view of whorl 1 and approximately the first
quarter of whorl 2. Lower whorl figured (parts of whorls 1 and 2)
has a diameter of about 2.3/4 mm. (7) Apical view of somewhat
more than the first two whorls. Maximum diameter of whorl 2 is about
699. P.R.I., No. 20062.

8-10. Fasciolariia apicina Dall ................................................... 34, 37

Apical whorls of adult individual with large initial bulb. (8) Side
view of whorls 1 and 2. The part of whorl 2 shown has a diameter of
about 1, 1/2 mm. (9) Side view of whorl 1 and approximately the first
half of whorl 2. Lower whorl figured has a diameter of about 4 mm.
(10) Apical view of slightly more than the first two whorls. Maxi-
mum diameter of whorl 2 is about 5 mm. Pliocene (Waccamaw).

11-13. Fasciolariia tulipa (Linné) ............................................ 34, 37

Young individual of about 2, 2, 3 whorls having a long dimension of
about 10 1/2 mm. (11) Nonapertural view. (12) Side view of whorls
1 and 2. The part of whorl 2 shown has a diameter of about 4 mm.
(13) Apical view of slightly more than the first two whorls. Maxi-
mum diameter of whorl 2 is about 4 1/2 mm. Recent. West coast of

14-16. Fasciolariia papillosa Sowerby ....................................... 33

Three views of the apical whorls in one individual. (14) Side view
of whorls 1 and 2 and part of whorl 3. Largest whorl figured (parts of
whorls 2 and 3) has a right-left diameter of about 2 1/2 mm. (15) An-
other side view but with specimen turned counter clockwise slightly.
Largest whorl figured (whorl 3) has a right-left diameter of about 4 1/2
mm. (16) Apical view of slightly more than the first two whorls. Maxi-
mum diameter of whorl 2 is about 2 mm. Recent. West coast of Florida.
Smith Coll., No. 1071. P.R.I., No. 20065.

17-19. Plicifusus kroyeri (Möller) ............................................. 34, 35, 37

Three views of the apical whorls of an individual with relatively small
and normal initial bulb. (17) Side view of whorls 1 and 2 and part of
whorl 3. The largest whorl figured (parts of whorls 2 and 3) has
a right-left diameter of about 2 1/2 mm. (18) Another side view but
with specimen turned about 1/2 whorl. The largest whorl figured has
a right-left diameter of about 4 mm. (19) Apical view of slightly more
than the first two whorls. Maximum diameter of whorl 2 is about 2 2/3
mm. Quaternary. Petite Rivière-aux-Loup, Province of Quebec, Can-

(Continued on previous page)
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To the

Invertebrate Paleontology

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Vol. III

No. 20, Some species of Platystrophia from the Trenton of Ontario and Quebec

By

G. Winston Sinclair

Sir George Williams College, Montreal

Notice!

This permanent record copy is printed on all rag paper.
NO. 20, SOME SPECIES OF PLATYSTROPHIA FROM THE TRENTON OF ONTARIO AND QUEBEC

By

G. WINSTON SINCLAIR
Sir George Williams College, Montreal

April 19, 1946

Palaeontological Research Institution
Ithaca, New York, U. S. A.
SOME SPECIES OF PLATYSTROPHIA FROM THE TRENTON OF
ONTARIO AND QUEBEC

By

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INTRODUCTION

I have been engaged in studying the Ordovician Trenton rocks of Ontario and Quebec for some time, and each year has seen a few specimens of Platystrophia set aside as "possibly new." These specimens have been allowed to accumulate in the hope that I might find material which would permit me to determine the extent to which early species of the genus varied and so to satisfy myself concerning specific limits.

Specimens of Platystrophia occur frequently in the Trenton group of central Ontario and the St. Lawrence Valley, but it is very seldom that enough well-preserved specimens can be collected from any one bed to allow reliable study of population variations. However, these early forms are of interest in throwing light on the first development of a stock which was later to become so prolific. The present paper is mainly concerned with the description of new species. The described specimens are in the writer's collection.

The first sound work on the genus was that of Cumings and Mauck (1902) and Cumings (1903). Their careful compilation and comparison of data are of great value. McEwan's study (1916) provided a large number of specific and varietal names for the forms which Cumings and Mauck had considered inseparable. This work would have gained greatly in value had the author shown where the analyses of Cumings and Mauck, which she discarded, were incorrect. Some of McEwan's species are sketchily described, and comparison with them is not always easy, especially where no measurements are given. Raymond (1921) added some notes on Trenton species. The 75 or so species and varieties described to 1930, including 21 from the Trenton, have been listed by Schuchert and Cooper (1932, p. 65). Since then two species have been described, one by Cooper (1930, p. 208) and another by Roy (1941, p. 86), both from the Upper Ordovician.

Schuchert and Cooper had trouble fixing the first appearance of the genus in America, owing to the unsettled correlation of the beds containing the earliest known forms. Kay (1937, p. 204) gives the lower Trenton Hull (=Kirkfield) formation as containing the first species. However, the first appearance of Platystrophia seems to have been a little earlier, as at least two species are present in the basal Trenton or Black River beds at Paquette Rapids on the upper Ottawa River. Throughout the Trenton species are locally common, but their distribution is irregular. Some thick Trenton formations (e.g., the Tetreauville at Montreal) seem to lack the genus entirely, and in others it is rare.

THE VALUE OF THE CONCEPT OF "GROUPS" IN PLATYSTROPHIA

Cumings (1903, p. 10, fn.) introduced the terms "biplicate, triplicate and uniplicate" as a matter of convenience in speaking of the method of origin of costae in the sinus of the pedicle valve. The "biplicate" forms have two primary costae arising in the beak; increase is generally by implantation in a mesial position. The "triplicate" forms have a primary mesial costa and add costae by lateral implantation. The "uniplicate" forms have only a single mesial costa.

McEwan used these terms as names of "groups," following Cumings, and divided the biplicate forms into four subgroups, and the triplicate into three. It is apparent from the discussion of Cumings and McEwan that they regarded these groups as genetically continuous and distinct sections of the genus. Schuchert and Cooper (1932) retained the groups, altering the names to "unicostate, bicostate and tricostate." They pointed out that the unicostate and tricostate are basically the same but kept them separate because "it is convenient to continue the two groups for their stratigraphic value." Since the two described unicostate species in America are from the lower Trenton and the Utica and are preceded, separated, and followed by tricostate forms, the stratigraphic value of the distinction is not apparent.

This division of the genus into groups was based on a recognition that there were two fundamentally different ways in which costae in the sinus could originate. The knowledge of American bicostate forms only in lower Trenton of the Champlain Valley and the Silurian, and the presumption that most European species were of this type, led Cumings to suggest that the group formed a distinct line, only represented on this continent by rare migrants from a European reservoir. It is now known that bicostate species occur well up into the Trenton, as far west as Minnesota. The European species, though not fully described, include representatives of all groups.

It will be shown that in the lower Trenton at Montreal there occur two species (P. minuta Raymond and P. champlainensis McEwan) which according to all other criteria are homogeneous but which include both bicostate and tricostate individuals. The same thing seems to happen in the Hermitage of Tennessee, where P. hermitagensis and P. extensa are said to occur together and differ only in costal pattern (McEwan, 1916, pp. 309, 416). Later forms seem to be more stable in their costal characteristics, but the bicostate species are more nearly similar to subcontemporaneous tricostate forms than to earlier or later bicostate species. (Compare P. trentonensis with P. anuna longicardinalis; P. intercalis (Cooper, 1930, p. 65) with P. regularis Shaler (Twenhofel, 1928, p. 177). This suggests that the bicostate group is not a continuous line but is made up of species which have appeared from time to time from tricostate forms.

The costal pattern is an "either-or" matter and allows no intergrading. It is thus tempting as a basis for division, but I believe that its ease of application is misleading. The terms are still useful in Cumings's original sense, as a shorthand way of describing patterns, but they should not be used in such a way as to imply relationships.
DESCRIPTION OF SPECIES

Genus PLATYSTROPHIA King

Platystrophia amena McEwan

P. amena McEwan, 1921, p. 412, pl. 43, figs. 1-8; Raymond, 1921, p. 17, pl. 6, figs. 1-5, 11.

This species, as Raymond remarked, is the most common and widespread of the Canadian Trenton Platystrophias. Our specimens tend to be a little larger than the type and are usually long-hinged, although at any locality the relative width of the hinge is very variable. Most of the specimens would be referred to P. amena longicardialis McEwan rather than to the species itself, but the constant association of short and long-hinged individuals in the same beds, with numerous intermediate specimens connecting them, makes the value of the subspecific name doubtful.

Platystrophia minuta Raymond

Plate 1, figures 59-63

P. minuta Raymond, 1921, p. 20, pl. 6, fig. 10.

The available material does not add much to Raymond's description of the species. It consists of eight pedicle and eight brachial valves, all dissociated, from the lower Trenton Mile End formation at Le Page Station, Terrebonne County, Quebec. The specimens agree with Raymond's type material in size and number of lateral costae. The costa of the fold and sinuses, however, are of interest.

The sinuses of the pedicle valves bear: (1) three costae in regular tricostate pattern (length of valve 6.0 mm.); (2) a single strong mesial costa and traces of two laterals, just appearing at the front of the shell (length, 5.7 mm.); (3) a single mesial costa (four specimens, lengths 6.5, 4.6 and 4.1 mm.); (4) no costa at all (length 6 mm.) and (5) a strong mesial costa which bifurcates about 2.6 mm. from the beak (length of valve 4 mm.).

The folds of the brachial valves are more regular. In three (lengths 6, 6.1 and 5 mm.) the two primary costae have bifurcated at about half the length of the valve. In two (length 3.8 and 4 mm.) the costae remain undivided, and in two (lengths 3.8 and 4 mm.) they have not divided but have broadened. Presumably had the latter two specimens reached a length of about 6 mm. they too would have had four costae on the fold.

In considering this variation in pattern it should be remembered that these specimens are all from precisely the same bed, agree in general configuration, and in always having five sharply angular costa on the slopes of the pedicle valve, and four on the brachial. There are no other Platystrophias in the bed, except the single specimen described below as P. minuta adulta. It is apparent that in this species the costal pattern had not become fixed, and individuals could be bicostate or tricostate without losing any of the characters of the species. I record the presence of the acostate specimen without attempting an explanation.

Platystrophia minuta adulta, n. var.

Plate 1, figure 48

Associated with P. minuta in the Mile End formation at Le Page Station, Quebec, is a single pedicle valve which looks like an overgrown specimen of that species. It has none of the characteristics of a gerontic individual but seems
rather to be the sort of shell *P. minuta* might grow into, were *P. minuta* a juvenile. But this does not seem to be the case, as we now have a score of specimens of the species, all agreeing generally in size, while there is only one of the form I am calling *adulta*.

The pedicle valve is widest at the hinge, gently convex. Each lateral slope bears six costae, of which the inner three are sharp, and the outer three more rounded. The sinus is very wide, and, considering the thinness of the valve, deep; it bears five costae in tricostate pattern. The primary mesial costa and two flanking ones, which originate about 2 mm. from the beak, are subequal at the anterior margin. Outside these is another pair which appears about 2.5 mm. from the front and do not become strong.

Length, 7.2 mm.; width, 10.6; width of sinus, 6.5; depth of sinus, 3.8.

This form differs from *P. minuta* in its larger size, wider hinge (age in most species of *Platystrophia* tends to decrease rather than increase the relative hinge width), additional lateral costae, and wider sinus, although this is a corollary of the number of costae in it. The exact relationship to *P. minuta* cannot be determined from the present material.

**Platystrophia champlainensis** McKean, emend. new

*Plate 1, figures 36-43*

*P. trentonensis champlainensis* McKean, 1916, p. 407, pl. 42, figs. 9-11.

*P. champlainensis* McKean, Raymond, 1921, p. 19, pl. 6, figs. 6-10.

*P. precedens* McKean, 1916, p. 405, pl. 42, figs. 7-8.

*P. uniflora* McKean, 1916, p. 905, pl. 42, figs. 4-2.

Shell small, rather thick, hinge narrow. Pedicle valve quite convex, lateral slopes with 6-11 sharp distant costae; sinus wide, rather deep. Brachial valve evenly convex, more convex than the pedicle, fold scarcely elevated.

In the lower Trenton Mile End formation at Montreal, and, according to the literature, in the Champlain Valley, there occur commonly *Platystrophia* which agree in their small size, plump shape, and number of lateral costae, and differ only in the costal pattern of the sinus and fold. Subgroups A and B of the bicostate group are represented, along with tricostate and unicostrate forms. Of 48 specimens selected for measurement, all from the same horizon at Montreal, 33 were the bicostate-B "*champlainensis*," 8 were the bicostate-A "*precedens*," 4 were "*uniflora*," and 4 were unicostrate but had incipient lateral costae in the sinus. The remaining specimen had four costae in the sinus, but unfortunately it did not show the method of origin.

These shells are all very similar in appearance, but they were divided into three groups on the basis of co-tal pattern and a few characteristics were analyzed. Some of the results follow, using the letters C, P, and U to indicate the "*champlainensis*," "*precedens*" and "*uniflora*" groups.

Ratio, length : width: C, 33 specimens, range 0.3-0.90, mode and median .77. 50% of specimens between .75 and .81; P, 8 specimens, range .67-0.93, median .78; U, 6 specimens, range .69-.83, median .74.

Number of costae on one lateral slope of pedicle valve: C, 30 specimens, range 6-9 (plus one case of 11), median and mode 8, 87% of specimens between 7 and 9; P, 6 specimens, range 7-9, median 9; U, 6 specimens, range 6-9, median 8.
Width of shell: C, 33 specimens, range 6.4-16 mm., median and mode 11. 50\% of specimens between 9.9 and 13; P, 8 specimens, range 4.3-15, median 13.5; U, 6 specimens, range 6-12, median 10.6.

Ratio sinus width :: shell width: C, 26 specimens, range 30-64, median .50, 50\% of specimens between .47 and .54; P, 5 specimens, range .42-.60, median .45; U, 6 specimens, range .41-.49, median .43.

I think the agreement between these rough figures is striking. The uniplicate forms are a little smaller than the average (but the type specimen of \textit{P. uniplicata} was 12 mm. wide), and there are few small "\textit{precedens}," but considering the limits of the commoner form I think the discrepancies can be charged to the small number of specimens. The width of the sinus seems to be a function of the number of costae in it, as might be expected. Measurements are not given for depth of sinus which seems to vary with age and thickness, nor for the ratio sinus depth :: thickness which is similar in the three groups.

It seems to me highly improbable that three (or four) true species would exist in the same place at the same time, differing among themselves only in one character. Shape in \textit{Platystrophia} tends to be variable; here it is quite constant, with the same norm in all groups; no group is long hinged nor auriculate nor markedly quadrate. Many species of \textit{Platystrophia} have stabilized the number of lateral costae; so have these three, all at the same figure. In spite of phylogenetic theories I find it easier to think of a single species in which the manner of costal origin was a matter of indifference, except that once initiated it could not be reversed. This irrevocable "choice," of course, makes it easy to separate individuals into groups, but I consider that giving these groups names is a meaningless procedure.

For that reason I have united McEwan's three species under the name \textit{champlainensis} because most of the individuals have the form of the types of that species. The same distribution seems to hold in the New York beds from which the three species were originally described, as McEwan had only two specimens of "\textit{uniplicata}" and notes that "\textit{precedens}" occurred in "relatively small numbers."

If I am right, then we would expect to find specimens with two primary costae in the sinus and a mesial one just starting near the anterior margin; in other words, forms transitional between bicostate subgroups A and B. This I have not found. In all the "\textit{champlainensis}" type, the three costae in the sinus are subequal and originate very close to the beak.²

This species is locally abundant in the Mile End formation near Montreal, although really well-preserved specimens are rather rare. The specimens examined in detail came from quarries at De Fleurimont and Marquette streets, in Montreal, and at St. Vincent de Paul, just north of the city.

\textit{Platystrophia molra}, n. sp.

Plate 1, figures 17-19

Shell small, quadrate, rather thin, uniplicate. Pedicle valve gently convex, each lateral slope with six sharp distant costae; sinus narrow, rather deep, with

² A recent day's intensive collecting at St. Vincent de Paul produced 102 specimens well enough preserved to show the costal pattern. Of these 102 "\textit{champlainensis}," 37 were "\textit{precedens}," 16 were "\textit{uniplicata}," and 3 had the intermediate bicostate pattern postulated above.

Recent work has also shown that this horizon in the Mile End formation is lower than that at Le Page Station, in which \textit{P. molra} and \textit{P. mirabilis} were found.
a single sharp mesial costa. Brachial valve evenly convex, fold scarcely elevated, with two costa which retain their identity to the beak.

Width, 10.5 mm; width of hinge, 10; length, 8.4; thickness, 0.5; width of sinus, 4.5; depth of sinus, 2.5 mm.

Occurrence.—Kirkfield formation (lower Trenton), along the Moira River in Belleville, Ontario.

Discussion.—The holotype is not so well preserved as could be wished but is chosen because it is complete. The species is distinguished from P. cygnus by its unicostrate sinus, which seems to be constant, and from P. champlainensis by the pauciplicate lateral slopes, wider hinge, and narrower sinus. A specimen which seems referable to this species was found at Paquette Rapids, where it was associated with larger tricostrate forms. The latter specimens are in the collections of the Geological Survey of Canada and are not described here.

Platystrophia canadensis, n. sp.

Plate 1, figure 22

Shell of medium size, thin, widest at hinge. Pedicle valve very gently convex, each lateral slope with seven rounded, distant costa; sinus wide, rather shallow, with three equal costa in bicostate pattern, more angular than those on the rest of the valve. Brachial valve crushed, fold apparently very low, with four subequal costa.

Width, 14 mm.; width of hinge, 14.8; length, 10.5; width of sinus, 7; depth of sinus, about 2.8 mm.

Occurrence.—Lower Trenton Kirkfield formation, at Kirkfield, Ontario.

Discussion.—The holotype, like most brachiopods in the shaly interbeds of the Kirkfield, is beautifully preserved but crushed. The species seems closest to P. trentonensis, but is smaller, thinner, and has fewer lateral costa. From P. trentonensis perplana McEwan, which occurs with it at Kirkfield, the species is distinguished by its quadrate rather than transverse shape.

Platystrophia lacerta, n. sp.

Plate 1, figures 20-21

Shell of medium size, widest at hinge, thin, quadrate. Pedicle valve gently convex, lateral slopes with 14 sharply rounded costae; sinus wide, rather shallow, with a strong rounded mesial costa and two feeble lateral costa which first appear about mid-length of the shell and never become prominent. Brachial valve of the only specimen badly weathered.

Width, 15 mm.; width of hinge, 14; length, 10; thickness, about 6; width of sinus, 6; depth of sinus, 3 mm.

Occurrence.—Sherman Fall formation, near Trenton, Ontario.

Discussion.—Similar to P. amana in shape, this species is distinguished chiefly by the larger number of lateral costa. The costal pattern resembles that of P. sera,
which occurs with this species, but an examination of growth varices indicates that the two are of fundamentally different shape. The young of *P. incerta* is more transverse than the adult, but the outline never approaches that of *P. sera*.

**Platystrophia egens**, n. sp.
Plate 1, figures 24-30

Shell of medium to small size, transverse or subquadratic in shape, pauciplicate. Pedicle valve gently and evenly convex, except immediately at the cardinal angles, where the slope becomes concave. Lateral slopes with six angular costae, with sometimes traces of another posteriorly. Sinus wide, rather deep, with three subequal costae in tricosate pattern. Brachial valve more convex, almost evenly so. Fold but slightly elevated, costae bifurcating within 1.5 mm. of the beak.

Width, 13 mm.; width of hinge, 11.5; length, 10; thickness, 8; width of sinus, 6.2; depth of sinus, 3 mm.

**Occurrence.**—Frequent in the Rosemount member of the Montreal formation at Montreal North (holotype and 4 paratypes); Rivière des Prairies (2 paratypes); Boulevard Pie IX about one mile north of the Chemin de la Côte St. Michel (2 paratypes). All the localities mentioned are on Montreal Island.

**Discussion.**—The above description is drawn from the holotype, a specimen with prominent growth varices, showing that the width of the hinge did not increase after the shell had attained a length of 7 mm. At that time the width at the middle of the shell was 10 mm. The number of costae was already fixed. The holotype has a nonypical fourth costa in the sinus, very small, and appearing at about 6.5 mm. length, intercalated between the left and central costae. On the fold the inner costa of the right-hand pair bifurcates.

*P. egens* is rather common in the Rosemount in the Montreal area and varies considerably in shape and size. The small number of lateral costae seems to be constant, except that young individuals may have only five. This characteristic distinguishes it from the somewhat similar *P. amena*.

Young shells are transverse and thin, with shallow sinuses, and become thicker and relatively narrower with age. The holotype is a little under the average size. The width, length, and thickness of seven paratypes are: 10, 7.5; 10, 7.5, 5.5; 14.5, 10.5, 9; 14.5, 11, 9; 15, 11.2, 10; 15, 12, 9.7; 15, 11.3, 12.8 mm. The relative width of the hinge varies about a norm of a little less than the greatest width of the shell.

**Platystrophia avoris**, n. sp.
Plate 1, figures 1-18

Shell of medium size, robust, short hinged, subovate in outline. Pedicle valve quite convex, evenly so, lateral slopes with 8-12 rather sharp costae. Sinus wide, deep, typically with three subequal sharp costae, in bicostate pattern. Brachial valve more convex, except toward the cardinal angles. Fold low, with 4 subequal costae.

Width, 20.1 mm.; width of hinge, 17; length, 25.3; thickness, 12; width of sinus, 10; depth of sinus, 5.8 mm. (holotype).

The largest specimen measured: width, 23 mm.; width of hinge, 20; length, 26;
thickness, 15; width of sinus, 10; depth of sinus, 8 mm. A small, juvenile specimen; width, 12 mm.; width of hinge, 10; length, 9.43; thickness, 7; width of sinus, 6; depth of sinus, 3 mm.

Occurrence.—Rosemount member of Montreal formation, at Montreal North, Quebec.

Discussion.—The 37 specimens measured all came from one bed of limestone, and presumably the smaller thinner specimens are the young forms. The holotype is typical of the mature specimens. There is some variation in the number of costae in the sinus. Thirty specimens have the typical three costae. Three specimens have five, but here it is evident that the first two costae of the lateral slopes have “slipped” into the sinus. One otherwise typical specimen has four costae, the median one having bifurcated shortly after its appearance; on the fold a median fifth costa is implanted. Two specimens have only two costae; one of these has a normal sinus width and the costae are low and broad instead of being sharply angular; the other specimen has more normal costae and a narrow sinus. One specimen has only a single broad costa in the sinus. Unfortunately, it is only a pedicle valve, and it is not possible to say what the fold was like.

The number of lateral costae varies to some extent. Two specimens have eight on each side of the pedicle valve, seven have nine, 17 have 10, three have 11, and six have 12. Those having less than 10, and most of those with 10, show a smooth area adjacent to the hinge, which in the others is occupied by small costae. The number of costae does not correlate with the size of the shell.

Bicostate Platystrophia occurs in adjacent beds, but none have been found in the stratum from which all the specimens of P. texanus came. The species has not been found elsewhere. It is somewhat similar to P. texanus but differs in its larger size, short hinge, and wider sinus.

The specific name is for my wife, who collected the material with me.

Platystrophia precax, n. sp.

Plate I, figure 23

Shell of medium size, transverse, thin. Pedicle valve only slightly convex, becoming concave at the cardinal angles. Each lateral slope has eight rather sharp, well-separated costae. Sinus broad and shallow, with two very strong distant primary costae, and two smaller ones outside these; the four are equidistant at the front, the lateral costae appear when the shell has reached about half its length. Brachial valve a little more convex, the fold very low and spreading, too weathered to allow detailed observation of the costal pattern.

Width, 15 mm.; width of hinge, about 14; length, 10; thickness, 8; width of sinus, 7; depth of sinus, 3 mm.

Occurrence.—Rosemount member of the Montreal formation; Botanical Gardens Quarry, Rosemount, Montreal.

Discussion.—The unique holotype is a free weathered specimen which would not be described except for its peculiar costal pattern. There is no associated species of which it could be a variant. Following McEwan’s classification, this specimen would be put in subgroup C of the bicostate group, a subgroup containing only P. brachignata (Hall), P. reversata Foerste, and P. camerata Twenhotel.
The former two are from the Silurian of the interior, the latter is from the Gamachian Ellis Bay formation of Anticosti. None of these species is similar to _P. praecox_, except in costal pattern. _P. praecox_ seems most similar to _P. amana_ and _P. egens_. It differs from _P. amana_ in being smaller, shorter in the hinge, and having fewer lateral costae. It is longer hinged and thinner than _P. egens_.

The specimen is mainly interesting as an indication that the Trenton tricostate Platystrophias were capable of producing at least one individual of wholly different costal pattern. Addition of secondary costae at the sides of the sinus is, of course, a tricostate feature, but here it is superimposed on a bicostate base.

**Platystrophia longa**, n. sp.

*Plate 1, figures 44-47*

Shell of medium size, quadrata, auriculate. Pedicle valve very gently convex, a little concave near the ears, hinge line always wider than the shell immediately anterior to it, but sometimes less and sometimes more than the greatest width of the shell. Lateral slopes with two rounded costae. Sinus wide, shallow, with three subequal costae in tricostate pattern. Brachial valve much more convex, also becoming concave near the ears; fold very low.

*Holotype.*—Width, 13.6 mm.; width of hinge, 15; length, 11; width of sinus, 6.6; depth of sinus, about 2.5 mm. *Paratype I.* width, 15.5; width of hinge, 15; length 12.5; thickness 11.5; width of sinus, 7.2; depth of sinus, 3.6 mm. *Paratype II.* width, 16; width of hinge, 16; length, 16; width of sinus, 8 mm.

*Occurrence.*—Middle Trenton, near Grondines, Quebec.

*Discussion.*—This species is represented by rather frequent poorly preserved specimens, almost all dissociated valves. The holotype is a typical specimen and is thin, as are almost all the specimens. The paratype I is exceptionally thick and is one of the few specimens with the valves joined. Paratype II is the longest specimens seen and is larger than usual. It is only moderately convex. This species is smaller than _P. globosa_ McIlwain (1911, p. 413), much thinner, and has an extra costae on each lateral slope. The presence of the subglobose paratype I suggests that the relationship to _P. globosa_ may be close. No other comparable species is so long.

**Platystrophia sera**, n. sp.

*Plate 1, figures 33-35*

Shell of medium size, widest at hinge, acuminate, thin. Pedicle valve very gently convex medially, becoming flat toward the cardinal angles. Lateral slopes with eight rather sharp, broadly sigmoid costae; the ears are smooth or have obscure undulations parallel to the costae. Sinus rather shallow, with a mesial costa and two smaller lateral costae which appear in tricostate pattern when the shell is about 6 mm. long. Brachial valve not quite so convex, but more regularly so, more convex at the cardinal angles. Fold very low, with four low costae, resulting from the late bifurcation of the two primaries.

Width, 14.3 mm.; width of hinge, about 20; length, 10.7; thickness, 8; width of
sinus, 6; depth of sinus, 3.3 mm.

Occurrence.—Middle Trenton cystid beds of the Ottawa limestone at Philmon Island, Hull, Quebec (holotype); Sherman Fall formation near Trenton, Ontario.

Discussion.—No other Trenton species has a shape similar to P. scra, but the Arnheim P. acuminata James seems to be very similar in size and shape. The only difference noted from McEwan's description (1919, p. 420, pl. 40, figs. 5-8) is a much deeper sinus and higher fold in the Richmond form. One of the specimens figured as P. amena longicardinalis (McEwan, 1919, pl. 43, fig. 11) approaches this in outline, but has a wider fold and larger lateral costa.

Platystrophia felis, n. sp.
Plate 1, figures 31, 32

Shell large, plump, hinge line extended. Pedicle valve gently convex, flattened or concave near the cardinal angles, each lateral slope with 13 sharp costa. Sinus wide, rather deep, with three subequal costae in tricostate pattern. Brachial valve more convex, flattening near the ears but still more convex than the pedicle valve. Fold low but distinct.

Width, 20 mm.; width at hinge, 27; length, 16; thickness, about 12; width of sinus, 10; depth of sinus, 4 mm. A larger paratype measures: width, 22 mm.; width of hinge, 32; length, 16; thickness, 13; width of sinus, 11; depth of sinus, 6.5 mm.

Occurrence.—Holotype from the Sherman Fall formation three miles north of Picton, Ontario. Paratype from the lower (?) Cobourg in a road cut on the second hill going east from Watertown, New York, on the Carthage Road, about 10 feet below the crest of the hill.

Discussion.—The brachial valve of the holotype is a little crushed, so that the exact thickness cannot be measured. This specimen has an additional small costa in the sinus, implanted on the right-hand lateral slope. The species is distinguished from all eastern Trenton forms by its large size. In this it agrees more with P. precursor and its varieties from the Kentucky-Tennessee area (none of which has been reported from the East), but none of them has such an extended hinge. The species is more probably related to P. amena, a much smaller shell, with fewer lateral costae, and a shorter hinge.

Platystrophia cf. trentonensis McEwan
Plate 1, figure 49

P. trentonensis, McEwan, 1919, p. 407, pl. 42, figs. 3-6.

This species, which I have found to be rather common in the middle Trenton of New York, seems to be rarer in Ontario, where I have found only a few specimens. The specimen I am comparing with the species is one from the lower Trenton at Eganville, Ontario. It occurs there on a small island in the middle of the village, with other silicified brachiopods (Dinorthis, Rafinesquina, etc.), in beds of whose exact age I am uncertain. It is much larger than the type of the species and must have been considerably thicker, but considering the variation I have found to occur in the New-York specimens I do not feel it would be wise to name this single brachial valve.
Width, 27.5 mm.; width of hinge, about 28.5; length, 16; thickness of brachial valve, 10; width of fold, 10 mm. Coste on fold, 5, in bicostate pattern; on each lateral slope, 14.

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PLATES

PLATE I ( VOL. PL. 24 )
EXPLANATION OF PLATE I (24)

Figure Page

1-16. Platystrophia uxoris, n. sp. ........................................ 9
   1-3. Holotype; 4-6, paratype with 2 wide sinal costa; 7, paratype with
   single costa; 8-10, small, juvenile, paratype; 11-13, paratype with 2 narrow
   costa; 14-16, paratype with 4 costa. All from Rosemount member of Mon-
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NO. 21, OBSERVATIONS ON GASTROPOD Protoconchs

PART III—SOME Protoconchs IN BUSYCON, FUSINUS,
HEILPRINIA, HESPERISTERNIA, AND UROSA LPINX

By

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</node><node class="item para"><p>Introduction</p></node><node class="item para"><p>Acknowledgments</p></node><node class="item para"><p>Part III.—Some protoconchs in Busycon, Fusinus, Heilprinia, Hesperisternia, and Urosalpinx</p></node><node class="item para"><p>The protoconch of Busycon</p></node><node class="item para"><p>Protoconch in Busycon contrarium</p></node><node class="item para"><p>Protoconch in Busycon cf. rapum</p></node><node class="item para"><p>Protoconch in Busycon cf. planulatum</p></node><node class="item para"><p>Protoconch in Busycon pyrum</p></node><node class="item para"><p>Interpretations</p></node><node class="item para"><p>The protoconch of Fusinus</p></node><node class="item para"><p>Protoconch in Fusinus exilis</p></node><node class="item para"><p>Interpretations</p></node><node class="item para"><p>The protoconch of Heilprinia</p></node><node class="item para"><p>Protoconch in Heilprinia caloosaensis carolinensis</p></node><node class="item para"><p>Interpretations</p></node><node class="item para"><p>The protoconch of Hesperisternia</p></node><node class="item para"><p>Protoconch in Hesperisternia filicata</p></node><node class="item para"><p>Interpretations</p></node><node class="item para"><p>The protoconch of Urosalpinx</p></node><node class="item para"><p>Protoconch in Urosalpinx trossulus</p></node><node class="item para"><p>Interpretations</p></node><node class="item para"><p>Summary of Part III</p></node><node class="item para"><p>Bibliography</p></node><node class="item para"><p>Plate</p></node><node class="item para"><p>CONTENTS</p></node><table><thead><tr><th>Introduction</th><td>5</td></tr><tr><th>Acknowledgments</th><td>5</td></tr><tr><th>Part III.—Some protoconchs in Busycon, Fusinus, Heilprinia, Hesperisternia, and Urosalpinx</th><td>6</td></tr><tr><th>The protoconch of Busycon</th><td>6</td></tr><tr><th>Protoconch in Busycon contrarium</th><td>6</td></tr><tr><th>Protoconch in Busycon cf. rapum</th><td>6</td></tr><tr><th>Protoconch in Busycon cf. planulatum</th><td>7</td></tr><tr><th>Protoconch in Busycon pyrum</th><td>7</td></tr><tr><th>Interpretations</th><td>8</td></tr><tr><th>The protoconch of Fusinus</th><td>8</td></tr><tr><th>Protoconch in Fusinus exilis</th><td>9</td></tr><tr><th>Interpretations</th><td>10</td></tr><tr><th>The protoconch of Heilprinia</th><td>10</td></tr><tr><th>Protoconch in Heilprinia caloosaensis carolinensis</th><td>11</td></tr><tr><th>Interpretations</th><td>11</td></tr><tr><th>The protoconch of Hesperisternia</th><td>12</td></tr><tr><th>Protoconch in Hesperisternia filicata</th><td>12</td></tr><tr><th>Interpretations</th><td>13</td></tr><tr><th>The protoconch of Urosalpinx</th><td>13</td></tr><tr><th>Protoconch in Urosalpinx trossulus</th><td>14</td></tr><tr><th>Interpretations</th><td>14</td></tr><tr><th>Summary of Part III</th><td>15</td></tr><tr><th>Bibliography</th><td>16</td></tr><tr><th>Plate</th><td>17</td></tr></thead></table>
OBSERVATIONS ON GASTROPOD PROTOCONCHS

By

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PART III.—SOME PROTOCONCHS IN BUSYCON, FUSINUS, HEILPRINIA, HESPERISTERNIA, AND UROSALPINX

INTRODUCTION

Parts I and II of these studies appeared as No. 19 of Volume III of Palaeontographica Americana (Smith, 1945). Part I consists of a review of selections from the literature with republication of some earlier figures. Part II contains descriptions and figures of protoconch and younger conch whorls in species belonging to the genera Busycon, Fasciolaria, and Plicifusus. Additional Busycon material has now become available and this is treated first in the present paper. Following are descriptions and figures of apical whorls of species in the genera Fusinus, Heilprinia, Hesperisteria, and Urosalpinx. So far, it has not been practicable to take up the early whorls of all of the species in any one genus and Part III, like Parts I and II, should be regarded merely as a contribution to our slowly accumulating knowledge of the gastropod protoconch.

ACKNOWLEDGMENTS

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Publication on the Busycons here considered was made possible through the kindness and generosity of the late Helen Tucker Rowland and the liberal attitude of Doctor Richards Atwell Rowland.

Mr. Druid Wilson of Frostproof, Florida, who took part in the collection of the Helen Tucker Rowland material, has contributed supplementary notes on the Florida localities which are especially useful in bringing them up to date with respect to recent highway construction. This help is gratefully acknowledged.

As in the illustrating of Parts I and II the writer is particularly indebted to Mrs. Ethel Ostrander Smith of Skaneateles, New York, for skilful drawing and preparation of the plate.
SOME PROTOCONCHS IN BUSYCON, FUSinus, HEILPRINIA, HESPERISTERNIA, AND UROSALPINX

THE PROTOCONCH OF BUSYCON

This was discussed in Part I (Smith, 1945, p. 14) and in Part II (Smith, 1945, pp. 23-29, 37, pls. 2, 3). In Part II the early whorls of Busycon contrarium, B. cf. fusiforme, B. coronatum or B. rugosum, B. incile, B. pyrum, B. excavatum, and B. cf. excavatum were described and figured. It is now possible to present descriptions and figures of the apical whorls of B. contrarium from the Caloosahatchee Pliocene, of B. pyrum from the Caloosahatchee Pliocene, and of B. pyrum from the Florida Pleistocene together with two forms, not considered in the earlier paper, which are assigned tentatively to B. rapum, and to B. planulatum.

PROTOCONCH IN BUSYCON CONTRARIUM

In Part II the early whorls of Busycon contrarium (Conrad) (Conrad, 1840, p. 387; 1861, republication of 1893, p. 81, pl. 45, fig. 11) were described and figured in specimens from the Duplin Miocene of North Carolina, the Waccamaw Pliocene of North and South Carolina, and the Recent fauna of North Carolina. In the present paper the apical whorls of a specimen from the Caloosahatchee Pliocene (Helen Tucker Rowland Collection 37F/55) are figured and briefly described. Its locality is Caloosahatchee River (north bank), about 3 miles east of Fort Denard, Florida. This is apparently in section 12, T. 43 S., R. 28 E. Hendry County. Figure 1 of Plate 1 depicts the apical whorls of this individual. The smooth and rounded stage can be seen early in whorl 1 and the change from the riblet or curved-rib stage to the noded and angulated stage of the conch at about the end of whorl 1. The largest whorl illustrated (parts of whorls 2 and 3) shows the noded and angulated stage of the conch.

PROTOCONCH IN BUSYCON CF. RAPUM

Well-preserved apical whorls are found in a specimen of the Helen Tucker Rowland Collection (71F/24) which is referred with doubt to Busycon rapum (Heilprin) (Heilprin, 1887, p. 71, pl. 2, fig. 4). The age is probably Caloosahatchee Pliocene. The locality is about halfway between Clewiston, Florida, and Labelle, Florida at the intersection of Highway 25 with a canal. The point is two miles west of the intersection of Highways 25 and 67. It is mapped as Pleistocene (Cooke and Mossom, 1929, pl. 2) but the material came from spoil banks, and it is believed that the specimen is referable to the underlying Pliocene (Cooke and Mossom, 1929, pp. 154, 155). Figure 2 of Plate 1 shows the smooth and rounded stage of whorl 1 followed by axial riblets and faint spirals late in whorl 1 and early in whorl 2. Incipient angulation can be seen at left of second whorl illustrated. Largest whorl illustrated (mostly whorl 2) shows the noded and angulated stage of the conch. Figure 3 is of the same individual turned counter clockwise about 1/4 whorl. In the second whorl shown the transition into the noded and angulated stage can be seen. The largest whorl at bottom (parts of whorls 2 and 3) shows the noded and angulated stage of the conch. Figure 4 depicts the individual in apical view. Smooth and round-
ed stage of the protoconch is followed by a ribbed stage which passes into the noded and angled stage of the conch. The figure shows somewhat more than the first three whorls and displays well the relatively simple growth lines of whorl 2 and the decidedly curved growth lines of whorl 3.

**Protoconch in Busycon cf. planulatum**

Figure 3 of Plate 1 depicts a side view of the apical whorls of an individual in the Helen Tucker Rowland Collection (36F/18) which is tentatively referred to *Busycon planulatum* (Dall) (Dall, 1890, p. 114). The specimen corresponds rather well with Dall's description of the species but it is deemed wiser to make the identification provisional. The locality is canal bank 12 and 7/10 miles from Moore Haven, Florida, at the intersection of Highways 67 and 25 in Hendry County. The horizon is Caloosahatchee Pliocene. In whorl 1 is seen the smooth and rounded stage and indications of sculpture in the last 1/4 whorl. The noded and angled stage is established by the beginning of whorl 2. The largest volutions illustrated (parts of whorls 2 and 3) shows the noded and angled stage of the conch. Figure 6 gives an apical view of slightly more than the first four whorls of the same individual. The smooth and rounded stage occupies about 3/4 whorl and is followed by ribbing in the last quarter of whorl 1. The noded and angled stage characterizes whorl 2 and persists through whorl 3. In whorl 4 the noded and angled stage passes into the keeled stage.

Figures 7 and 8 of Plate 1 represent another individual of the Helen Tucker Rowland Collection (61F/50) which is tentatively assigned to *Busycon planulatum* (Dall). This specimen is from the spoil banks of the pits at Aclene, Florida, which apparently yield fossils of more than one horizon (Tucker and Wilson, 1932, p. 357). However, the age in this case is probably Pliocene. Figure 7 gives a side view of the apical whorls. The smooth and rounded stage is seen at top. Axial ribs or riblets show late in whorl 1 and these are followed by the noded and angulated stage in whorl 2. The largest volutions illustrated (parts of whorls 2 and 3) shows the noded and angled stage of the conch. Figure 8 gives the apical view of a little more than the first two whorls of the same individuals. The smooth and rounded stage is followed by ribbing and this by the noded and angulated stage which persists through whorl 3. In this Aclene specimen the nodes are relatively few and elongated in a spiral direction. Early in whorl 4 the nodes pass into the keel of the keeled stage which occupies the remainder of the whorl.

**Protoconch in Busycon pyrum**

In Part II (Smith, 1945, pp. 27, 28, pl. 2, figs. 19-21) occurred a discussion and figures of the apical whorls of a form usually assigned to *Busycon pyrum* (Dillwyn) (Dillwyn, 1817, vol. 1, p. 485; Dillwyn (Lister), 1823, pl. 877, fig. 1). The figures were of Recent individuals from Sanibel Island, Florida. It is now possible to add data derived from two Florida fossils.

Figures 9 and 10 of Plate 1 are side views of the apical whorls of a small and apparently immature individual (Helen Tucker Rowland Collection 36F/7) which can be assigned to *Busycon pyrum* in the sense adopted in Part II of these
studies. Rather coarse spirals in its later whorls cause a resemblance to Busycon pyrum amyphotum (Dall) (Mansfield, 1930, p. 69, pl. 8, figs. 1-6). The specimen is attributed to the Caloosahatchee Pliocene and its locality is canal bank 12 and 7/10 miles from Moore Haven, Florida, at the intersection of highways 67 and 25 in Hendry County. In figure 9 can be seen the smooth and rounded stage and the early sculpture in whorl 1. The larger volutions illustrated shows the nodded and angulated stage of the conch. Figure 10 is of the same individual turned slightly. This brings to view (middle volution illustrated) the transitional passage from the early sculpture to the nodded and angulated stage. The volution at bottom (parts of whorls 2 and 3) shows the nodded and angulated stage of the conch.

Figure 11 of Plate 1 depicts the apical whorls of an immature individual of Busycon pyrum in the Helen Tucker Rowland Collection (5F/111). Its age is Pleistocene and the locality is between the Highway 23 bridge and the next bridge upstream on Sixmile Creek at Orient, Florida. The figure shows the smooth and rounded stage at top and the transitional passage from the early sculpture into the nodded and angulated stage late in whorl 1 and early in whorl 2. At bottom the illustrated volution (parts of whorls 2 and 3) shows the nodded and angulated stage of the conch.

INTERPRETATIONS

In addition to the Busycon data considered in Part II there are now published figures and brief descriptions of protoconch and early conch features in six individuals of Busycon as follows: Busycon contrarium from the Caloosahatchee Pliocene, B. cf. rapum probably from the Caloosahatchee Pliocene, B. cf. planulatum from the Caloosahatchee Pliocene, B. cf. planulatum of probable Pliocene age, B. pyrum from the Caloosahatchee Pliocene, and B. pyrum from the Pleistocene of Florida.

The Busycons studied in the present paper bear out the general conclusions already stated (Smith, 1945, pp. 24, 26) that the protoconch is relatively uniform throughout the group and is characterized by an early smooth and rounded stage and by a later very short stage of simple sculpture on a rounded whorl. This is followed by transition into the nodded and angulated stage of the conch.

THE PROTOCONCH OF Fusinus

The protoconch of Fusinus has been considered at some length by Grabau (1903, pp. 8, 9, text-figs. 1-3, pl. 17, figs. 1-4). He figures the protoconch in Fusinus porrrectus (Solder), Eocene; F. acuminatus (Sowerby), Eocene; F. asper (Sowerby), Eocene; F. turriculus (Kiener), Recent; F. longirostris (Brocchi), Pliocene; F. brede (Michelotti), Pliocene and emphasizes its relative uniformity of character throughout the genus. References and quotations from Grabau’s work have been given in Part I of these studies (Smith, 1945, pp. 13, 14).

As noted in Part I (Smith, 1945, p. 14) the uniformity of the Fusinus protoconch is relative and not absolute. Sturany (1904, pp. 220, 221, pl. 1, figs. 1a, 2a, 3a, 3b, 4a, 4b, 4c) has demonstrated a protoconch difference between the species Fusinus bifrons (Sturany) and F. paucicostatus (Sturany).

Mansfield (1935, p. 31, pl. 2, fig. 9) has figured and briefly described the protoconch in Fusinus alaquaeensis Mansfield from the upper middle Miocene of the Alaka Creek Valley, Florida.
A recent discussion and illustration of the *Fusinus* protoconch are to be found in the work of Gardner (1944, pp. 447, 448, pl. 49, fig. 8). Under the generic diagnosis she writes: "Protoconch of about 1 1/2 volutions, the first, large, smooth, and tipped up slightly, the last half turn axially costate and delimitd from the conch by a varical riblet. Conch strongly threaded with spiral cords and axially rippled with obtuse ribs most prominent peripherally." The species described with protoconch figured is *Fusinus waltonensis* Gardner from the Alum Bluff group (middle Miocene) of Florida. Its protoconch is stated to be "rather small, obtuse, including two smooth whorls and usually about half a whorl that bears an axial sculpture; initial turn inflated, immersed at the tip, coiled in a single plane; succeeding volution also timid at its beginning, flattening toward its close, the axially sculptured portion feebly convex; riblets narrow but rather heavy, 15 or 16 of them crowded into half a whorl subequal and uniform in prominence between the sutures. Dividing line between the conch and protoconch clearly indicated by a varico riblet and by the abrupt beginning of the post-nuclear sculpture. Both axial and spiral sculpture strongly developed on the conch." The figure given shows the smooth and rounded and riblet stages of the protoconch followed by the conch sculpture of axial undulations crossed by spirals.

Typically the protoconch in *Fusinus* consists of one smooth and rounded whorl followed by an axial riblet stage of about 1/2 whorl. This latter stage is usually terminated by a riblet strong enough to be described as a varix.

The protoconch of another American Miocene *Fusinus* will now be taken up.

**PROTOCONCH IN FUSINUS EXILIS**

The protoconch and other apical parts are well shown by a specimen (Smith Collection, 1222, Pal. Research Inst., No 20317) from the Yorktown Miocene at the western end of Fort Boykin bluffs, Burwell Bay, James River, Virginia (Yorktown quadrangle). It can be rather confidently assigned to *Fusinus exilis* (Conrad) (Conrad, 1832, republication of 1803, p. 17, pl. 3, fig. 2; 1801, republication of 1803, p. 85, pl. 49, figs. 1, 4). The term *Fusinus exilis* (Conrad) is here used to include *F. burnsii* (Dall) (Dall, 1890, pp. 126, 127) which would appear to be at most a subspecies of *F. exilis*. The absence of axial undulations in the later whorls of Dall's form does not seem to constitute a difference of sufficient importance to warrant the erection of a separate species. That the adult and later ontogenetic stages in *Fusinus* are subject to great, and what may well be individual variation, is indicated by the work of Grabau (1904, pp. 21-23, 24-30, 46-48, pls. 2, 5). It is believed that *F. burnsii* represents nothing more than an individual variant of *F. exilis*.

Figures 12 and 13 of Plate 1 depict the apical whorls of the specimen of *Fusinus exilis* which forms the subject of this note. Figure 12 shows the smooth and rounded stage of the protoconch and late in whorl 1 the beginning of the riblet stage of the protoconch. The largest volution illustrated (parts of whorls 2 and 3) shows the conch sculpture of axial undulations crossed by raised spirals.
Figure 13 gives the smooth and rounded stage of the protoconch, at top and just below is seen end of protoconch riblet stage and beginning of conch sculpture. The largest volution illustrated (whorl 3) shows the conch sculpture.

Shell shape and conch sculpture both indicate that the specimen belongs in *Fusinus*. When to these the characters of the protoconch are added there can be no doubt that *Fusinus* is the proper genus for the specimen.

Grabau (1904, pp. 90, 91) places "*Fusus exilis Conrad" in the genus *Heilprinia*. This he probably would not have done had the protoconch been known to him.

**INTERPRETATIONS**

In the present paper the protoconch and early conch features of *Fusinus exilis* (Conrad) have been figured and briefly described. The protoconch is of the "*Fusus*" or *Fusinus* type so well described by Grabau (1904) and which appears to be relatively uniform in its characters throughout the genus. The conch of *Fusinus exilis* likewise points to a *Fusinus* reference. In discussing the species as a *Heilprinia* Grabau (1904, p. 90) says: "The protoconch has not been observed, but it is most probably of the same type as that of *H. caloosaensis*.

The protoconch of the specimen of *Fusinus exilis* here considered can in no way be referred to *Heilprinia* (see Grabau, 1904, pl. 18, fig. 5).

**THE PROTOCONCH OF HEILPRINIA**

The genus *Heilprinia* of Grabau (1904, p. 87) is based very largely on the characters of the protoconch. The protoconch of the genotype, *Fusus caloosaensis* Heilprin (Heilprin, 1887, pp. 68, 69, pl. 1, fig. 1), is described by Grabau (1904, pp. 87, 88) as follows:

"The protoconch in the specimens seen has a small rather pointed end, and is smooth for about a third of a volution. There is, however, a slight hollow in the upper whorl of some specimens, as if a partial volution had been broken away. The smooth whorls are followed by whorls with narrow sharp riblets, which are close together on the upper part of the whorl, but separate towards the center until they are from two to four times their width apart, and then approach each other again towards the umbilical side of the whorl, their lower ends being hidden by the succeeding whorl. This type of riblets continues for about a third or a half volution, after which the riblets become concave forward, on the upper part of the volution and convex forward on the lower portion. The outline is something like a reversed letter S. The general slope of the riblets is downward and forward. After the completion of the first ribbed volution the riblets become more crowded, but the interspaces are of irregular width. Fine spiral lines make their appearance between the ribs, where they are hardly visible even with a magnifier. After the completion of over one and a half ribbed volutions of the protoconch the riblets merge into the ribs of the conch, there being no definite varix. Towards the end the ribs are vertical and subequally spaced. There appears to be a very fine barely visible spiral sculpture on the ribbed portion of the protoconch, traces of which have been seen throughout."

Grabau’s text leaves no room for doubting that *Heilprinia* has a protoconch decidedly different from that of *Fusinus*. His figure of the protoconch in
Heilprinia caloosaensis (1904, pl. 18, fig. 5) further demonstrates not only this difference from Fusinus but also serves to emphasize the rather unusual characters of the early whorls in Heilprinia.

The species Heilprinia caloosaensis was first described from the Caloosahatchee Pliocene of Florida. It, or its variety carolinensis, has since been reported from the Waccamaw Pliocene of South Carolina (Dall, 1892, p. 234) and from the Waccamaw Pliocene of North Carolina (Miller, 1912, p. 256).

It is now proposed to submit figures and brief descriptions of the apical whorls in two specimens from the Carolinas.

 Protoconch in Heilprinia caloosaensis carolinensis

An individual (Smith Collection, 1218, Pal. Research Inst., No. 20318) from the Waccamaw Pliocene of Acme, North Carolina, shows rather well some of the riblets of the protoconch. The specimen is referred to Heilprinia caloosaensis (Heilprin) variety carolinensis (Dall) (Dall, 1892, p. 234, pl. 14, fig. 44a). Figure 14 of Plate 1 gives the apical view of the protoconch and in outline a small portion of the conch. The smooth and rounded stage of the protoconch is seen in the first 1/4 or 1/3 of whorl 1 and is followed by the riblet stage of the protoconch, partly obscured by weathering, but persisting through about 2/3 of whorl 2. The early conch sculpture is also obscured by weathering and this part of whorl 2 is shown in outline only. Figure 15 is a side view of the apical whorls of the same individual. A little of the smooth and rounded stage of the protoconch is seen in whorl 1 and this is followed by the riblet stage of the protoconch in whorls 1 and 2. The largest volutions illustrated (whorl 3) shows a weathered conch sculpture of axial undulations crossed by raised spirals.

Figures 16 and 17 of Plate 1 are of an individual (Smith Collection, 1217, Pal. Research Inst., No. 20316) which is likewise referred to Heilprinia caloosaensis (Heilprin) variety carolinensis (Dall). It came from the Waccamaw Pliocene of Nixons Landing, Waccamaw River, South Carolina. Figure 16 is a side view of the apical whorls. The riblets of the protoconch in whorl 1 are much weathered and barely recognizable but in whorl 2 they are better displayed. The largest volutions illustrated (whorl 3) shows the conch sculpture of axial undulations crossed by raised spirals. Figure 17 gives another side view of the apical whorls of the same individual. Here the specimen is turned slightly so as to show end of protoconch and beginning of conch. The riblets are obscured by weathering in this view of whorl 1 but they are well displayed in whorl 2 where they cease abruptly at the end of the protoconch. The conch sculpture of axial undulations and raised spirals occupies the rest of whorl 2 and all of whorl 3 which is the largest volutions illustrated.

Interpretations

Protoconch and early conch features have now been figured and briefly described for two individuals of Heilprinia caloosaensis carolinensis. In neither of these Carolina specimens is the preservation perfect but between them they give a very fair picture of the features in question. There is a rather good agreement with Grabau's description and figure of the genotype (1904, pp. 87, 88, pl. 18, fig. 5). Although Heilprinia and Fusinus are superficially much alike
in conch sculpture and in fusiform shape their protoconchs are quite different. The protoconch in *Heilprinia* has a small initial bulb and a very short smooth and rounded stage as a rule. A longer smooth and rounded stage (Grabau, 1904, p. 89) may constitute an individual variation. The riblet stage of the protoconch, on the other hand, is long and the dispositions, characters, and variations in shape of the riblets are unusual. The present writer is not a believer in the doctrine that protoconch characters should always govern in classification. Nevertheless here the differences between the protoconchs of *Heilprinia* and *Fusinus* are so profound that they add great weight to the justification for separation of the two genera. However, the two genera appear to be separable on conch characters alone (see Cossmann, 1906, p. 227, pl. 13, figs. 1, 2).

**THE PROTOCONCH OF HESPERISTERIIA**

The genus *Hesperisteriia* was instituted by Gardner (1914, p. 445) for "a small group of species characterized by a naticoid protoconch," etc. The genotype was designated as *Hesperisteriia valtonia* Gardner. The protoconch of the genotype (Gardner, 1914, p. 446) is "rather small, smooth, highly polished, naticoid including three volutions; initial turn strongly inflated, immersed at the tip; remaining volutions convex, increasing rather rapidly both in height and diameter. Close of protoconch indicated by a slight thickening of the shell and by the first appearance of faint spiral lirae and sharp, crowded incrementalts." etc. The first half turn assigned to the conch is "threaded with 3 fine spirals, the anterior just visible behind the suture, the medial slightly in front of the median horizontal and the posterior midway between the medial lira and the posterior suture." The early axials are fine and sharp, resembling growth lines. Near the close of the first ½ turn of the "conch" the sculpture changes abruptly.

This assignment of early sculpture to the conch may be questioned but the sequence observed can be recognized and seems to agree fully with that of the apical whorls of *Peristernia filicata* (Conrad) (Conrad, 1861, republication of 1803, p. 85, pl. 39, fig. 2). The figures given by Gardner (1914, pl. 39, figs. 14, 15, 16) also indicate that *Hesperisteriia* should include Conrad's species which is accordingly placed in that genus. It is now proposed to submit figures and brief descriptions of the apical whorls in *Hesperisteriia filicata* (Conrad).  

**PROTOCONCH IN HESPERISTERIIA FILICATA**

The apical whorls are present and well preserved in a specimen (Smith Collection, 1234, Pal. Research Inst., No. 20320) of *Hesperisteriia filicata* (Conrad) (Conrad, 1861, republication of 1803, p. 85, pl. 39, fig. 2). It came from the western end of Fort Boykin bluffs, Burwell Bay, James River, Virginia (Yorktown quadrangle). The age is Yorktown Miocene. "Figure 18 of Plate 1 gives an apical view of the first three whorls. Whorl 1 shows the minute initial bulb and the smooth and rounded stage of the protoconch which also persists through whorl 2 and goes slightly into whorl 3. Early in whorl 3 appear fine spirals which are later accompanied by fine axials. This sculpture persists to slightly beyond the first ¼ of whorl 3. The remainder of whorl 3
shows conch sculpture of axial undulations crossed by raised spirals. Figure 19 depicts the apical whorls of the same individual in side view. Whorls 1 and 2 show the smooth and rounded stage. Whorl 3 shows its end and the beginning of faint sculpture early in the whorl. The largest volutions illustrated (parts of whorls 3 and 4) is occupied by the conch stage of axial undulations crossed by raised spirals. Figure 20 is another side view of the apical whorls of the same individual. Smooth and rounded stage shows in whorls 1 and 2. In whorl 3 is seen the change from the faint early sculpture to the coarser sculpture of axial undulations crossed by raised spirals. The largest volution illustrated (whorl 4) likewise shows the axial undulations crossed by raised spirals.

INTERPRETATIONS

The apical whorls of an individual assignable to Peristernia filicata (Conrad) have now been figured and briefly described. The sculptural sequence in these early whorls is very like that described and figured by Gardner for the genus Hesperisternia. Gardner’s three species of Hesperisternia and the form here considered are believed to be congeneric. Apparent discrepancies in the lengths of their early stages are not regarded as important. The first fine sculpture is placed in the conch by Gardner. The present writer is more inclined to interpret this first sculpture as either (1) the equivalent of the protoconch riblet stage of Fusinus and other genera or to regard it as (2) comparable to the protoconch-conch transition seen in Busycon.

Mansfield (1930, p. 64) places Conrad’s species, here called Hesperisternia filicata (Conrad), in the Fasciolariidae. Gardner (1944, pp. 442-445) assigns the genus Hesperisternia to the same family. If the more or less bifurcated columellar ridge or plait in Conrad’s species confirms its proximity to Fasciolaria we are again confronted with the question of different protoconch types in closely related forms. Whatever its boundaries the protoconch in Hesperisternia filicata is quite different from the protoconchs found in Fasciolaria tulipa, F. apicina, and F. papillosa (Smith, 1945, pl. 3, figs. 4-16).

THE PROTOCONCH OF UROSALPINX

The somewhat limited and imperfect evidence in the possession of the writer indicates that the protoconch in the genus Urosalpinx is large, prominent, and erect in position. The first half whorl may have an axis of coiling seemingly discordant with that of the remainder of the whorl. The initial bulb is large. The volutions are few and probably do not exceed one and one-half. The protoconch is apt to terminate in a strong varix.

The protoconch has been described and figured in Urosalpinx phriknos Gardner and Aldrich (Gardner and Aldrich, 1919, p. 35, pl. 4, figs. 2, 4, 6, 7). The description is—“Protoconch including 1½ small, smooth, somewhat flattened whorls. First half turn partially submerged in the succeeding volutions. Differentiation between conch and protoconch very sharp.”

Figures and brief descriptions of some apical whorls in Urosalpinx will now be given.
Protoconch in Urosalpinx Trossulus

The protoconch and other apical whorls may be present and well preserved in *Urosalpinx Trossulus* (Conrad) (Conrad, 1852, republication of 1893, p. 18, pl. 3, fig. 5; 1893, republication of 1893, pp. 84, 85, pl. 48, fig. 6). Figures 21, 22, and 23 of Plate 1 show the apical whorls of an individual (Smith Collection, 1207, Pal. Research Inst., No. 20321) from the western end of the Fort Boykin bluffs, Burwell Bay, James River, Virginia (Yorktown quadrangle). The age is Yorktown Miocene. Figure 21 is an apical view of slightly more than the first two whorls. In whorl 1 can be seen the relatively large initial bulb and smooth and rounded stage of the protoconch. This stage also persists into the early portion of whorl 2. It is terminated by a strong varix. The conch sculpture then begins abruptly and occupies the remainder of whorl 2. Figure 22 is a side view of the apical whorls of the same individual in it can be seen the smooth and rounded stage in whorl 1 and in the early part of whorl 2. The volutions at bottom (parts of whorls 2 and 3) shows conch sculpture. In figure 23 the same individual is turned slightly so as to bring to view the end of the smooth and rounded stage of the protoconch with its strong terminal varix. This is followed by the abrupt commencement of conch sculpture. The largest volutions illustrated (parts of whorls 2 and 3) shows the conch sculpture.

Figure 24 of Plate 1 is a side view of the apical whorls of another individual (Smith Collection, 1219, Pal. Research Inst., No. 20322) of *Urosalpinx Trossulus* from the Yorktown Miocene. This specimen was collected a short distance northwest of Edenhouse Point, Chowan River, North Carolina (Edenton quadrangle). The figure shows the smooth and rounded stage of the protoconch ended by a comparatively weak varix. Conch sculpture begins abruptly in whorl 2 and can be seen in whorl 3, the largest volutions illustrated.

**Interpretations**

The apical whorls of two individuals of *Urosalpinx Trossulus* have now been figured and briefly described. In the example from Virginia the protoconch has a strong terminal varix. In the specimen from North Carolina the varix is relatively weak. Neither individual shows a true riblet stage in the protoconch although one may interpret the terminal varix as the vestigial remnant of this stage. Differences in the strength of the varix are regarded as falling under the heading of individual variation.
SUMMARY OF PART III

BUSYCON

The forms here considered are *Busycen contrarium*, *B. cf. rapum*, *B. cf. planulatum*, and *B. pyrum*. The protoconch is relatively uniform and its late sculpture passes gradually into the conch sculpture.

FUSINUS

The apical whorls of *Fusinus exilis* have been figured and described. The protoconch is of the *Fusinus* type. Both protoconch and conch characters preclude a reference to *Heilprinia*.

HEILPRINIA

The apical whorls of *Heilprinia calooasaensis carolinensis* are considered. The characters of these whorls are much like those found in the corresponding whorls of the genotype. Both protoconch and conch features justify the placing of the subspecies in *Heilprinia*.

HESPERISTERNIA

The apical whorls of *Hesperisteriina flicata* are studied. The protoconch is remarkable for its minute initial bulb and its relatively long smooth and rounded stage. The earliest sculpture may be the equivalent of the protoconch riblet stage or it may represent a transitional sculpture between protoconch and conch. However bounded the protoconch is quite different from that in certain Fasciolarias—possible near relatives.

UROSALPINX

The apical whorls of *Urosalpinx trossulus* are figured and described. The protoconch has a relatively large and somewhat discordant initial bulb and is without a riblet stage. Its terminal varix may be strong. The conch sculpture begins abruptly.
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PLATE

PLATE 1 (VOL. PL. 25)

volution shown is about 1.25 mm. (15) Side view of apical whorls of same individual. The largest volution illustrated (whorl 3) has a right-left diameter of about 2.5 mm. at the shoulder angle. Pliocene (Waccamaw). Acme, North Carolina. Smith Coll., No. 1218. P. R. I., No. 20318.

16, 17. Heilprinia caloosensis carolinensis (Dall) .......................... 11

Apical whorls of one individual. (16) Side view. Largest volution illustrated (whorl 3) has a right-left diameter of about 2.5 mm. at the shoulder angle. (17) Another side view, the individual being turned slightly so as to display end of protoconch and beginning of cone. Largest volution illustrated (whorl 3) has a right-left diameter of about 2.66 mm. at the shoulder angle. Pliocene (Waccamaw). Nixons Landing, Waccamaw River, South Carolina. Smith Coll., No. 1217. P. R. I., No. 20319.

18-20. Hesperisternia flicita (Conrad) ........................................ 12

Apical whorls of one individual. (18) Apical view of the first three whorls. Whorl 3 has a diameter of about 1.25 mm. (19) Side view of the apical whorls of the same individual. The largest volution illustrated (parts of whorls 3 and 4) has a maximum right-left diameter of about 1.5 mm. (20) Another side view. The largest volution illustrated (whorl 4) has a maximum right-left diameter of about 1.75 mm. Miocene (Yorktown). Western end of Fort Boykin bluffs, Burwell Bay, James River, Virginia (Yorktown quadrangle). Smith Coll., No. 1234. P. R. I., No. 20320.

21-23. Urosalpinx trossulus (Conrad) ....................................... 14

Apical whorls of an individual with strong varix. (21) Apical view of slightly more than the first two whorls. Maximum diameter of whorl 2 is about 1.5 mm. (22) Side view of apical whorls. Volution at bottom (parts of whorls 2 and 3) has a right-left diameter of about 1.66 mm. at the lower suture. (23) Another side view of the apical whorls of the same individual. Volution at bottom (parts of whorls 2 and 3) has a right-left diameter of about 2 mm. at the lower suture. Miocene (Yorktown). Western end of Fort Boykin bluffs, Burwell Bay, James River, Virginia (Yorktown quadrangle). Smith Coll., No. 1207. P. R. I., No. 20321.

24. Urosalpinx trossulus (Conrad) ........................................ 14

Side view of the apical whorls. Largest volution illustrated (whorl 3) has a right-left diameter of about 1.5 mm. at the lower suture. Miocene (Yorktown). A short distance northwest of Edenhouse Point, Chowan River, North Carolina (Edenton quadrangle). Smith Coll., No. 1219. P. R. I., No. 20322.

(Figures of Plate 1, drawings by Ethel Ostrander Smith)
EXPLANATION OF PLATE 1 (25)

Figure

1. *Busycon contrarium* (Conrad) .............................................. 6

   Side view of the apical whorls. Largest volutions illustrated (parts of
   whorls 2 and 3) has a left-right diameter of about 6 mm. at the shoulder
   angle. Pliocene (Calooshahatchee). Calooshahatchee River, about 3 miles
   east of Port Deurnal, Florida. Helen Tucker Rowland Coll., No. 67F/55.

2-4. *Busycon cf. rapium* (Heilprin) ........................................... 6

   (2) (3) Side views of the apical whorls of one individual. In figure
   2 the largest volution illustrated (mostly whorl 2) has a right-left diam-
   eter of about 5 mm. at the shoulder angle. In figure 3 the largest volu-
   tion illustrated (parts of whorls 2 and 3) has a right-left diameter of
   about 6 mm. at the shoulder angle. Figure 4 is an apical view of the
   same individual. It shows somewhat more than the first three whorls.
   Maximum diameter of whorl 3 is about 9 mm. Probably Pliocene
   (Calooshahatchee). About halfway between Clewiston, Florida and La-

5-6. *Busycon cf. planulatum* (Dill) ........................................... 7

   (5) Apical whorls in side view. Largest volutions illustrated (parts
   of whorls 2 and 3) has a right-left diameter of about 3 mm. at the shoul-
   der angle. (6) Apical view of slightly more than the first four
   whorls of the same individual. Whorl 4 has a maximum diameter of
   about 11 mm. at the shoulder angle. Probably Pliocene. Acline, Flor-
   4ida. Helen Tucker Rowland Coll., No. 61F/50.

7-8. *Busycon planulatum* (Dall) ............................................... 7

   (7) Apical whorls in side view. Largest volution illustrated (parts
   of whorls 2 and 3) has a right-left diameter of about 3 mm. at the
   shoulder angle. (8) Apical view of slightly more than the first four
   whorls of the same individual. Whorl 4 has a maximum diameter of
   about 11 mm. at the shoulder angle. Probably Pliocene. Acline, Flor-
   4ida. Helen Tucker Rowland Coll., No. 61F/50.

9-10. *Busycon pyrum* (Dillwyn) ............................................... 7

   Apical whorls of a probably immature individual. (9) Side view.
   Larger volution illustrated has a right-left diameter of about 3 mm. at
   the shoulder angle. (10) Another side view, the specimen being turned
   slightly. Volution at bottom (parts of whorls 2 and 3) has a right-
   left diameter of about 4 mm. at the shoulder angle. Pliocene (Caloo-
   shahatchee). Twelve and 7/10 miles from Moore Haven, Florida, at the
   intersection of Highways 67 and 25 in Hendry County. Helen Tucker
   Rowland Coll., No. 36F/18.

11. *Busycon pyrum* (Dillwyn) ............................................... 8

   Side view of the apical whorls of an immature individual. Volution
   illustrated at bottom (parts of whorls 2 and 3) has a right-left diam-
   eter of about 4 mm. at the shoulder angle. Pleistocene. Sixmile Creek,
   at Orient, Florida. Helen Tucker Rowland Coll., No. 5F/11.

12-13. *Fusinus exile* (Conrad) .............................................. 9

   Apical whorls of an immature individual. (12) Side view. Largest
   volution illustrated (parts of whorls 2 and 3) has a right-left diameter
   of about 2 mm. (13) Another side view. Specimen turned slightly.
   Volution at bottom (whorl 3) has a right-left diameter of about 3 mm.
   Miocene (Yorktown). Western end of Port Boykin bluffs, Burwell Bay,
   P. R. I., No. 20317.

14-15. *Heilprinia caloosaensis carolinensis* (Dall) ...................... 11

   Apical whorls of one individual. (14) Apical view of protocoen and
   in outline a small portion of the conch. Maximum diameter of largest

(Continued on the previous page.)
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TO THE

INVERTEBRATE PALEONTOLOGY

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By

BURNETT SMITH

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## CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Introduction</td>
<td>5</td>
</tr>
<tr>
<td>Acknowledgments</td>
<td>5</td>
</tr>
<tr>
<td>Petite Rivière-du-Loup</td>
<td>5</td>
</tr>
<tr>
<td>Field Evidence</td>
<td>5</td>
</tr>
<tr>
<td>Interpretations</td>
<td>7</td>
</tr>
<tr>
<td>Rivière-du-Sud</td>
<td>7</td>
</tr>
<tr>
<td>Field Evidence</td>
<td>7</td>
</tr>
<tr>
<td>Interpretations</td>
<td>8</td>
</tr>
<tr>
<td>Bibliography</td>
<td>10</td>
</tr>
<tr>
<td>Plates</td>
<td>11</td>
</tr>
</tbody>
</table>
TWO MARINE QUATERNARY LOCALITIES

By

BURNETT SMITH

INTRODUCTION

Not counting damage due to human activities the mature geologist may see localities of great interest deteriorate markedly during the course of his lifetime. Such deterioration may affect the bedrock but is apt to be much more pronounced and rapid in the usually soft and unconsolidated surface materials. In these latter, however, there may also be relatively sudden happenings of an opposite nature, very trying to the landowner perhaps, but of no small benefit to the geologist. This paper is intended to present data overlooked or unstressed and also to record very recently exposed and probably temporary sections which may be useful in dating the marine Quaternary fossils involved. The localities considered are in the Province of Quebec, Canada. The first is the long-known collecting ground of the Petite Rivière-du-Loup, near the city of Rivière-du-Loup in the county of that name. The second, much less well known, is to be found in the bluffs of the Rivière-du-Sud near St. François Montmagny (Orleans Sheet), Montmagny County.

The primary emphasis in this paper is stratigraphic. Geologic processes, physiography, and lithology are regarded as of secondary importance. For those interested chiefly in processes a very useful discussion is to be found in the recent work of Washburn (1947, especially p. 82).

To avoid misunderstanding the present writer points out that the term “Post-Glacial” has a regional or locality value and is used in this sense here. (See Flint, 1947, p. 207).

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PETITE RIVIERE-DU-LOUP

FIELD EVIDENCE

This locality has been known for a long time (Dawson, 1865, pp. 82, 85; Dawson, 1894, p. 104) but has usually been cited as simply “Riviere du Loup”. As a result one can not be sure whether a fossil so reported has come from the stream described by Dawson or from the marine beds, very much higher in altitude, which have been found within the city of Rivière-du-Loup (Goldthwait, 1913, p. 66). A further complication is caused by Dawson’s use of the term “boulder clay” to include fossiliferous marine clays which contain ice-rafted
boulders (Dawson, 1894, pp. 160-162). Apparently some later writers have considered that Dawson's boulder clay was necessarily glacial till. Coleman has presented evidence for two glaciations at Rivière-du-Loup (Coleman, 1927, pp. 385-403) but his text shows clearly that he was not studying the Petite Rivière-du-Loup of Dawson.

The Petite Rivière-du-Loup roughly parallels the shore of the St. Lawrence and also the ridge behind Cacouna noted by Dawson (1894, p. 82). It has excavated a valley in the marine till of the low ground. The surface of this till, now approximately 75 feet in altitude, constitutes a definite terrace on each side of the stream. Its surface is flat and even, varying little in altitude in a stream-wise direction, but sloping very gently from the north toward the stream. This is the only well-developed terrace along the Petite Rivière-du-Loup. For purposes of identification it will be referred to as the Petite Rivière-du-Loup terrace. See Plate 1, figure 1. Two comparatively small areas on this terrace appear to be boulder covered if one may so interpret their rounded and protuberances. These areas are very small compared to the generally smooth terrace on which boulders are very few indeed. In any event there is nothing on the terrace surface to suggest the uneven topography of ground moraine.

In the terrace sections so far examined no glacial till has been found by the writer. Several of these sections go to the terrace top. Boulders, it is true, are present in the terrace material in which the marine fossils occur. However, they are not numerous enough to suggest till and the many unbroken marine fossils would seem to negative the conclusion that one is dealing with a glacier-shoved sea bottom.

The evidence, physiographic and geologic, indicates that the Petite Rivière-du-Loup terrace is simply the remnant of a miniature coastal plain which once filled the depressions in the Rivière-du-Loup region.

Near the mouth of the Petite Rivière-du-Loup and extending some distance up its valley is a lower plain 40 to 45 feet below the Petite Rivière-du-Loup terrace already noted. See Plate 1, figure 1. This lower plain may possibly correlate with Goldthwait's Micmac terrace (Goldthwait, 1911, pp. 301-317) though it appears a little too high for a Micmac reference.

Marine fossils so far found by the writer along the Petite Rivière-du-Loup are rather surely from the material of the terrace and not from this lower plain.

In October, 1946 a recent landslide south of the stream showed a fair section of the Petite Rivière-du-Loup terrace materials. In October, 1947 still further sliding had taken place. The section extended to the top of the terrace and demonstrated beyond question that here the fossiliferous deposit is not overlain by glacial till.

On the other side of the valley but farther upstream a number of slumped sections also extended to the top of the terrace but showed no till. Unfortunately some of these places have been used for the dumping of rubbish including oyster shells. These latter may in time cause trouble for the paleontologist.

The information gathered from the series of sections just considered is most helpful in interpreting the conditions at the locality shown in Plate 1, figures 2, 3. This station is of especial interest because it has furnished a specimen of Plirifiusus kroyeri (Moller) with protoconch rather well preserved. The apical whorls of this individual have been described and figured (Smith, 1945, pp. 34, 35, 37; text fig. 4, pl. 3, figs. 17-19) and any evidence helping to date the specimen becomes of value.
Here most of the fossils are found in what is rather surely landslide or land-
slip material. The stream is eroding the lower portions of this slide exposing oc-
casional fossils. Passing upward the grass-covered surface of the slide or slip-
izes gradually and then more steeply until it reaches the edge of the Petite Rivière-
du-Loup terrace surface. In the steeper parts of this slope more or less slid-
ing has exposed the terrace material below the soil. Here also fossils are found.
The evidence points not to a violent landslide but to a slow creep or flow of the
material toward the stream. Trees on the slope have been tilted without being
overturned. The fence at the terrace border has not been destroyed, but portions
of it have been left "dangling". In October, 1936, a crack was seen on the terrace
surface roughly parallel to the terrace margin and close to it. The undisturbed sur-
f ace of the terrace gives no indication of glacial till. The same is true of the slop-
ing disturbed surface of the terrace.

INTERPRETATIONS

The evidence so far gathered leads to the conclusion that the marine hill of
the Petite Rivière-du-Loup terrace has never been covered by till and that the
fossils coming from it are to that extent Post-Glacial.

RIVIÈRE-DU-SUD

FIELD EVIDENCE

Between Valleville and Montmagny the Rivière-du-Sud valley in the larger
sense is from two to four miles wide and the higher land both northwest and
southeast of the valley is composed of bedrock often much disturbed. Inside of
these rock walls is a relatively flat plain or terrace ranging in altitude from 100
to 150 feet (Orleans Sheet). This may in places be quite smooth and level for a
distance of nearly two miles at right angles to the general trend of the valley or
general course of the river. The contours on the Orleans Sheet indicate that the
surface of this plain descends gently when followed downstream. The Rivière-du-
Sud has cut an inner valley, widened by meanders, through this plain thereby
producing an extensive terrace on each side of the stream. Wherever ob-
erved this plain is composed of soft or loose materials, prevailingly clay or mud.
No unquestionable glacial deposits were seen either in the river bluffs or upon
the surface of the plain or terrace.

Near St. François-Montmagny a northwestward-cutting meander has pro-
duced a more or less connected series of bluffs. See Plate 2, figure 4 and Plate 3,
figures 8, 9. These bluffs, though considerably slumped, combine to give a very
fair picture of the conditions from river's edge to the terrace surface which here
is approximately 125 feet in altitude. The bluffs are made up of fossiliferous
marine clay except for some four or five feet at the top. Under favorable condi-
tions the marine beds can be seen in place extending downward to the river and
passing under water. Their known thickness at this locality is 45 to 50 feet. How
much more may lie below the river is unknown.

The fundamental cause of the exposure of terrace materials is, of course,
erosion by the Rivière-du-Sud. Very fair, small, and temporary sections have as
immediate causes rain wash and rilling, slumping, and landslides.

In October, 1936 an apparently very recent landslide was observed. The sec-
tion produced was insignificant but the slide must have been of considerable vi-

precisely truncated by river erosion. In one place above the slide the otherwise undisturbed clay presented a curving lined gouge which might be likened to slickensiding in bedrock.

Between October 7, 1946 and October 8, 1947 minor slides laid bare a number of new sections in the Rivière-du-Sud terrace near St. François Montmagny. Two of these will now be considered.

One section is seen in Plate 2, figures 5, 6. Figure 5 shows the relation of section to the almost undisturbed terrace surface while figure 6 gives the details of the section. In this closer view (fig. 6) the marine fossiliferous clay can be seen at base. It is much jointed both vertically and horizontally but the vertical joints are predominant. The horizontal jointing is probably determined by bedding planes. The marine clay is overlain by a wedge of gravel and cobbles with one relatively large boulder. Above the gravel come one from one and one-half to two feet of laminated sandy material. In places the lamina are brecciated and folded though the bed as a whole is not disturbed. Above the laminated bed come about two feet of soil to the top of the terrace. Minor unconformities are believed to separate the laminated material from lower units and the gravel from the marine clay. Fossils occur in the marine clay and have also been found in the gravel. These latter were probably derived from the the marine clay. No fossils have been seen in the laminated bed.

About 150 feet east of the station just discussed a more extensive, if less accessible, section was found in the Rivière-du-Sud terrace. This is shown in Plate 3, figure 7. Shrunken and gullied or rain-rilled marine beds below are overlain by a discontinuous layer of gravel and cobbles which is in turn overlain by about three feet of laminated material. Above the last is soil. The figure shows the terrace surface virtually uneroded at left but passing into the scarp at right.

Proximity and similar sequence in these two Rivière-du-Sud sections make the equivalency of their respective units a practical certainty.

In the Rivière-du-Sud terrace near St. François Montmagny boulders are found in the marine clay but not in such numbers as to suggest till. The presence of numerous unbroken marine shells may be taken as ruling out the conclusion that the deposit is glacier-overridden sea bottom. Ice-rafting of the boulders seems to give the only logical explanation of their presence in the clay.

A boulder in the discontinuous gravel and cobble bed is shown in Plate 2, figure 6. A boulder in the second section discussed occurred at the top of the laminated bed and was apparently in place.

As already noted no till has been seen in the sections and the smooth and flat terrace surface shows no evidence of ground moraine topography.

The Rivière-du-Sud terrace at this locality is of particular interest to the writer because from it came a specimen of *Plicatula kroyeri* (Möller) with a rather well-preserved, large, and perhaps abnormal protoconch. The apical whorls of this specimen have been described and figured (Smith, 1945, pp. 34-36, plate 3, figures 20-22). It is therefore important that any evidence on the dating of the specimen should be a matter of record.

**Interpretations**

For the Rivière-du-Sud bluffs near St. François Montmagny evidence at hand indicates a thickness of some 45 to 50 feet of fossiliferous marine clay or mud
overlain by a discontinuous layer of gravel and cobbles which in turn is overlain by a laminated sandy bed of fine grain. Minor unconformities separate these three stratigraphic units. The laminated bed is capped by a few feet of material which has been classified as soil and which can probably be disregarded in any attempt to date the deposits of the terrace. The marine clay or mud at base is definitely, even if obscurely, stratified and yields unbroken fossils, some in an excellent state of preservation. That such material could have been overridden or pushed along by glacial ice is out of the question. Any included boulders are therefore interpreted as ice-rafted, that is, dropped on the sea bottom by the melting of floating sea ice (see Dawson, 1894, pp. 190-192). The overlying discontinuous gravel and cobbles layer is thin and has not the characteristics of glacial till. Although marine fossils are found in it these have probably been derived from the clay or mud below. As previously stated (Smith, 1945, pp. 35, 36) this coarse deposit is believed to represent a transient fluvial episode. A like interpretation can be given the laminated bed which probably accumulated in some short-lived back water or ox-bow. The laminae may well depict seasonal changes, but there seems to be no reason for invoking the proximity of glacial ice to explain them. The climate was, however, almost certainly cold. The brecciation and minute folding of some of the laminae would seem to correspond with structures encountered in shallow water Paleozoic deposits such as the Chrysler formation and the Elmwood waterline (Smith, 1929, pp. 28-30; Smith, 1935, pp. 14, 16, 17, 22, 23). The laminated bed as a unit is undisturbed, only its laminae are folded or contorted and these very locally and not universally. This latter point is stressed for the conditions here are in no way comparable to those produced by glacial ice which has overridden and folded stratified beds and truncated their folds (Clapp, 1908, p. 528, plate 58, figs. 1, 2 and text fig. 5 on p. 540).

The Rivière-du-Sud terrace has an extremely even and flat, if somewhat sloping, top (Plate 2, figure 4). There is nothing on its surface resembling ground moraine topography. It is interpreted as the remnant of a miniature coastal plain (Post-Glacial for this locality) which extended tongue-like up a valley flanked by bedrock. Its present surface has undergone so little erosion that the original evenness has come down to us intact. In this part of the valley the only erosion of any magnitude is that which has been accomplished by the Rivière-du-Sud.

When one attempts a more precise dating of the stratigraphic units of this terrace the matter becomes more speculative. However, as a working hypothesis the writer favors the following interpretations. The fossiliferous marine clay is assumed to be a single unit until proved otherwise. It was initiated during the period of early subsidence (or rise in sea level) and ice-margin retreat (see Brøgger, 1900, 1901, pp. 650a, 670-685; Johnston, 1917, pp. 9-11, 28, 30). It was completed after emergence set in. The gravel and overlying laminated bed are of fresh-water origin and belong to the period of emergence (or sea withdrawal). The marine clay at the start was contemporary with not distant glacial ice but the deposit as a whole is Post-Glacial in a local sense. The gravel and the laminated bed are Post-Glacial in the generally accepted broader sense.
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Washburn, A. Lincoln
PLATES

PLATE 1 (VOL. PL. 26)
EXPLANATION OF PLATE 1 (26)

Figure Page

1. Petite Rivière-du-Loup .... 6
   Terrace (Petite Rivière-du-Loup terrace) about 45 feet above the
   Highway 10 bridge over the stream. Taken from Highway 10 looking
   upstream. At right a lower plain about 45 feet below the terrace.

2. Petite Rivière-du-Loup 6
   Stream-eroded creep landslide material from the Petite Rivière-du-
   Loup terrace which shows in the background.

3. Petite Rivière-du-Loup 6
   A slightly different view of the creep-slide shown in figure 2. Note
   effect of slide on fence at edge of terrace and on tree (extreme left).

(Figures of Plate 1, photographs by Ethel Ostrander Smith, October, 1947.)
EXPLANATION OF PLATE 2 (27)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>4. Rivière-du-Sud, near St. François Montmagny</td>
<td>7, 9</td>
</tr>
<tr>
<td>View from highway on southeast side of river. Note bluffs and extremely flat top of 125 foot terrace. St. François Montmagny in the background.</td>
<td></td>
</tr>
<tr>
<td>5. St. François Montmagny</td>
<td>8</td>
</tr>
<tr>
<td>Small slide section in the 125 foot terrace of the Rivière-du-Sud. Camera points away from river.</td>
<td></td>
</tr>
<tr>
<td>6. St. François Montmagny</td>
<td>8</td>
</tr>
<tr>
<td>Closer view of the slide section shown in figure 5. Much jointed marine beds (specimen P.R.I., No. 20383) below overlain (just above glove) by a wedge of gravel and cobbles which in turn is overlain by laminated material (specimen P.R.I., No. 20382). Above the last is soil. Note contortion and brecciation of laminae in the laminated bed.</td>
<td></td>
</tr>
</tbody>
</table>

(Figures of Plate 2, photographs by Ethel Ostrander Smith, October, 1947.)
PLATE 3 (VOL. PL. 28)
EXPLANATION OF PLATE 3 (28)

7. St. François Montmagny
   Relatively extensive section at top of the 125 foot terrace of the Rivière-du-Sud. This is about 150 feet east of the station shown in figures 5 and 6. Silted and gullied marine beds below are overlain by a discontinuous layer of gravel and cobbles which in turn is overlain by about 3 feet of laminated material. Above the last is soil. Approximate scale may be obtained from the pasture vegetation at top of terrace.

8. Rivière-du-Sud, near St. François Montmagny
   Bluffs and ravine-like landslide scar with cone at base, Camera points approximately northwest.

9. Rivière-du-Sud, near St. François Montmagny
   View of bluffs, camera pointing downstream.

(Figures of Plate 3, photographs by Ethel Ostrander Smith, October, 1947.)
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OF

AMERICA

VOLUME III

NO. 23: STUDIES OF CARBONIFEROUS CRINIDS

Part I. A Group Of Pennsylvanian Crinoids From The Ardmore Basin
Part II. Delocrinids Of The Brownville Formation Of Oklahoma
Part III. Description Of Two New Cromyocrinids From The Pennsylvanian Of Nebraska
Part IV. On New Species Of Alcimocrinus And Ulrichickinus From The Fayetteville Formation Of Oklahoma

By

Harrell L. Strimple

May 20, 1949

Paleontological Research Institution

Ithaca, New York
U. S. A.
STUDIES OF CARBONIFEROUS CRINOIDS

PART I.—A GROUP OF PENNSYLVANIAN CRINOIDS FROM THE ARDMORE BASIN

By

HARRELL L. STRIMPLE

INTRODUCTION

A most interesting assemblage of crinoids has been collected from Pennsylvanian rocks of the Ardmore Basin in Oklahoma, by Frank Crane of Fort Worth, Texas, and Wm. T. Watkins of San Antonio, Texas. These advanced amateur paleontologists are to be highly commended for their diligence in the field and for their cooperation in placing this material into scientific channels. Specimens were collected from the Arnold limestone member, Deese formation, the Pumpkin Creek limestone and the Otterville limestone members of the Dornick Hills formation. Certain lower members of the Dornick Hills formation are considered by Tomlinson (1929) as of Morrow (lowermost Pennsylvanian) age. All species studied have been proven new and distinct from those found in other Mid-Continent or Texas areas. However, the genera have all been previously described. This is to be expected since the Ardmore Basin is known to have been more or less isolated from the oceans covering adjacent areas during Pennsylvanian time. Most Pennsylvanian crinoids are primarily statozoic and could not be expected to migrate freely under such conditions.

Three forms are assigned with reservation to the genus Paradelocrinus and are described as P. crani, n. sp., P. regulatus, n. sp., and P. discitus, n. sp. In the discussion of Ethelocrinns watkinsi, n. sp., the weakness of the genus Paradelocrinus is pointed out, and it is proposed that the older genus, Ethelocrinns, be given preference in the assignment of species having a low dorsal cup with only two plates in the posterior interradius and for which the arms are not known. The species E. ardmorensis, n. sp., E. peridous, n. sp., and E. variabilis, n. sp. are described. E. sphaeri, n. sp. is presented. However, assignment of the latter to Ethelocrinns is with hesitation due to the upflared attitude of the infrabasal plates which indicates close affinity with such forms as Ulocrinns. Three species of Placocrinus are described as P. dornickei, n. sp., P. tumulosus, n. sp., and P. putens, n. sp. The latter species is different from most forms assigned to the genus. Two species of Delocrinus are present and are described as D. armatura, n. sp., and D. aristatus, n. sp. Of unusual interest is the occurrence of a bona fide representative of the Permian genus Malalocrinus which is described as M. acygonis, n. sp. One species of Lecythoocrinus is described as L. fusiformis, n. sp. Several undescribed species are known from disassociated ossicles and from material found on more recent field trips to the Ardmore Basin in southern Oklahoma.
SYSTEMATIC DESCRIPTIONS

Genus PARADELOCRINUS Moore and Plummer, 1940

Remarks.—Paradelocrinus was proposed for the reception of forms having nearly regular, strong curvature of the sides in profile of the cup, no anal plate below the upper limits of the cup, and the subcircular outline in dorsal or ventral view. Normal representatives also possess a strong basal invagination somewhat similar to Delocrinus. None of the species described below have a tunnel-like basal concavity and so assigned to the genus with reservation.

Paradelocrinus cranii, n. sp.

Plate 1, figures 1, 2, 3, 7

Description.—Infrabasal circlet is flat, and outer extremities of the five elements are readily visible beyond the large proximal columnal. Basals (BB) are small, six-sided plates, slightly longer than wide with proximal portions forming walls of the broad, shallow basal concavity. Two BB are larger than the others, and are apparently post. B and 1. ant. B. Radials (RR) are unusually large, long elements, with proximal extremities curved slightly inward to participate in basal depression. Distal portions have a strong regular curvature.

Articular facets are strongly developed. Outer ligamental areas form a thin excavation for almost the entire width of the radial and have a short, sharp ligamental pit in mid-section. Transverse ridge occupies entire width of facet but is not particularly well defined. A central pit is present, also a short intermuscular furrow. The intermuscular notch is very slight and adsutural slopes are interrupted by ridges. The distal surface of radials extend beyond outer marginal ridges of the facets.

No anal plate is preserved in the calyx proper, and arm segments cover the area where a small, rudimentary anal X would normally be found in the intermuscular area.

Only one primibrach (PBr) is preserved. It is low, wide, and the length of the lateral sides is almost as great as the maximum height of the plate. Strong facets for the reception of two equal-sized SBrBr are present.

Measurements.—

<table>
<thead>
<tr>
<th>Holotype</th>
<th>Mm.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum width of dorsal cup</td>
<td>23.9</td>
</tr>
<tr>
<td>Height of cup</td>
<td>7.7</td>
</tr>
<tr>
<td>Diameter of proximal columnal</td>
<td>4.5</td>
</tr>
<tr>
<td>Width of primibrach</td>
<td>14.6</td>
</tr>
<tr>
<td>Height of primibrach</td>
<td>5.2</td>
</tr>
</tbody>
</table>

Remarks.—The only described specimen closely approaching P. cranii is a paratype of P. brachiatius Moore and Plummer (1940, pl. 16, fig. 7). That specimen differs, however, in having a small column with IBB extending well beyond the impression, and BB are more pointed than observed in P. cranii.

Occurrence and horizon.—Pumpkin Creek limestone member, Dornick Hills formation, Pennsylvanian; west side of Lake Murray, south of Ardmore in Love County, Oklahoma.

Holotype.—Collected by Frank Crane. To be deposited in the U. S. National Museum.
Paradelocrinus regulatus, n. sp.
Plate 1, figures 13, 15, 17; Plate 2, figures 2, 5

Description.—Dorsal cup has a broad, flat basal area, within which are found the following elements:—a rather large columnar impression; pentagonal-shaped IBB disk extending well beyond the circumference of stem; all of the small BB except for their distal extremities; and the incurved proximal tips of the large RR. 1 B circlet has the outline of a star. The effort of RR to reach the IBB circlet leaves a short suture between BB. When viewed from above or below the cup is seen to have a subcircular outline.

Articular facets are well preserved; ligamental pit is sharp and narrow; transverse ridge is weak; intermuscular furrow well defined and is flanked at mid-length by two rounded oblong pits; intermuscular notch is hardly perceptible; adsutural slopes are negligible. There is a notch for the reception of rudimentary anal X between articular facets.

Measurements.—

<table>
<thead>
<tr>
<th>Measure</th>
<th>Holotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum width of dorsal cup</td>
<td>14.0</td>
</tr>
<tr>
<td>Height of dorsal cup</td>
<td>5.7</td>
</tr>
<tr>
<td>Diameter of proximal columnal</td>
<td>3.0</td>
</tr>
</tbody>
</table>

Remarks.—The elongate radials of this species is similar to both P. cranie and P. brachiatus Moore and Plummer. However, P. regulatus is readily distinguished by its broad, flat basal plane. Structure of the basal elements is rather close to P. brachiatus as shown by the paratype illustrated by Moore and Plummer (1940, pl. 16, fig. 1), but the BB are more elongated and pointed in that specimen. There are other obvious fundamental differences.

Occurrence and horizon.—Pumpkin Creek limestone member, Dornick Hills formation, Pennsylvanian; west side of Lake Murray, south of Ardmore in Love County, Oklahoma.

Types.—Collected by Wm. T. Watkins. To be deposited in the U. S. National Museum.

Paradelocrinus disculus, n. sp.
Plate 3, figures 15, 16

Description.—Dorsal cup broad and very shallow. Basal plane unusually broad with slight depression except for the mildly impressed columnar impression. Five regular IBB form a moderate-sized pentagonal-shaped disk. Five small BB form a more or less star-shaped outline. The RR are exceptionally large in comparison to the other calyx plates. Lateral sides of the cup are formed by the sharply upcurved outer extremities of RR. Articular facets are normal subhorizontal shelves. The author has failed to find any evidence of a notch between the articular facets for reception of a rudimentary anal plate.

Measurements.—

<table>
<thead>
<tr>
<th>Measure</th>
<th>Holotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>Width of dorsal cup</td>
<td>14.1 mm.</td>
</tr>
<tr>
<td>Height of dorsal cup</td>
<td>3.1 mm.</td>
</tr>
<tr>
<td>Ratio of height to width</td>
<td>0.22</td>
</tr>
<tr>
<td>Diameter of stem impression</td>
<td>1.9 mm.</td>
</tr>
</tbody>
</table>
Remarks.—*P. discus* is a highly divergent representative of the genus, if indeed these forms under present study are true members of *Paradelocrinus*. It is readily distinguished from all other described forms by the broad, flat, shallow nature of the dorsal cup.

*Occurrence and horizon.*—Otterville limestone member, Dornick Hills formation, Pennsylvanian; approximately five and one-half miles north of Ardmore, Oklahoma, on U. S. Highway 77.

*Holotype.*—Collected by Frank Crane. To be deposited in the U. S. National Museum.

Genus *ETHELOCRINUS* Kirk, 1937

*Ethelocrinus watkinsi*, n. sp.

Plate 3, figures 10, 17; text figure 1

*Description.*—Dorsal cup is large, shallow and bowl-shaped. BBB circle is not preserved but the structure of basals indicates a shallow invagination. BB are five robust elements. Post. B is truncated for the reception of the large anal X above and is restricted in development by RA to the right. KR are five moderate-sized pentagonal plates. L. post. R is not preserved. L. ant. B and r. post. R are small and have less than r. ant. R or ant. R. RA is slightly smaller than anal X. No RX is present. There is no definite evidence of ornamentation except for an irregular appearance of the outer surfaces of the plates.

There are 12 bona fide biserial arms. However, in the r. post. ramus the outer ray divides in its upper portion with no evidence of an axillary SBr. This is considered by the author to be an abnormality, probably representing a regenerative mutation through accidental loss of a portion of the arm. All rami bifurcate with the PBrBr and apparently the inner rays bifurcate again with the

Figure 1. Diagrammatic sketch of the holotype of *Ethelocrinus watkinsi*, n. sp.
first SBBr in the two posterior rami. At least this is the case in the r. post. ramus, and there are three arms known to be present in the l. post. ramus. Pin-

nules are of moderate size and attain considerable length.

Column has not been observed.

**Measurements.**

<table>
<thead>
<tr>
<th>Metric</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height of dorsal cup</td>
<td>21.0*</td>
</tr>
<tr>
<td>Maximum width of dorsal cup</td>
<td>52.0</td>
</tr>
<tr>
<td>Length of r. ant. B</td>
<td>15.6</td>
</tr>
<tr>
<td>Width of r. ant. B</td>
<td>15.3</td>
</tr>
<tr>
<td>Width of r. post. R</td>
<td>15.1</td>
</tr>
<tr>
<td>Length of r. post. R</td>
<td>7.1</td>
</tr>
<tr>
<td>Length of r. ant. R</td>
<td>7.0</td>
</tr>
<tr>
<td>Width of r. ant. R</td>
<td>10.0</td>
</tr>
<tr>
<td>Width of anal X</td>
<td>14.2</td>
</tr>
<tr>
<td>Length of anal X</td>
<td>13.0</td>
</tr>
<tr>
<td>Length of arms as preserved</td>
<td>51.5</td>
</tr>
</tbody>
</table>

**Remarks.**—*Ethelocrinus rotkiusi* is another example of the varied manifestations found among representatives of this genus. If only the dorsal cup were preserved, assignment of the species would be to *Paruloerinus* Moore and Plummer (1940) rather than to *Ethelocrinus* Kirk (1937), not on the basis of the genotype, but through precedent established by Moore and Plummer in 1940, and subsequently followed by most authors. In *Ulocrinus blairi* Miller and Gurley (taken as the genotype of *Paruloerinus*) the IBB have a decided upflared attitude, albeit these plates are barely visible in side view of the dorsal cup. Sutures are flush with the outer surfaces, and the calyx has a spherical shape which, due to the protrusion of the left posterior region, is asymmetrical in outline. The form used as typical, *ipso facto*, for the genus is *Paruloerinus marquisi* Moore and Plummer, in which species there is indication of a mild basal concavity, strongly impressed sutures, and ten biserial arms. When dealing with calices devoid of arms it has become common to assign only those forms having strong tubercles to *Ethelocrinus*, mainly because *E. magister* (Miller and Gurley), the genotype, possesses tubercles. The weakness in classification is demonstrated by *E. millsapensis* Moore and Plummer, which, although devoid of tubercles, was of necessity assigned to the genus due to the arm structure. Another demonstration of fallacy was disclosed by a specimen of *E. oklahomensis* Moore and Plummer figured by Strimple (1940, pl. 1, figs. 1-3) wherein ten biserial arms were recorded for that species. Apparently Moore and Plummer were inclined to assign *E. oklahomensis* to their *Paruloerinus* on the basis of this evidence because they listed the species as *P. oklahomensis* (1940, p. 364) although elsewhere in the paper they assigned it to *Ethelocrinus*. The specimen in question did not conform to the assumed generic characteristics and subsequently has been ignored, probably on the grounds that the dorsal cup was not connected to the arms *in toto*. Even

* Estimated.
casual comparison of the ornamentation shown on the PBrBr with that of the calyx plates (which were actually found intimately associated with the arms) discloses they are of one and the same species. Although not figured, some of the fractured portions of the radial plates match the portions of the radial plates attached to the PBrBr.

In recent years, four specimens have been found which prove beyond doubt that *Ethelocrinus plattsburgensis* Strong is properly assigned to *Ethelocrinus* on the basis of arm structure. It has been listed under *Parulocrinus* by Moore and Plummer (1940), Bassler and Moody (1943), and Moore and Laudon (1944). As additional specimens are found with arms preserved the problem will solve itself, but on the basis of existing evidence *Parulocrinus* has no valid standing. There is no apparent justification for separation of *U. blairi* from other species of *Ulocrinus* Miller and Gurley; therefore, it is proposed to place *Parulocrinus* in synonymy under that genus. The balance of described species formerly assigned to *Parulocrinus* should be designated as *Ethelocrinus*; however, it is recognized that a separate genus is desirable for such species as *Ethelocrinus marquisci* (Moore and Plummer) and *E. oklahomensis* (Moore and Plummer), where only ten biserial arms are present. Future studies will probably disclose the regressive evolution of *Ethelocrinus* to ten-armed forms. The author has observed the evolution of *Ulocrinus* to forms having a basal concavity; however, without knowledge of the arm structures it is impossible to determine whether such species are ethelocrinids or uocrinids. In the meanwhile the older genus, *Ethelocrinus*, is best adapted for the reception of species having a low dorsal cup with only two anal plates present.

*Ethelocrinus watkinsi* is characterized by the robust anal X, relatively small and obliquely placed RA and the irregular-sized RR.

Occurrence and horizon.—Arnold limestone member, Deese formation, lower Pennsylvanian; west side of Lake Murray, south of Ardmore in Love County, Oklahoma.

Holotype.—Collected by Wm. T. Watkins. To be deposited in the U. S. National Museum.

*Ethelocrinus sphaeri*, n. sp.

Plate 1, figures 4-6, 9

Description.—This species is represented by a single well-preserved dorsal cup. IBB are five regular elements forming a slightly convex, pentagonal-shaped disk which rests slightly above the basal plane. BB are five tumid elements. That of the posterior carries anal X above and the large quadrangular RA to the right. RR are considerably wider than high, with articular facets sloping inward. Outer ligamental area is narrow and bounded externally by a slight marginal ridge, internally by a strong transverse ridge.

Outer surfaces of calyx elements are rough appearing but there are no decided nodes. Borders of all plates except IBB are bent inward to produce moderately deep furrows. Regularly spaced ridges along the sutures occur about one to a millimeter. Just above midheight of RR a strong ridge is present causing distal portion of each radial to have a subhorizontal position.

Measurements.—

Greatest width of cup

Holotype

21.8 mm.
Height of dorsal cup 10.7 mm.
Ratio height to width 0.52
Diameter of body cavity 9.9 mm.
Height of basal cavity 1.0 mm.
Width of IBB circle 7.8 mm.
Width of stem impression 3.8 mm.
Length of basal plate 10.8 mm.
Width of basal plate 10.8 mm.
Length of radial plate 8.8 mm.
Width of radial plate 13.6 mm.
Length of transverse ridge 9.6 mm.
Length of infrabasal plate 4.9 mm.
Width of infrabasal plate 4.3 mm.
Length of radialis 6.5 mm.
Width of radialis 5.4 mm.
Length of anal X 6.8 mm.
Width of anal X 3.9 mm.
Length of suture between basals 5.2 mm.
Length of suture between radials 4.0 mm.

Remarks.—The most distinctive characteristics of this species are: irregular surface of all calyx elements, approaching but not attaining nodose ornamentation; almost horizontal surface formed in the distal portion of each radial; mildly convex IBB circle which is above the basal plane and therefore not visible in side view of cup; and tumidity of BB. *E. marquisi* (Moore and Plummer) has a strong ridge forming a girdle near the rim of the dorsal cup, but the area above it is in the form of a shallow furrow, and in addition the species has nodose ornamentation.

Occurrence and horizon.—Pumpkin Creek limestone member, Dornick Hills formation, Pennsylvanian; west side of Lake Murray, south of Ardmore in Love County, Oklahoma.

Holotype.—Collected by Wm. T. Watkins. To be deposited in the U. S. National Museum.

*Ethelocrinus ardmorensis*, n. sp.

Plate 2, figures 9, 12, 15

Description.—Although the holotype of this species is not perfectly preserved, all essential calyx elements are present and familiarity with the group permits reasonable accuracy in reconstruction. Of considerable interest and diagnostic importance is the strongly downflared attitude of the IBB. BB are five, large plates, that of the posterior sacrificing considerable area to the large RA. RR are wide, heavy elements, curving evenly inward to form a subhorizontal shelf terminating with a thin ridge forming the outer boundary of the outer ligamental area. Ligamental pit is well defined and is backed by a sharp transverse ridge. Articular facets slope slightly inward; adsutural slopes are almost absent; and muscle areas are shallow.

No granular or nodular ornamentation is present; however, the calyx elements are not perfectly smooth. Sutures between the cup plates are in deep, V-shaped depressions, and are marked by alternating pits and ridges—approximately four ridges to three millimeters.
Stem impression is small, round, heavily crenulated, and is pierced by a pentalobate lumen.

**Measurements.**

- Greatest width of dorsal cup: 26.0 mm. (est.)
- Height of cup: 13.5 mm.
- Ratio height to width: 0.52 (approx.)
- Height of basal concavity: 2.7 mm.
- Width of IBB circle: 7.3 mm.
- Width of stem impression: 1.8 mm.
- Length of basal plate: 12.5 mm.
- Width of basal plate: 13.3 mm.
- Length of radial plate: 11.0 mm.
- Width of radial plate: 17.2 mm.
- Length of transverse ridge: 11.4 mm.
- Length of infrabasal plate: 5.3 mm.
- Width of infrabasal plate: 3.7 mm.
- Length of RA: 6.5 mm. (est.)
- Width of RA: 6.5 mm.
- Length of suture between basals: 9.3 mm.
- Length of suture between radials: 8.0 mm.

**Remarks.**—No described species of this group has an IBB circle similar to that found in *E. ardmoreanus*, i.e., strongly downflared but curved sharply upward prior to junction with BB. There are some forms known which have decided invagination but none compare to this extreme development.

**Occurrence and horizon.**—Pumpkin Creek limestone member, Dornick Hills formation, Pennsylvanian; west side of Lake Murray, south of Ardmore in Love County, Oklahoma.

**Holotype.**—Collected by Wm. T. Watkins. To be deposited in the U. S. National Museum.

_Ethemocerius magnus_, n. sp.

Plate 2, figures 1, 3, 4, 6

**Description.**—Dorsal cup of holotype is somewhat compressed but all features are excellently preserved. IBB circle is flat, has a pentagonal outline, and extends well beyond the columnar scar. BB are five large elements with proximal portions curved under to form much of the shallow basal concavity. Post.B is smaller than others due to large, quadrangular-shaped RA to the right and relatively large anal X above. RR are five wide elements, those of the posterior being slightly smaller than the other three.

Ornamentation consists of large tubercles. There is a tendency toward swelling in the distal median portions of IBB. A row of circular-shaped nodes are found around the outer portion of RR, either three or four to each side, and some ten nodes occupy the median area of each radial. Sutures between plates are deeply impressed. Large nodes are also found along the proximal border of RR. However, some are inclined to be vertically elongate, particularly along the lateral sides of the radials. Tubercles have almost entirely fused to form a solid, heavy horizontal ridge which curves sharply over and produces a depressed upper
facet at the distal extremities of KR.

Outer ligamental area is pronounced and is bound by a strong ridge. There is a sharp ligamental pit. Transverse ridge is well developed and has a tendency to become narrow in midlength. Light intermuscular furrow is flanked by two circular depressions and three or four shallow elongate furrows radiate from these pits. The entire articular facet slopes slightly inward.

Measurements.—

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Holotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>Greatest width of cup</td>
<td>32.2 mm.</td>
</tr>
<tr>
<td>Height of dorsal cup</td>
<td>12.1 mm.</td>
</tr>
<tr>
<td>Ratio height to width</td>
<td>0.38  *</td>
</tr>
<tr>
<td>Diameter of body cavity</td>
<td>14.2 mm.</td>
</tr>
<tr>
<td>Width of IBB circle</td>
<td>10.7 mm.</td>
</tr>
<tr>
<td>Width of stem impression</td>
<td>5.0 mm.</td>
</tr>
<tr>
<td>Length of basal plate</td>
<td>15.7 mm.</td>
</tr>
<tr>
<td>Width of basal plate</td>
<td>15.7 mm.</td>
</tr>
<tr>
<td>Length of radial plate</td>
<td>13.2 mm.</td>
</tr>
<tr>
<td>Width of radial plate</td>
<td>19.0 mm.</td>
</tr>
<tr>
<td>Length of infrabasal plate</td>
<td>5.0 mm.</td>
</tr>
<tr>
<td>Width of infrabasal plate</td>
<td>5.0 mm.</td>
</tr>
<tr>
<td>Length of transverse ridge</td>
<td>13.3 mm.</td>
</tr>
<tr>
<td>Length of radial</td>
<td>11.5 mm.</td>
</tr>
<tr>
<td>Width of radial</td>
<td>9.0 mm.</td>
</tr>
<tr>
<td>Length of anal X</td>
<td>10.0 mm.</td>
</tr>
<tr>
<td>Width of anal X</td>
<td>6.9 mm.</td>
</tr>
<tr>
<td>Length of suture between basals</td>
<td>9.0 mm.</td>
</tr>
<tr>
<td>Length of suture between radials</td>
<td>5.7 mm.</td>
</tr>
</tbody>
</table>

Remarks.—*Ethelocrinus magnus* is similar to *E. marquisi* (Moore and Plummer) from which it differs mainly in having more pronounced ornamentation and in the position of the articular facets of RR. The outer ligamental area of *E. marquisi* is plainly visible in side view of the dorsal cup but is entirely obscured from side view in *E. magnus*. The present species also has a more decidedly depressed area above the girdlelike rim formed at the upper extremities of RR. Another significant difference is the greater H/W ratio of RR in *P. marquisi*.

Occurrence and horizon.—Pumpkin Creek limestone member, Dornick Hills formation, Pennsylvanian; west side of Lake Murray, south of Ardmore in Love County, Oklahoma.

Holotype.—Collected by Wm. T. Watkins. To be deposited in the U. S. National Museum.

*Ethelocrinus peridous*, n. sp.

Plate 2, figures 11, 13, 14, 16

Description.—This form is represented by two dorsal cups and is the largest of the group under study. Dorsal cup is broad and shallow with base shallowly invaginated. IBB are five, confined to basal invagination, and subhorizontal in

* Approximate
attitude. BB are five very large plates which sweep out of the concave base. Post. B is narrow due to encroachment of large quadrangular-shaped RA. Anal X is robust and rests solidly on truncated upper extremity of post. B. RK are large five-sided elements with a subhorizontal area in front of articular facets. Excessive weathering has almost obliterated details of large articular facets. A ridgelike development accentuates the outline of every plate, and the sutures rest in V-shaped depressions. Minute pits and ridges interrupt the sutures. Surfaces of all plates are uneven in a manner indicating weak nodular ornamentation.

Measurements.—

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Greatest width of cup</td>
<td>38.5 mm.</td>
</tr>
<tr>
<td>Height of dorsal cup</td>
<td>15.7 mm.</td>
</tr>
<tr>
<td>Ratio height to width</td>
<td>0.41</td>
</tr>
<tr>
<td>Diameter of body cavity</td>
<td>20.3 mm. *</td>
</tr>
<tr>
<td>Height of basal cavity</td>
<td>2.7 mm.</td>
</tr>
<tr>
<td>Width of IBB circlet</td>
<td>9.8 mm.</td>
</tr>
<tr>
<td>Width of stem impression</td>
<td>4.8 mm.</td>
</tr>
<tr>
<td>Length of basal plate</td>
<td>19.6 mm.</td>
</tr>
<tr>
<td>Width of basal plate</td>
<td>17.7 mm.</td>
</tr>
<tr>
<td>Length of infrabasal plate</td>
<td>6.3 mm.</td>
</tr>
<tr>
<td>Width of infrabasal plate</td>
<td>4.2 mm.</td>
</tr>
<tr>
<td>Length of radianal</td>
<td>13.2 mm.</td>
</tr>
<tr>
<td>Width of radianal</td>
<td>10.7 mm.</td>
</tr>
<tr>
<td>Length of anal X</td>
<td>9.2 mm.</td>
</tr>
<tr>
<td>Width of anal X</td>
<td>6.8 mm.</td>
</tr>
<tr>
<td>Length of suture between basals</td>
<td>12.7 mm.</td>
</tr>
<tr>
<td>Length of suture between radials</td>
<td>5.1 mm.</td>
</tr>
</tbody>
</table>

Remarks.—Ethelocrinus peridous is most readily distinguished from other described species by the profile of the cup and in various proportionate ratios.

Occurrence and horizon.—Otterville limestone member, Dornick Hills formation, Pennsylvanian; approximately 5½ miles due north of Ardmore, Oklahoma, on U. S. Highway 77.

Holotype.—Collected by Frank Crane. To be deposited in the U. S. National Museum.

Ethelocrinus variabilis, n. sp.

Plate 1, figures 8, 10, 11

Description.—Dorsal cup is very deep and has a broad flat base. IBB disk is large and is almost flat. Stem facet is proportionately small, round, and pierced by a pentalobate lumen. BB are large full elements; that of the posterior is larger than normal for these forms due to pronounced reduction in size of RA. Connection between RA and r. post. B is entirely lost, and RA is in strong contact with l. post. R, supporting a slightly smaller anal X above. There are no V-shaped impressions at the sutures. However, the sutures are mildly depressed and have the typical interruption caused by small pits. Surfaces of calyx plates are mildly uneven but no decided ridges or nodes are present. There is a slight flattened

* Approximate
area beyond the outer ligamental pit, and the articular facets slope slightly inward.

**Measurements.**

- Greatest width of cup: 28.2 mm.
- Height of dorsal cup: 15.1 mm.
- Ratio height to width: 0.54.
- Diameter of body cavity: 14.1 mm.
- Height of basal concavity: 0.0 mm.
- Width of IBB circle: 10.1 mm.
- Width of stem impression: 3.7 mm.
- Length of basal plate: 15.1 mm.
- Width of basal plate: 15.5 mm.
- Length of radial plate: 17.3 mm.
- Width of radial plate: 17.2 mm.
- Length of infrabasal plate: 5.3 mm.
- Width of infrabasal plate: 5.0 mm.
- Length of transverse ridge: 13.2 mm.
- Length of radial:
  - radial: 6.4 mm.
  - Width of radial: 6.4 mm.
- Length of anal X: 8.4 mm.
- Width of anal X: 5.9 mm.
- Length of suture between basals: 8.1 mm.
- Length of suture between radials: 6.7 mm.

**Remarks.**—*Ethelocrinus variabilis* is easily distinguished from other described forms by its unusual height, tumid basals, structure of post. IR, and flat basal area.

**Occurrence and horizon.**—Ottenville limestone member, Dornick Hills formation, Pennsylvanian; approximately 4 3/4 miles due north of Ardmore, Oklahoma, on U. S. Highway 77.

**Holotype.**—Collected by Frank Crane. To be deposited in the U. S. National Museum.

*Plaxocrinus dornickensis, n. sp.*

Plate 2, figures 7, 8, 10; text figure 2

**Description.**—The species has a large, low, smooth, unornamented dorsal cup, and rather deep, broad basal invagination. Columnar scar is circular in outline and is crenulated. IBB circle extends well beyond the stem impression, is slightly downflared, and is pentagonal in outline. BB are five, of moderate size, and curve evenly out of basal concavity. Post. B carries anal X above and RA to the right. RX rests directly on RA and obtains support from anal X to the left. There is an even curvature to the RR with proximal portions extending into the basal plane. Posterior interradius is depressed and well defined.

Articular facets are strong, slope decidedly outward, and are narrower than the greatest width of RR. Outer ligamental area is narrow, occupies the full width of articular facet, and is bounded by a fine outer ridge. A sharp ligamental pit is in midportion of the ligamental area. Transverse ridge is not particularly pronounced but is rather broad except just above the ligamental pit where it becomes very narrow. There are well-defined intermuscular notches, muscle areas, and adsutural slopes. When the calyx is viewed from above the outer
ligamental area is not visible.

Measurements—

<table>
<thead>
<tr>
<th>Description</th>
<th>Holotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum width of dorsal cup</td>
<td>21.2</td>
</tr>
<tr>
<td>Height of dorsal cup (to transverse ridge)</td>
<td>5.5</td>
</tr>
<tr>
<td>Width of posterior interradius</td>
<td>5.8</td>
</tr>
<tr>
<td>Width of columnar impression</td>
<td>3.9</td>
</tr>
</tbody>
</table>

Remarks.—All Plaxocrinus species are similar in general appearance but are readily separable under close study. P. perundatus Moore and Plummer is the only described species that might be confused with P. dornickensis. In P. perundatus the basal concavity is not so pronounced, depression of post. IR is more moderate, and the articular facets do not slope so strongly outward.

This is the most common species found in the formation. A peculiar primibrach is found imbedded in the matrix covering the upper portion of a paratype. The same type, PBr Br, is rather common in the formation and is also certain to belong to the species. Basal facet of PBr is rectangular in outline; lower outer surface curves strongly downward from the base and thence evenly upward to a point about even with the midsection of basal facet, after which it progresses more gradually to the point. Upper facet is divided into two triangular-shaped muscle areas by a strong ridge which would receive the two secundibrachs. Each large area is divided into two more or less triangular-shaped muscle areas. A somewhat similar PBr is described by Moore, 1938, as Acantharthropteryum acutum (group and section designations), from the Cherokee shale, Des Moines series. The main difference seems to lie in the muscle (or articular) facets.

Occurrence and horizon.—Pumpkin Creek limestone member, Dornick Hills formation, Pennsylvanian; west side of Lake Murray, south of Ardmore in Love County, Oklahoma.

Types.—Collected by Wm. T. Watkins and Frank Crane. To be deposited in the U. S. National Museum.

Plaxocrinus tumulosus, n. sp.

Plate 1, figures 12, 14, 16, 19

Description.—Calyx structure is normal for the genus. IBB circlet is slightly concave, extending beyond the columnar impression. BB are five large, tumid elements. Post. B supports anal X above, RA is in an oblique position to the right and in turn supports RX above. RR do not participate in basal plane due to bulosity of BB. Outer surfaces of RR are nearly horizontal in the proximal region, curve strongly upward in midsection, and are almost vertical in distal
region. Articular facets are sloping mildly outward and do not quite cover the entire width of RR; no intermuscular furrow is present; and intermuscular notch is broad and weak. Posterior interradius is slightly depressed.

**Measurements.**

<table>
<thead>
<tr>
<th></th>
<th>Holotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum width of dorsal cup</td>
<td>29.1 Mm.</td>
</tr>
<tr>
<td>Height of dorsal cup (to transverse ridge)</td>
<td>4.5</td>
</tr>
<tr>
<td>Width of post. IR</td>
<td>6.3</td>
</tr>
<tr>
<td>Width of columnar impression</td>
<td>4.7</td>
</tr>
</tbody>
</table>

**Remarks.**—The only described species which are closely similar to *P. tumulosus* are *P. perundatus* Moore and Plummer and *P. obesus* Moore and Plummer. In both of these species the distal portions of RR are almost vertical. *P. perundatus* has no strong tumidity of BB, deep basal concavity, and the area between articular facets is wider. In *P. obesus* the BB are smaller and narrower and do not reach the basal plane. Also the posterior interradius is convex rather than concave.

**Occurrence and horizon.**—Pumpkin Creek limestone member, Dornick Hills formation, Pennsylvanian; west side of Lake Murray, south of Ardmore in Love County, Oklahoma.

**Holotype.**—Collected by Wm. T. Watkins. To be deposited in the U. S. National Museum.

**Placovcrinus putens**, n. sp.

Plate 3, figures 1, 2, 5, 7

**Description.**—Five IBB form a pentagonal disk which is downflared and is covered in the main by the round stem impression. Five BB are bulbous and curve strongly out of the basal concavity. Five RR are strongly convex with articular facets inclined evenly outward. Each radial carries a pair of mild bulges which unite with neighboring bulges of the adjoining basals. In addition a raised ridge diverges from the point of maximum bulge on each radial to almost meet similar ridges of adjacent RR. This feature accentuates the hollows formed at the angles between plates of the radial and basal circlets, particularly at the distal tip of each basal plate. All angles between plates of the posterior interradius are marked by dimplelike depressions. Post. IR is rather broad and is composed of three large plates. Anal X is in solid contact with post. B; RA is obliquely placed in contact with r. post. B below, with anal X to the left, r. post. R to the right and RX above. The articular facets are less than the greatest width of RR. Ligamental pit furrow is thin with a wide ligamental pit in midsection. A central pit is present but there is no intermuscular furrow connecting it to the intermuscular notch. Lateral furrows are pronounced and together with the lateral ridges, surround triangular-shaped muscle areas.

**Dorsal cup plates are devoid of ornamentation.**

**Measurements.**

<table>
<thead>
<tr>
<th></th>
<th>Holotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height of dorsal cup</td>
<td>4.9 mm.</td>
</tr>
<tr>
<td>Maximum width of dorsal cup</td>
<td>17.6 mm.</td>
</tr>
<tr>
<td>Ratio of height to width</td>
<td>0.28</td>
</tr>
</tbody>
</table>

- **Measurements.**
- **Remarks.**
- **Occurrence and horizon.**
- **Holotype.**
- **Placovcrinus putens**, n. sp.
- **Description.**
- **Measurements.**
Height of basal concavity 1.6 mm.
Diameter of stem impression 3.3 mm.

Remarks.—Although a moderately deep basal concavity is present in Plaxocrinus putusus and BB, and plates have a downflared attitude as found in Perimestocrinus Moore and Plummer, there are no steep walls formed by the proximal extremities of BB. Assignment to Plaxocrinus Moore and Plummer is made with reservation. The species is readily distinguished from other described forms by the dimple-like depressions formed at the angle of meeting between plates of the BB and RR circllets and between plates of the post. IR.

Occurrence and horizon.—Otterville limestone member, Dornick Hills formation, lower Pennsylvanian; approximately 5½ miles north of Ardmore, Oklahoma, on U. S. Highway 77.

Holotype.—Collected by Frank Crane. To be deposited in the U. S. National Museum.

Genus DELOCRINUS Miller and Gurley, 1890

Delocrinus armatura, n. sp.

Plate 3, figures 3, 4

Description.—Dorsal cup is small and heavily ornamented. HB are five small elements confined to the funnel-shaped basal concavity. BB are five moderate-sized elements with proximal portions forming walls of basal invagination and curving outward and upward so that upper extremeties participate in outer calyx walls. Post B is truncated for reception of the small narrow, elongate anal X. RR are five pentagonal-shaped elements with greater width than length. Articular facets are subhorizontal. Sutures between plates of BB and RR circllet are mildly impressed. Ornamentation consists of irregular swollen tubercles which are more pronounced on the RR than on the BB. Stem impression is circular in outline. Arms are unknown.

Measurements.—

<table>
<thead>
<tr>
<th>Description</th>
<th>Holotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height of dorsal cup</td>
<td>5.0 mm.</td>
</tr>
<tr>
<td>Maximum width of dorsal cup</td>
<td>11.0 mm.</td>
</tr>
<tr>
<td>Ratio of height to width</td>
<td>0.45</td>
</tr>
<tr>
<td>Height of basal concavity</td>
<td>1.0 mm.</td>
</tr>
<tr>
<td>Diameter of stem impression</td>
<td>1.4 mm.</td>
</tr>
</tbody>
</table>

Remarks.—Delocrinus armatura is somewhat similar to D. parinodosaurus Stimpie from the Wewoka formation. In the latter species the nodes are more spinelike, sutures are more impressed, and the upper extremeties of RR curve inward to form a subhorizontal area.

Occurrence and horizon.—Pumpkin Creek limestone member, Dornick Hills formation, lower Pennsylvanian; west side of Lake Murray, south of Ardmore in Love County, Oklahoma.

Types.—Collected by Wm. T. Watkins. Holotype to be deposited in the U. S. National Museum.

Delocrinus aristatus, n. sp.

Plate 3, figures 18-21

Description.—Dorsal cup large with deep, wide basal invagination. HB are five, confined to the bottom of well-like basal concavity. BB are five, large hexagonal plates which participate in the basal invagination but curve strongly out to form the broad basal plane. The median section of each basal plate is depressed so that proximal tips of RR and the area adjoining the sutures between BB are protruded. Post. B is larger than other BB and is truncated for the
reception of anal X. RR are five wide elements forming the outer walls of the calyx. Near the upper extremity of each radial, a row of weak nodes are found after which the surface curves inward to form a small arcuate area below the outer ligamental area. Articular facets are broad horizontal shelves. The outer ligamental area is shallowly excavated; transverse ridge is well defined; two ligamental fossae lie subparallel to the transverse ridge near its extremity; intermuscular notch is broad and shallow; and adsutural areas are shallow and widen toward the body cavity. Anal X curves sharply inward and has a distinctive appearing muscle scar.

The round proximal columnal is unusually small when compared with the size of the cup. In addition to the weak tubercles mentioned above the entire surface of the cup plates is delicately granular appearing.

**Measurements.**

<table>
<thead>
<tr>
<th>Description</th>
<th>Holotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height of dorsal cup</td>
<td>9.0 mm.</td>
</tr>
<tr>
<td>Maximum width of cup</td>
<td>27.0 mm.</td>
</tr>
<tr>
<td>Ratio of height to width</td>
<td>0.33</td>
</tr>
<tr>
<td>Height of basal concavity</td>
<td>4.3 mm.</td>
</tr>
<tr>
<td>Width of stem impression</td>
<td>2.4 mm.</td>
</tr>
</tbody>
</table>

**Remarks.**—In ornamentation this species closely approaches *D. granulosus* Moore and Plummer. The cup of *D. aristatus* is broader and the articular facets are quite different. In *D. granulosus* the muscle scars are more pronounced. The adsutural slopes are steep with no flattened areas present. The broad almost flattened articular facets of *D. aristatus* with a triangular-shaped adsutural area near the body cavity are distinctive. In addition the proportionately smaller stem and structure of the distal portion of the anal plate serve to readily differentiate *D. aristatus* from other described species.

**Occurrence and horizon.**—Pumpkin Creek limestone member, Dornick Hills formation, lower Pennsylvanian; west side of Lake Murray, south of Ardmore, in Love County, Oklahoma.

**Holotype.**—Collected by Wm. T. Watkins. To be deposited in the U. S. National Museum.

**Genus MALAIOCRINUS** Wanner, 1923;

**Malaiocrinus azygus**, n. sp.

Plate 8, figures 4, 8, 9, 12

**Description.**—Dorsal cup is bowl-shaped with a slightly convex base and steep lateral sides. Five IBB form a broad disk the median portion of which is occupied by the large round stem impression. Five are small triangular-shaped elements with that of the posterior truncated for the reception of anal X. All other BB are four-sided and none have contact with each other, which unusual arrangement is due to the meeting of RR circle with IBB circle. RR are five pentagonal plates only slightly wider than high. Articular facets slope slightly outward and are mildly horseshoe-shaped. The outer ligamental furrow is modest in size and is of particular interest because of the strong pattern of denticles. Ligamental pit and its furrow are well defined and the transverse ridge is sharp. Intermuscular furrow is broad and the lateral furrows are negligible. Adsutural slopes are broad and pass onto outer surfaces of RR. Plates of the posterior interradius are distinctive elements. Anal X is robust, elongate, seven-sided plate. RA is pentagonal-shaped, of moderate size, erect in attitude, and has the lowermost extremity in contact with r. post. IB. RX is hexagonal and not quite so broad
as anal X. Another plate rests solidly and evenly in the notch formed by the
distal extremities of anal X and RX. It is technically a tegmen plate but in the
present species is obviously a member of the anal series, or post. IR, which nor-

mally only consists of three plates or less. Five tegmen plates surround the
lateral sides and upper portion of the extra anal plate.

Numerous heavy plates are present indicating a short, stout tegmen. Median
sections of most plates are protruded in the form of a single short spine.

Arms are unknown except for the upper portion of an axillary brachial which
protrudes under some of the slightly displaced tegmen plates in the r. post.
radius. This plate indicates an hourglass shape of the brachials. Calyx plates
are unornamented.

Measurements.—

<table>
<thead>
<tr>
<th>Holotype</th>
<th>Height of dorsal cup</th>
<th>3.8 mm.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Maximum width of cup</td>
<td>12.9 mm.</td>
</tr>
<tr>
<td></td>
<td>Ratio of height to width</td>
<td>0.29</td>
</tr>
<tr>
<td></td>
<td>Diameter of stem impression</td>
<td>3.3 mm.</td>
</tr>
<tr>
<td></td>
<td>Width of IBB circle</td>
<td>5.5 mm.</td>
</tr>
</tbody>
</table>

Remarks.—Malaiocrinus parvisculus Moore and Plummer from the Des Moines
(Pennsylvanian) is the only recorded North American species referred to the
genus, and it does not closely agree with the characteristics of M. sundiacus
Wanner, the genotype. M. sundiacus has a broad, flat IBB circle almost entirely
covered by the large stem, and all other Pennsylvanian species referred to the genus have
unusually large stems. The articular facets of M. sundiacus are long (deep)
and are accentuated by a robust outer ligamental facet which is marked by radi-
ating ridges or denticles. The infrabasal circle of M. parvisculus rests in a
shallow concavity, is small, and the stem is of modest size. Articular facets are
not so deep as found in Permian forms, and there is no extension of the outer
ligamental area. Although M. azzyus is readily distinguished from the known
Pennsylvanian species, it conforms to the generic characteristics.

Occurrence and horizon.—Pumpkin Creek limestone member, Dornick Hills
formation, Pennsylvanian; west side of Lake Murray, south of Ardmore, Love
County, Oklahoma.

Holotype.—Collected by Wm. T. Watkins. To be deposited in the U. S.
National Museum.

Genus LECYTHIOCRINUS White, 1880

Lecythiocinus fusiformis, n. sp.
Plate 3, figures 11, 13, 14

Description.—Dorsal cup is elongate with swollen midsection and a slight twist
from right to left in proximal region. The base is formed by three unequal IBB,
the smallest of which is right posterior in position. IBB are long hexagonal plates
of somewhat unequal size. RR are five pentagonal elements which are constricted
at the top and have small horseshoe-shaped articular facets which are distinctive.
The facets slope outward, are smaller than the width of RR, and each has a long
slender intermuscular notch. The distal opening into body cavity is rather small.
Anal opening is relatively large and occupies the area at the upper extremity of
post, B and equal portions of r. post. R and l. post. R. Slight stress ridges are
present, diverging from the raised area in median portion of BB to the articular facets of adjoining RR.

Under weak magnification the outer surface of the dorsal cup plates have a porous appearance. Arm structure is unknown.

**Measurements.**

<table>
<thead>
<tr>
<th></th>
<th>Holotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height of dorsal cup</td>
<td>11.7</td>
</tr>
<tr>
<td>Maximum width of cup</td>
<td>9.5</td>
</tr>
<tr>
<td>Height of IBB circle</td>
<td>3.3</td>
</tr>
<tr>
<td>Maximum width of IBB circle</td>
<td>7.3</td>
</tr>
<tr>
<td>Diameter of stem scar</td>
<td>1.3</td>
</tr>
<tr>
<td>Length of r. post B</td>
<td>6.3</td>
</tr>
<tr>
<td>Width of r. post. B</td>
<td>5.0</td>
</tr>
<tr>
<td>Length of r. ant. R</td>
<td>4.3</td>
</tr>
<tr>
<td>Width of r. ant. R</td>
<td>4.2</td>
</tr>
<tr>
<td>Diameter of body opening</td>
<td>2.3</td>
</tr>
<tr>
<td>Diameter of anal opening</td>
<td>2.3</td>
</tr>
</tbody>
</table>

**Remarks.**—L. *jusiformis* is distinctive in having an elongate dorsal cup with unusually pronounced constriction at the upper extremity of cup. *L. urnaiformis* Strimple is comparable in length, but the outline of the cup is different in that its maximum width is closer to the basal region. *L. ollineiformis* White has a broader cup and a larger body opening, and *L. adamsi* Worthen also has a larger body opening.

**Occurrence and horizon.**—Pumpkin Creek limestone member, Dornick Hills formation, lower Pennsylvanian; west side of Lake Murray, south of Ardmore in Love County, Oklahoma.

**Types.**—Holotype was collected by Wm. T. Watkins. To be deposited in the U. S. National Museum.

**REFERENCES**


Strimple, H. L.  
1940. *Four new crinoid species from the Wenoka and one from the Ochelata group.* Bull. Amer. Paleont., vol. 25, No. 92, pp. 1-10, pl. 1.


Tomlinson, C. W.  

Wanner, J.  

White, C. A.  

Worthen, A. H.  

PART II.—DELOCKINIDS OF THE BROWNVILLE FORMATION OF OKLAHOMA

INTRODUCTION

The outcrop of Brownville limestone located some seven miles west of Strohmi, Osage County, Oklahoma, consists of a railroad cut which at the time of its discovery as a crinoidal horizon by two amateurs, E. L. Banion and Paul McGuire, contained numerous forms of crinoids, mainly in the material thrown up on the banks of the cut. By the time this author became aware of the outcrop all the loose material had been thoroughly collected, and it was necessary to work in the limited exposures of the cut proper. In the meantime the entire outcrop is slowly and surely being covered by weeds and grass. Two dorsal cups collected by Paul McGuire and 11 dorsal cups and loose ossicles collected by Mrs. Melba Strimple and the author probably represent the main results of collecting subsequent to the study of Brownville crinoids presented by Raymond C. Moore (1939). All calices in hand belong to the genus Delocrinus and are assigned to two species, *Delocrinus brownvillensis,* n. sp. and *Delocrinus ponderosus,* n. sp. The more common form is *D. brownvillensis* which was assigned to *D. vulgatus* Moore and Hummer by those authors (1940). However, there are several differences which are discussed below in the Remarks under description of species.

SYSTEMATIC DESCRIPTIONS

**Delocrinus brownvillensis**, n. sp.

*Plate 4, figures 1-4*

*Description.*—Dorsal cup is moderately deep, full, and basal area is invaginated. When viewed from above or below the cup has a slight pentagonal outline except at the posterior interradius which area is depressed. Five small IBB are present in the basal invagination and are downward in attitude. BB are five large elements, curving strongly out of the basal invagination. Anal X is elongate, almost rectangular in outline, and is curved longitudinally. Approximately two-thirds of the anal plate is below the upper limits of the dorsal cup. RR are five large pentagonal-shaped elements. Articular facets are well defined. The entire surface of the dorsal cup is finely granular.
Measurements.—

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height of dorsal cup</td>
<td>9.6 mm</td>
</tr>
<tr>
<td>Greatest width of cup</td>
<td>27.2 mm</td>
</tr>
<tr>
<td>Ratio of height to width</td>
<td>0.35</td>
</tr>
<tr>
<td>Height of basal concavity</td>
<td>3.7 mm</td>
</tr>
<tr>
<td>Width of basal concavity</td>
<td>11.5 mm</td>
</tr>
<tr>
<td>Diameter of stem impression</td>
<td>2.7 mm</td>
</tr>
<tr>
<td>Length of basal</td>
<td>11.8 mm</td>
</tr>
<tr>
<td>Width of basal</td>
<td>10.8 mm</td>
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<tr>
<td>Length of suture between basals</td>
<td>8.0 mm</td>
</tr>
<tr>
<td>Length of radial</td>
<td>9.3 mm</td>
</tr>
<tr>
<td>Width of radial</td>
<td>16.0 mm</td>
</tr>
<tr>
<td>Length of suture between radials</td>
<td>6.8 mm</td>
</tr>
<tr>
<td>Length of anal X</td>
<td>12.2 mm</td>
</tr>
<tr>
<td>Greatest width of anal X</td>
<td>4.4 mm</td>
</tr>
<tr>
<td>Width of body cavity</td>
<td>16.1 mm</td>
</tr>
</tbody>
</table>

Remarks.—It is necessary to briefly review the status of D. vulgaris Moore and Plummer because three dorsal cups from the Brownville limestone were designated as paratypes of that species. Two specimens, both from Harpersville formation, Cisco group, Virgil series of Texas, were figured by those authors, one designated as holotype (P-10325) and the other as paratype (KU 4584). Even a cursory examination of the illustrations discloses considerable difference between the holotype and paratype; for example, the sharp angulation at the basal plane and the mildly pentagonal outline of the dorsal cup when viewed from above or below in the holotype as compared to the circular outline of the cup and the even longitudinal curvature of BB in the paratype. The species is reported to be devoid of ornamentation, and there is no depression of the post. IR recorded which is sufficient to distinguish the Texas forms from D. brownvilleensis as represented by specimens at hand.

Type.—Holotype, No. D-28, Strimple Collection, collected by Paul McGuire. Paratype, No. 894, Strimple Collection, collected by Harrell L. Strimple.

Occurrence and horizon.—Railroad cut at Kief, about seven miles west of Strohm, Osage County, Oklahoma; Brownville limestone formation, Wabashian group, Virgil series, Pennsylvanian.

*Delocrinus ponderosus*, n. sp.

Plate 4, figures 5-8

Description.—Dorsal cup is large, full, basal invagination rather shallow. When viewed from above or below the outline of cup is mildly elliptical. Five small BB are confined to the basal concavity and are mainly covered by the round stem impression. Five large BB have proximal extremities in the basal invagination and are curved longitudinally. Post. B is truncated for the reception of a single anal plate (X) of robust size. RR are five large pentagonal plates. Articular facets are developed inwardly as horizontal shelves of unprecedented size. The unusual appearance of the facets are well shown by the illustration.
Entire surface of the cup is delicately granular.

**Measurements.**—

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Holotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height of dorsal cup</td>
<td>10.8 mm.</td>
</tr>
<tr>
<td>Greatest width of cup</td>
<td>30.0 mm.</td>
</tr>
<tr>
<td>Ratio of height to width</td>
<td>0.36</td>
</tr>
<tr>
<td>Height of basal concavity</td>
<td>2.8 mm.</td>
</tr>
<tr>
<td>Width of basal concavity</td>
<td>10.0 mm.</td>
</tr>
<tr>
<td>Width of stem impression</td>
<td>3.0 mm.</td>
</tr>
<tr>
<td>Length of basal</td>
<td>14.0 mm.</td>
</tr>
<tr>
<td>Width of basal</td>
<td>13.0 mm.</td>
</tr>
<tr>
<td>Length of suture between basals</td>
<td>9.0 mm.</td>
</tr>
<tr>
<td>Length of radial</td>
<td>9.0 mm.</td>
</tr>
<tr>
<td>Width of radial</td>
<td>12.5 mm.</td>
</tr>
<tr>
<td>Length of suture between radials</td>
<td>6.9 mm.</td>
</tr>
<tr>
<td>Length of anal X</td>
<td>9.0 mm.</td>
</tr>
<tr>
<td>Maximum width of anal X</td>
<td>6.4 mm.</td>
</tr>
<tr>
<td>Width of body cavity</td>
<td>16.8 mm.</td>
</tr>
</tbody>
</table>

**Remarks.**—*D. ponderosus* is most readily distinguished from other described species by the unusual large size of the articular facets, robust nature of the cup, and the elliptical outline of the calyx.

**Type.**—Holotype, No. D-26, Strimple Collection, collected by Mrs. Melba Strimple.

**Occurrence and horizon.**—Railroad cut at Kief, about seven miles west of Strohm, Osage County, Oklahoma; Brownville limestone formation, Wabaunsee group, Virgil series, Pennsylvanian.

**REFERENCES**


**PART III.—DESCRIPTION OF TWO NEW CROMYOCRINIDS FROM THE PENNSYLVANIAN OF NEBRASKA**

**INTRODUCTION**

With the acquisition and recording of additional materials we are slowly acquiring comprehensive stratigraphic and morphologic knowledge which will be eventually of considerable value. *Ethelocrinus* is known to have great geologic range and considerable diversity. A new species from the Iatan limestone is presented as *Ethelocrinus latani*, n. sp. On the basis of the presence of three anal plates in the posterior interradius, a form from the Stanton formation is described as *Mooreocrinus meadowensis*, n. sp.
SYSTEMATIC DESCRIPTIONS
Genus ETHELOCRINUS Kirk
Ethelocrinus iatani, n. sp.
Plate 4, figures 9-11

Description.—Dorsal cup is large and comparable to other described representatives of the genus. Five small IBB are confined to a moderately deep basal invagination. Proximal areas form a sharp depression with the columnar scar in the center, but outer areas level out to become almost horizontal. Five large BB are typical of the genus with proximal areas participating slightly in the broad basal concavity, post B, encroached upon by a large quadrangular-shaped RA and supporting the large anal X above. RR are five prominent cup elements, wider than high with almost horizontal articular facets. Outer ligamental area is sharply defined, but the muscle areas are shallow, indicating weak articulation processes. Sutures are sharply impressed.

Posterior side of cup has a flattened appearance and actually curves inward. Anterior side of calyx is erect and is slightly higher than the posterior side. There is no evidence of distortion; however, the possibility of such is recognized.

Some plates appear to be smooth, while others have a mildly granular appearance and the suggestion of tubercles. It is possible the specimen was worn smooth by abrasive action.

Measurement.—

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Holotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height of dorsal cup</td>
<td>13.5 mm.</td>
</tr>
<tr>
<td>Greatest width of cup</td>
<td>31.5 mm.</td>
</tr>
<tr>
<td>Ratio of height to width</td>
<td>0.43</td>
</tr>
<tr>
<td>Height of basal cavity</td>
<td>3.7 mm.</td>
</tr>
<tr>
<td>Width of IBB circle</td>
<td>9.0 mm.</td>
</tr>
<tr>
<td>Diameter of stem impression</td>
<td>3.7 mm.</td>
</tr>
<tr>
<td>Length of basal plate</td>
<td>17.9 mm.</td>
</tr>
<tr>
<td>Width of basal plate</td>
<td>16.0 mm.</td>
</tr>
<tr>
<td>Length of radial plate</td>
<td>10.1 mm.</td>
</tr>
<tr>
<td>Width of radial plate</td>
<td>17.0 mm.</td>
</tr>
<tr>
<td>Length of transverse ridge</td>
<td>13.0 mm.</td>
</tr>
<tr>
<td>Length of IBB plate</td>
<td>6.0 mm.</td>
</tr>
<tr>
<td>Width of IBB plate</td>
<td>5.0 mm.</td>
</tr>
<tr>
<td>Length of radialal</td>
<td>12.0 mm.</td>
</tr>
<tr>
<td>Width of radialal</td>
<td>10.0 mm.</td>
</tr>
<tr>
<td>Length of anal X</td>
<td>9.6 mm.</td>
</tr>
<tr>
<td>Width of anal X</td>
<td>8.2 mm.</td>
</tr>
<tr>
<td>Length of suture between BB</td>
<td>10.7 mm.</td>
</tr>
<tr>
<td>Length of suture between RR</td>
<td>5.2 mm.</td>
</tr>
<tr>
<td>Width of body cavity</td>
<td>15.2 mm.</td>
</tr>
</tbody>
</table>

Remarks.—The distinctive shape and outline of dorsal cup along with various mathematical ratios serve to readily distinguish Ethelocrinus iatani from other
described species. It might be noted that the form would probably have been assigned to *Parulocrinus* Moore and Plummer prior to the placement of that genus in synonymy with *Ulocrinus* by Strimple (1949).

**Holotype.**—Collected by Mr. Robert Berry of Omaha, Nebraska. To be deposited in the U. S. National Museum.

**Occurrence and horizon.**—Iatan formation, Douglas group, Missouri series, Pennsylvanian; near Richfield, Nebraska.

**Genus MOOREOCRINUS** Wright and Strimple

**Mooreocrinus meadowensis**, n. sp.

Plate 4, figures 12-14

**Description.**—The species is based on a single large, magnificently preserved dorsal cup. The calyx is mildly disturbed by lateral compression which has the effect of causing the RA and adjoining area to be more protruded than would have been normal.

Basal area is deeply invaginated with five downwarded IBB confined to the depressed area. BB are large with proximal portions participating in the basal depression but curving strongly out of the cavity. R post. B is considerably larger than the other BB. Five RR are normal elements, wider than high, with outer ligamental area well defined, articular facets subhorizontal in position and muscle area poorly defined.

**Measurements.**—

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Holotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height of dorsal cup</td>
<td>15.2 mm.</td>
</tr>
<tr>
<td>Greatest width of cup</td>
<td>31.0 mm. (average)</td>
</tr>
<tr>
<td>Ratio of height to width</td>
<td>0.49</td>
</tr>
<tr>
<td>Height of basal cavity</td>
<td>3.4 mm.</td>
</tr>
<tr>
<td>Diameter of IBB circle</td>
<td>7.5 mm.</td>
</tr>
<tr>
<td>Diameter of stem impression</td>
<td>3.6 mm.</td>
</tr>
<tr>
<td>Length of basal plate</td>
<td>17.8 mm.</td>
</tr>
<tr>
<td>Width of basal plate</td>
<td>15.9 mm.</td>
</tr>
<tr>
<td>Length of radial plate</td>
<td>10.9 mm.</td>
</tr>
<tr>
<td>Width of radial plate</td>
<td>16.8 mm.</td>
</tr>
<tr>
<td>Length of transverse ridge</td>
<td>13.2 mm.</td>
</tr>
<tr>
<td>Length of infrabasal plate</td>
<td>4.6 mm.</td>
</tr>
<tr>
<td>Width of infrabolus plate</td>
<td>4.0 mm.</td>
</tr>
<tr>
<td>Length of RA</td>
<td>13.8 mm.</td>
</tr>
<tr>
<td>Width of RA</td>
<td>10.5 mm.</td>
</tr>
<tr>
<td>Length of anal X</td>
<td>10.0 mm.</td>
</tr>
<tr>
<td>Width of anal X</td>
<td>8.0 mm.</td>
</tr>
<tr>
<td>Length of suture between BB</td>
<td>10.3 mm.</td>
</tr>
<tr>
<td>Length of suture between RR</td>
<td>5.5 mm.</td>
</tr>
<tr>
<td>Width of body cavity</td>
<td>13.0 mm. (approximate)</td>
</tr>
</tbody>
</table>
Remarks.—The genus Mourecrinus was established for the reception of cromyocrinids having three anal plates within the dorsal cup and a flattened or depressed basal area. The genotype is known to have ten biserial arms, and a Chester species, M. bowsheri Strimple which has been tentatively assigned to the genus, has ten arms. Until definite knowledge of the arm structure is obtained assignment of this species to the genus is desirable. M. meadowensis is a very distinctive form and is not closely approached by any described species.

Type.—Holotype collected by Robert Berry of Omaha, Nebraska. To be deposited in the U. S. National Museum.

Occurrence and horizon.—Meadow limestone member, Stanton limestone formation, Lancing group, Missouri series, Pennsylvanian; Kiewitz Quarry, Meadow, Nebraska.

REFERENCES

Wright, James, and Strimple, Harrell L.
1945. Mourecrinus and Ureocrinus gen. nov., with notes on the family Cymocrinidae. Geol. Mag., vol. LXXXII, No. 5, pp. 221-228, pl. 9.

Strimple, Harrell L.

PART IV.—ON NEW SPECIES OF ALCIMOCRINUS AND ULRICHICRINUS FROM THE FAYETTEVILLE FORMATION OF OKLAHOMA

ABSTRACT

Many crinoids of the upper Chester series demonstrate close affinity with Lower Pennsylvanian forms. A. ornatus, new species and U. chesterensis, new species are described here.

INTRODUCTION

The prolific and highly variable crinoid faunas of Mississippian (Lower Carboniferous) age have almost disappeared in Upper Chester strata with the exception of two or three camerates, a few flexibles and a highly interesting inadunate fauna. Close affinities are more readily found among Pennsylvanian forms than in older Mississippian faunas.

Comparison of the new Chester species, A. ornatus, with A. girtyi (Springer) from the Morrow series discloses a trend toward the addition of arms as an evolutionary factor. In this particular instance the genus appears to terminate without fulfilling the full evolutionary cycle, i. e., eventual reduction in number of arms and simplicity in structure. The new Chester species, U. chesterensis, also seem to evolve to a form with more numerous arms in the Morrow species, U. oklahoma Springer. However, it is probable that
this group survives and is represented in later Pennsylvanian forms. Exact affinities are not determinable from existing literature.

SYSTEMATIC DESCRIPTIONS

**Genus ALCIMOCRINUS** Kirk

**Aleiocrinus ornatus**, n. sp.

Plate 5, figures 1-7

*Description.*— *Dorsal cup.* Shallow with deeply invaginated base. Five small IBB are confined to basal concavity. Five small BB are also entirely within basal concavity and form a star-shaped disk. Three anal plates are within the cup, radial (RA) placed obliquely and supporting RX above, and together with post. B supports anal X to the left. No decided tendency has been observed toward modification, or evolution, of the anal series except toward *loss of contact between RA and r.* Post. B. Five RR are the most prominent elements of the calyx. They participate in the basal concavity and curve upward to form the lateral sides of the cup. Articular facets slope outward. The entire cup is covered by minute spindelike granules.

*Arms.*—First bifurcation takes place in PBrBr₂ in all rays. There is another equal branching which may take place on the fourth, sixth, eighth or tenth SBrBr. From this point on the branching is endotomous. Normally the eighth, tenth, twelfth or fourteenth brachial is axillary in the outer rays. From eight to ten arms to a ray have been observed. In the holotype 44 pinnulate arms are preserved. All plates are granular appearing.

*Tegmen.*—The tegmen is known to be club-shaped and extends beyond the upper extremity of the arms in three observed specimens but does not normally attain such a length. Tegmen plates are minute ossicles.

*Stem.*—Only proximal columnals are known. The column is circular in outline, pierced by a small, round lumen, and is rather large in comparison to the size of the cup.

*Measurements.*—

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Holotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of crown</td>
<td>33.7 mm.</td>
</tr>
<tr>
<td>Height of dorsal cup</td>
<td>2.0</td>
</tr>
<tr>
<td>Maximum width of dorsal cup</td>
<td>10.2</td>
</tr>
<tr>
<td>Diameter of proximal columnal</td>
<td>2.2</td>
</tr>
</tbody>
</table>

*Remarks.*—This species is closely related to *Aleiocrinus girtyi* (Springer) from the Morrow series of Oklahoma. In *A. ornatus* the RR are more tumid, the arms are slender with less numerous bifurcations, and the crown is not so robust. Apparently this genus climaxed and terminated in the lower beds of the Pennsylvanian since no similar forms have appeared in middle or upper strata of the period.

*Occurrence and horizon.*—Fayetteville formation, Chester group, Mississippian; *Primitive Type A* after Wright (1926) and Strimple (1948).
6 miles SW. of Afton, Craig County, Oklahoma.

Types.—Figured holotype and paratypes collected by Mr. and Mrs. H. L. Strimple. To be deposited in the U. S. National Museum.

Genus ULRICHICRINUS Springer (1926)

Remarks.—This genus was proposed for the reception of a form from the Moral series described as Ulrichicrinus oklahoma. However, the genotype was not actually designated. Bassler and Moody (1943) have listed U. oklahoma as the genotype and since such was the obvious intent it should so stand. Springer's description of the species and the genus leaves much to be desired, particularly with regard to the exact mode of arm bifurcation. Under generic description it is mentioned that from three to four branches are present in each rami but under his, "Analysis of the Genera" (p. 70), he shows as follows:

"Arms branching once on IBr
Arms not abutting; 4 to the ray exceptionally 3 or 2 . . . Ulrichicrinus"

Examination of the illustration shows all arms branch once with PBrBr (IBr) and again with SBrBr (IBr) in some rays. The left posterior ray has four arms in both types and the right posterior ray appears to have only two arms. The anterior ray has four and the left anterior has three arms.

Ulrichicrinus chesterensis, n. sp.
Plate 5, figures 8-11

Description.—The crown is elongate with a high turbinate-shaped dorsal cup. IBB are five erect elements. BB are five plates of hexagonal outline except where in contact with post. IR. Three normally arranged anal plates occupy the wide post. IR. RR are five pentagonal-shaped plates.

There are normally 13 pinnular bearing arms. First bifurcation occurs with PBrBr1 in all rays. A second branching takes place with SBrBr1 in all outer rays except for the anterior where only two arms are developed. Occasionally the left anterior ray develops only two arms.

All caylx plates and the lower brachials are ornamented by thin elongate ridges which roughly take the form of concentric rings following the perimeter of the plates.

The column is circular in outline and is comprised of alternating expanded columnals.

Measurements.—

<table>
<thead>
<tr>
<th></th>
<th>Holotype</th>
<th>Figured paratype</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of crown</td>
<td>Not available</td>
<td>166.0</td>
</tr>
<tr>
<td>Height of IBB circllet</td>
<td>3.7</td>
<td>4.0</td>
</tr>
<tr>
<td>Width of IBB circllet</td>
<td>7.7</td>
<td>7.5*</td>
</tr>
<tr>
<td>Height of dorsal cup</td>
<td>13.1</td>
<td>17.0</td>
</tr>
<tr>
<td>Width of dorsal cup</td>
<td>17.5*</td>
<td>21.0*</td>
</tr>
<tr>
<td>Diameter of proximal columnals</td>
<td>3.6</td>
<td>5.5</td>
</tr>
</tbody>
</table>

* Computed.
Remarks.—*U. chesterensis* is readily distinguished from other species assigned to the genus by the distinctive ornamentation and arm structure. *U. oklahoma* has a greater number of arms which trend toward cuneate brachials.

Occurrence and horizon.—Fayetteville formation, Chester group, Mississippian; 6 miles SW. of Afton, Craig County, Oklahoma.

Types.—Figured types collected by Mr. and Mrs. H. L. Strimple. To be deposited in the U. S. National Museum.

REFERENCES

Kirk, Edwin

Springer, Frank

Strimple, Harrell L.

Wright, James
EXPLANATION OF PLATE 1 (29)

Figure Page
1-3. 7. *Paraecococrinus cranci*, n. sp. .......................................................... 6

4-6. 9. *Ethelocrinus sphacri*, n. sp. ................................................................. 10
  4. Posterior view, ×2 1/4. 5. Summit view, ×1 1/2. 6. Anterior view, ×1 1/2. Holotype, Pumpkin Creek limestone, Love County, Oklahoma.

8, 10, 11. *Ethelocrinus variabilis*, n. sp. .......................................................... 14

12, 14, 16, 18. *Plexocrinus tumulosus*, n. sp. .................................................. 16

13, 15, 17. *Paraecococrinus regulatus*, n. sp. ................................................... 7
EXPLANATION OF PLATE 2 (30)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
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<tbody>
<tr>
<td>1, 3, 4, 6. <em>Ethelocrinus magnus</em>, n. sp.</td>
<td>12</td>
</tr>
<tr>
<td>2, 5. <em>Paradelocrinus regulatus</em>, n. sp.</td>
<td>7</td>
</tr>
<tr>
<td>7, 8, 10. <em>Plavocrinus dormickensis</em>, n. sp.</td>
<td>15</td>
</tr>
<tr>
<td>9, 12, 15. <em>Ethelocrinus ardmorensis</em>, n. sp.</td>
<td>11</td>
</tr>
<tr>
<td>11, 13, 14, 16. <em>Ethelocrinus peridens</em>, n. sp.</td>
<td>13</td>
</tr>
</tbody>
</table>
**EXPLANATION OF PLATE 3 (31)**

**Figure**

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
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</thead>
<tbody>
<tr>
<td>1, 2, 5, 7. <em>Placocrinus patens</em>, n. sp.</td>
<td>17</td>
</tr>
<tr>
<td>3, 6. <em>Delocrinus armatura</em>, n. sp.</td>
<td>18</td>
</tr>
<tr>
<td>4, 8, 9, 12. <em>Malalocrinus azygous</em>, n. sp.</td>
<td>19</td>
</tr>
<tr>
<td>10, 17. <em>Ethelocrinus zweikinsii</em>, n. sp.</td>
<td>8</td>
</tr>
<tr>
<td>10. Right anterior view of crown, small right posterior radial plate is seen to the left. 17. Left anterior view of crown. Holotype, ×2. Arnold limestone, Love County, Oklahoma.</td>
<td></td>
</tr>
<tr>
<td>11, 13, 14. <em>Lecythocrinus fusiformis</em>, n. sp.</td>
<td>20</td>
</tr>
<tr>
<td>15, 16. <em>Paradelocrinus discus</em>, n. sp.</td>
<td>7</td>
</tr>
<tr>
<td>18-21. <em>Delocrinus aristatus</em>, n. sp.</td>
<td>18</td>
</tr>
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</table>
### EXPLANATION OF PLATE 4 (32)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
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</thead>
<tbody>
<tr>
<td>1-4. Delocerinus brownvillensis, n. sp.</td>
<td>Holotype. View from below, posterior, anterior, and summit views.</td>
<td>22</td>
</tr>
<tr>
<td>5-8. Delocerinus ponderosus, n. sp.</td>
<td>Holotype. View from below, posterior, anterior, and summit views.</td>
<td>23</td>
</tr>
<tr>
<td>9-11. Ethelocerinus iatuni, n. sp.</td>
<td>Holotype. View from below, posterior and summit views.</td>
<td>25</td>
</tr>
<tr>
<td>12-14. Moorcocrinus meadensis, n. sp.</td>
<td>Holotype. View from below, posterior and summit views.</td>
<td>26</td>
</tr>
</tbody>
</table>

All figures enlarged two times.
EXPLANATION OF PLATE 5 (33)

Figure | Page
---|---
1-7. *Heimocrinus ornatus*, n. sp. | 23

Figs. 1, 2. Summit and basal views of dorsal cup, paratype, enlarged ×4. Fig. 3. Portion of arms to show pinnular structure, paratype, enlarged ×2. Fig. 4. Upper portion of crown to show tegumen sac, paratype, enlarged ×2. Figs. 5-7. Basal, left anterior, and right anterior views of crown, holotype, enlarged ×2.

8-11. *Ulrichicrinus chestereensis*, n. sp. | 29

NO. 24. STEREOTOCERAS AND THE BREVICOERATIDÆ
Rousseau H. Flower
New York State Museum

June 1, 1930

Paleontological Research Institution
Ithaca, New York
U. S. A.
CONTENTS

<table>
<thead>
<tr>
<th>Title Page</th>
<th>1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Table of Contents</td>
<td>3</td>
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<tr>
<td>Stereotoceras and the Brevicoceratida</td>
<td>5</td>
</tr>
<tr>
<td>Nomenclatorial problems of Cyrtoceratites</td>
<td>9</td>
</tr>
<tr>
<td>Genus Stereotoceras, n. gen.</td>
<td>12</td>
</tr>
<tr>
<td>Genotype Stereotoceras oppletum, n. sp.</td>
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</tr>
<tr>
<td>Stereotoceras oppletum, n. sp.</td>
<td>13</td>
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<tr>
<td>Stereotoceras halli, n. sp.</td>
<td>16</td>
</tr>
<tr>
<td>Stereotoceras canadense, n. sp.</td>
<td>17</td>
</tr>
<tr>
<td>Stereotoceras citheron, n. sp.</td>
<td>18</td>
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<tr>
<td>Stereotoceras lentiexpansum, n. sp.</td>
<td>19</td>
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<td>Stereotoceras gibbosum, n. sp.</td>
<td>20</td>
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<tr>
<td>Stereotoceras impressum, n. sp.</td>
<td>21</td>
</tr>
<tr>
<td>Stereotoceras vetustum (Barrande)</td>
<td>22</td>
</tr>
<tr>
<td>Stereotoceras (?) cruciferum (Hall)</td>
<td>23</td>
</tr>
<tr>
<td>References</td>
<td>24</td>
</tr>
<tr>
<td>Plates</td>
<td>25 - 36</td>
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STEREOTOCERAS AND THE BREVICOCERATIDAE

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The present work is devoted to the description and illustration of the new genus Stereotoceras, together with its known species. All are rare forms, and the material described here is from the collection of a number of institutions. I am indebted to Dr. W. Storrs Cole and Dr. J. W. Wells for the loan of material from Cornell University, to Dr. W. A. Bell for material from the collections of the Geological Survey of Canada, to Dr. I. G. Reimann for material from the collections of the Buffalo Museum of Science, to Dr. R. S. Bassler for material from the U. S. National Museum, and to Dr. A. S. Romer and Mr. W. E. Schevill for material from the Museum of Comparative Zoology at Harvard.

The genus is an anomalous one, being one of the very few smooth-shelled gyroceracones of the Devonian, contrasting strongly with the contemporaneous Rutoceratidce which, with its excessive ornamentation, is one of the most characteristic of the Devonian developments in the Nautiloidea. Internally the genus is unique among gyroceracones in possessing well-developed cameral deposits which, by reason of their supposed hydrostatic function, I had not expected to find in this type of shell. In two respects the genus is a most interesting one; first, for the remarkable variation in form and coiling exhibited by the various species, and second, because of its affinities. Instead of being allied to other gyroceracones it belongs to the Brevicoceratidce, of which most other members are either brevicomes or trochoceroids.

In all, seven species are placed in the genus, and an eighth is included with doubt, because, while it is atypical, it fits here better than in any known genus at the present time. The shells are dominantly gyroceracones, broad whorled, the section varying from a depressed one, with a characteristic flattening of the dorsum, to one in which a ventral keel develops and the whorl is subtriangular. The sutures, normally otherwise simple, are commonly characterized by a lobe developed on the flattened dorsum. The ventral siphuncle is cyrtocoanitic and, where best known, contains irregular actinosiphonate deposits.

The species display wide variations in form, which might be wider were some of them better known. S. oppletum, the genotype, starts as a simple gyroceracone, but at the completion of the second volution the whorls come into contact in a most unexpected manner. At the same time, the adoral part of the shell suddenly ceases to increase in height, although the width increases as before. The mature living chamber is unknown. This same tendency is carried farther in the remarkable S. impressum of the Upper Devonian. This is known from a fragment of a shell which, by itself, would be considered cyrtocoanitic. However, the concavity of the dorsum here suggests that coiling was close enough, as in the genotype, to develop an impressed zone. Probably this obvious conclusion is incorrect, and the concavity of the dorsum, with its attendant lobation of the suture, is not caused
by having the whorls closely impressed. In the geronic stages the shell becomes straighter, as in many other coiled genera. Further, in this species the reduction in vertical expansion is carried to such an extent that the height of the shell is decreasing as the living chamber is approached.

*S. eitheron* of the Stafford limestone is specialized in a reduction of coiling. If coiling is uniform in this species, it is cyrtocone. The species is further specialized in that the sutures develop faint ventral as well as stronger dorsal lobes.

*S. lenticespansum* is peculiar in that the dorsum is nearly as broadly rounded in cross section as is the venter. In other respects it is quite typical. The lobes of the dorsum, an inherent feature of the genus, are well developed here. This is, in a way, surprising. More often in nautiloids the curvature of the septum is relatively uniform, and suture patterns vary with the cross section, compressed shells developing lateral lobes, depressed specimens developing lateral saddles.

This is the stable septum (Flower, 1946, p. 33). However, occasionally the suture pattern becomes fixed and may remain uniformly throughout a series of related species in spite of modifications of the cross section. This is the stable suture. The presence of the stable suture in this species is a clear indication that the suture pattern has become fixed in its ancestors, where it evidently appeared as the natural effect of the characteristically flattened dorsum upon a primitively stable septum, but at length the suture has become fixed instead of the septum. These indications show further that the temptation is to assume that the simple cross section of *S. lenticespansum* is not a primitive condition, but a specialized one. Indeed, it is one which is not now present in *Streotoceeras* but also in the ancestral *Nedyceras*.

*S. gibbosum* is generalized in all features but one, the living chamber, which expands laterally and then contracts to the aperture, giving the shell a brevicicone aspect. Irritatingly enough, it is only in this species that a mature aperture has been observed, but there is no basis for assuming that the living chambers behave similarly in the other species. On the other hand, a similar tendency has been noted in some species of the related genus, *Gyronedyceras*, as well as in the more primitive and, I believe, ancestral genera *Nedyceras* and *Gonionedyceras*.

The remaining species are more generalized. *S. halli* of the Schoharie grit is a fairly typical, rather rapidly expanding, gyroceracoid with the dorsum more flattened than the venter and with the usual dorsal lobes of the sutures. *S. canadense* of the Onondaga limestone is less closely curved, and shows a faint tendency toward the development of the ventral keel which appears in the more specialized *S. oppletum* and *S. impressum.* *S. velatum* of the Devonian of Bohemia is typical in section and is noteworthy for the relatively close coiling and the rapid vertical expansion of the shell in the known portion which gives it a completely deceptive resemblance to the stock of the Rhabdinoceratidae. *S. cruciferum*, a little known species of the Schoharie grit, is placed here largely because of the similarity of the cameral deposits with those of the genotype. The species is very inadequately known and is atypical in the relatively high and narrow cross section as well as in the considerable distance of the siphuncle from the venter. I have included it because *Streotoceeras* is the only known genus with which its anomalous features seem to be at all consistent.

With such variations in form as are exhibited by these species, several genera could be erected upon the basis of features which have at least the sanction of long usage. I have not done so because, in spite of form variation, these species
Stereotoceras and the Brevicoceratidae: Flower

obviously constitute a natural genetic unit. The use of more generic names would serve only to complicate the nomenclature, already had enough, and to obscure these relationships.

The affinities of the genus presented quite another problem. Most of the gyroceracones known in the Devonian belong to a stock characterized, above all else, by a surface pattern involving frills, spines, sometimes hollow, and again solid, and spout-like projections of the shell. These various markings appear on the shell at regular rhythmic intervals clearly to be interpreted as former apertures, and probably representing resting stages in the growth of the shell. A considerable number of generic names have been employed to express the varying external features within this group. It is represented by *Trocho cereas*, *Pi noceras*, *Phyll co ceras*, *Ad elphoceras*, *Homo adelphoceras*, *Rutoceras*, *Kop hino ceras*, *Heroceras*, *Tet ranodoceras*, *Hindeo ceras*, *Casteroceras*, *Tylorthoceras*, *Hallo ceras*, *Thea tocrates* and *Goldringia* (Flower, 1943). More recently (Flower, 1949) *Mu ioceras* and *Diademoceras* were added to this form group. Most of these genera have a slightly depressed section, the dorsum more flattened than the venter. The origin of the stock is obscure, and it is not even certain that we are not dealing here with several distinct lines in which a false similarity is presented by the development of similar patterns of frills and spines. Indeed, I believe that *Mu ioceras* is related to *Cyrtoceratites* and unrelated to other members of the stock. Within the other genera there is considerable variation in internal structure, *Trocho cereas* has a faintly expanded siphuncle with organic deposits, the nature of which requires further study. Some genera are actinosiphonate according to the extinct descriptions, including *P i noceras*, *Ad elphoceras* and *Homo adelphoceras*. *Rutoceras* itself has a broadly expanded siphuncle, but clear evidence of actinosiphonate structure within it is lacking. Most of the genera, including *Hallo ceras*, *Goldringia*, *Tetrano doceras*, *Hindeo ceras*, *Casteroceras*, *Diademoceras*, and *Tylorthoceras*, possess tubular, empty siphuncles. The evidence now at hand is not sufficient to warrant any conclusion as to whether internal structure has varied here within in a single stock, or whether two or more unrelated stocks are represented. If so, it will supply one of the most remarkable cases of contemporaneous convergence in paleontology.

Attempts to relate *Stereotoceras* to any of the members of this perplexing group were fruitless; the forms which approached the genus most closely in some respects showed such differences in others that it was clear any hypothesis involving a close relationship would be patently untenable.

The family Brevicoceratidae (Flower, 1941, 1945) represents an amazingly plastic stock consisting of trochoceroids, gyroceracones and, finally, brevicones, which are united as smooth-shelled forms with a deep hyponomic sinus, sutures which tend to develop a broad lobe on a flattened dorsum, and in which the ventral siphuncle, cyrtolobanitic but generally rather slender, typically retains discrete deposits which are in general actinosiphonate, though clearly degenerate in some forms and altogether absent in some members of the stock. The family is an unsatisfactory one from the point of view of succinct definitions. It is established with its present boundaries because the genera it embraces constitute a genetic stock, and, indeed, are sufficiently closely related that some species are embarrassingly close to the necessarily arbitrary boundaries which separate genera. A full account of the family will be delayed for another occasion when, it is hoped, descriptions and illustrations of the known species can be included. At the present time it will suffice to point out the relationship of *Stereotoceras* with the other genera.
The first appearance of the family in the American Devenian is an abrupt one, for in the Schoharie grit are represented the genera *Nycyceras, Goniomycyceras, Gyromycyceras, Wissenbachia, Stereotoceras, Brevicoceras* and *Exocystroceras*. The smooth trochoeroids of the Schoharie grit show great divergence of form. Those which exhibit the most marked trochoeroid coiling, typified by *Nycyceras engenium*, are relatively simple and essentially symmetrical in cross section and sutures. On the other hand, *Goniomycyceras*, typified by *Trochoceras pandion*, is characterized by a cross section and a suture pattern which are strongly asymmetric, considerably askew in relation to the position of the siphuncle, while at the same time these shells are so loosely coiled that they may be considered gyrocones rather than trochoeroids. Inspection of these species leads to the conclusion that the only possible explanation of the widely divergent forms exhibited by these evidently closely related species is that they are degenerate offshoots from a more perfectly trochoeroid ancestral form. Such ancestral types are found in the Upper Silurian genera *Mitrococeras* and *Foersteococeras* of the Cobleskill limestone of New York. Through these genera, it is possible to trace the family through the other whorled forms referred to *Oxygoniococeras* in the Middle Silurian, to *Oonoceras*, and finally to a beginning in the Ordovician *Onococeratidae*, to which *Oonoceras* is probably best referred.

From the narrow-whorled species of *Nycyceras* there developed *Gyromycyceras*, in which the shell became more slender and lost completely the trochoeroid condition. The genus is represented in the Schoharie grit by the genotype, *G. validum*, and reappears in the Milwaukee dolomite, where it is represented by *G. oryx* (Hall) and *G. wisconsinense*. *Nycyceras* itself is represented by some surprising species in beds younger than the Schoharie grit, including *N. gibbosum* and *N. contractum* of the Columbus limestone (Flower, 1845) of Ohio, while in New York the genus persists into the Ithaca and Chemung, being represented by undescribed species, and is present in the Middle Devonian Nevada limestone. Apparently *Stereotoceras* is a gyroconic expression of the broad-whorled species placed in *Nycyceras*, the group of *N. barrandeii* and *N. orion*. Indeed, the relationship between *Nycyceras oblignatum*, *N. expansum* and *Stereotoceras halli* is still quite close, and the generic division has been drawn necessarily at the distinction between the trochoeroid and the gyroconic shells. Once this relationship is seen some of the tendencies noted in *Stereotoceras*, formerly so perplexing, can be traced to tendencies already noted in *Nycyceras*; there is the tendency toward slight inflation of the living chamber so puzzling in *S. gibbosum*. *Nycyceras orion* shows only slight inflation, but the living chamber tapers gradually, contracting toward the aperture. Is the vertical contraction noted in *S. appletum* and *S. impressum* a tachyconic expression of this tendency? The similarity may be false, but it is at least comforting that such tendencies, rare alike in trochoeroids and gyrocones, are common to species of these two related genera. Likewise, the species of *Nycyceras* show unexpected changes in rate of curvature making understandable in *Stereotoceras*, as the gyroconic descendant, such things as the sudden appearance of whorls which attain contact at the completion of the second instead of the first whorl, and then apparently become free in a still later growth stage.

Strangely, foreshortening of the stock of these coiled genera has apparently produced brevicoceres. There are several species of *Nycyceras* which approach
rather close to the shell form of *Wissenbachia*; in the Schoharie we have one species which fulfills the requirements of this genus as defined by Foerste. There is not as marked a transition between *Stereotoceras* and *Brevicoceras*, but *Brevicoceras* is clearly a less curved and strongly abbreviated edition of that genus. Likewise, a genus, as yet undescribed, is the breviconic expression of *Goniocyclites*.

It is unnecessary at the present time to trace the family farther. This has already been done in a brief form (Flower, 1915), and a more extensive discussion should properly be accompanied by descriptions and illustrations of the species and genera concerned.

*Cyrtoceratites* Goldfuss is a genus externally similar to *Stereotoceras*. It differs in the more semicircular cross section and the more rapid vertical expansion of the shell. These obvious, but superficial, differences find further support in the concavosiphonate siphuncle which is filled with continuous vertical lamelle. It is quite probable that *Cyrtoceratites* is not related to *Stereotoceras* or the Brevicoceratid. Its origin is, however, uncertain.

**Nomenclatorial Problems of Cyrtoceratites**

Much perplexity surrounds the question of the valid form of the genus which has appeared under various spellings, *Cyrtoceratites*, *Cyrtocera*, *Cyrtoceratites*, and a few more. As generally used, under the spelling *Cyrtocera*, the type has been accepted as *C. depressa* (Goldfuss, 1832). The generic name was proposed by Goldfuss in 1830, in the Jahrbuch für Mineralogie, vol. 1, p. 228. Goldfuss in 1832, in the German edition of the De la Beche Handbuch der Geognosie, published the generic name *Cyrtocera* described as "Halbmondörig gebogene Orthocerae" and listed six species without description. Foord (1888) discussed *Cyrtoceras*, noting that it was first called *Cyrtocera* and stating: "Lastly, *depressa* and *lineata* remain to be disposed of, and as the former is found in a more perfect condition than the latter, it may well be adopted as the type of the genus." This statement has been taken, and, I think, correctly in spite of its tentative wording, as the designation of a type species. Subsequent authors have uniformly accepted the species *depressus* as the genotype of *Cyrtoceras*. There are, however, complications.

The generic name *Cyrtoceras* was first used by Sowerby in 1837 as pointed out by Teichert (1939, p. 107, footnote). Teichert stated that the only species referred to the genus is a gastropod. The writer is not completely convinced of this interpretation from Sowerby's figure, which might possibly represent a *Cyrtorizoceras* or an *Oonoceras*, both of which occur in the British Silurian. However, this matter has no bearing upon the problem, for *Cyrtoceras* was not accompanied here by the indication, description or definition required by the rules. Instead, there is a clear indication that Sowerby had no intention of proposing a new genus, but only an emendation of spelling of an old one. He writes as follows: "*Cyrtoceras laeve* Pl. 8, fig. 21. Also in Upper Ludlow rocks, pl. 5, fig. 34. (For the generic description of *Cyrtoceras* see Goldfuss.)" The remainder is a description of the species irrelevant to the present problem. It is clear from this reference to Goldfuss that *Cyrtoceras* was proposed as an emendation of either *Cyrtocer-
attics, Cyrtocera, or, more probably, both of these spellings. As an emendation, Cyrtoceras Sowerby is not proper under the rules.

The species which Goldfuss listed as Cyrtoceras depressus in 1830 was not valid at the time, since no description nor figure was given. The species dates from Bronn, 1837, in the second edition of vol. 1 of his Lethaea Geognostica, p. 101, tab. 1, fig. 5. The same species was figured and redescribed under the name Cyrtoceras depressus by D'Archiac and De Verneuil in 1842 (Geol. Soc. London, Trans., 2d ser., vol 6, pt. 2, p. 350, pl. 20, fig. 1, 1a). Cyrtoceras was used earlier by Goldfuss.

It is unfortunately legally possible under the rules of zoological nomenclature to designate different genotypes to these various spellings and to use them as distinct genera. In fact, this sort of thing has been done too often already. Usage has not been consistent. Teichert and Miller (1936, Amer. Jour. Sci., vol. 31, p. 360) recommended the revival of Orthoceras Brünnich, 1771. Teichert (1939, p. 163) recommended that Phragmoceratites d'Archiac and de Verneuil should not replace Archiaceras, over which it has priority since the authors indicated no intention of erecting a new genus and the generic name is not accompanied by a designation or description. Article 25 of the International Rules of Zoological Nomenclature requires a "description or a definition." Under this requirement, Orthoceras Brünnich, 1771, has no standing nor has Cyrtoceras. However, to prevent further complications, I designate types for those names for which no previous designation has been made. For Cyrtoceras Goldfuss, 1830, Teichert (1930, Jour. Paleont., vol. 14, p. 504) has already designated Cyrtocera depressa Bronn, 1837, Lethaea Geognostica, vol. 1, 2d ed., p. 101, pl. 1, fig. 5. For Cyrtocera Goldfuss, 1832, I designate Cyrtocera depressa Bronn, 1837, as above, and for Cyrtoceras Goldfuss, 1832, identical with Cyrtoceras d'Archiac and de Verneuil, 1842, I designate the same species as the type. This will reduce Cyrtocera and Cyrtoceras as synonyms of Cyrtoceras beyond any possible question.

Yet another aspect of the rules of nomenclature suggests that actually none of these designations are legal, and another solution is necessary. Article 30 of the International Rules of Zoological Nomenclature states specifically that species are not available as genotypes "which were not included under the genus at the time of its original designation." Dr. J. W. Wells has pointed out to me that this may very well be read as valid species. Quite probably, the makers of the rules, being sensible people, assumed that no one would bother with a species which was not valid. A survey of the recent literature impels me to conclude that if so, they led sheltered lives. In this case there are good grounds for confusion, for between 1830 and 1850 the manuscript names of Goldfuss keep appearing in the literature with such amazing uniformity of use, suggesting that descriptions and figures might have been circulated privately. At various times in this interval various of the species were validated by descriptions of different authors.

However, this is an ambiguous point. Dr. G. W. Sinclair (fide ltt.) brings up the question as to whether a species or a name is the type of a genus. If a species, as stated by the rules, the above solution is adequate. However, if a valid specific name is to be required, none of these designations are legal, as the species Cyrtoceras depressus is not available for selection as a genotype. None of the Goldfuss names of 1830 or 1832 are available, but Goldfuss lists as a synonym under Cyrtoceras compressus the previously described and therefore available species Orthoceras flexuosus Schlotheim 1820. As the
only valid species listed under Cyrtoccratites at the time of its original description, it is the only species available under this interpretation of Article 30 as a genotype; more, designation is not necessary for it becomes the genotype by monotypy.

Further, Goldfuss lists this as a synonym of Cyrtoccratites compressus. As this antedates all of the publications of Goldfuss in question, it has priority over C. compressus. Therefore, in listing C. compressus in this or any other genus, Goldfuss is automatically including within it Orthocerites flexuosus. In this way, the same nomenclatorial solution must be accepted for Cyrtocera Goldfuss 1832 and Cyrtoceratites Goldfuss.

This interpretation involves the status of two other generic names. Cranoceras Hyatt 1884, based upon "Cyrtoceras" depressus Goldfuss (Cyrtoceratites depressus Goldfuss, Cyrtocera depressa Bronn) has been suppressed as a synonym of Cyrtoceras Goldfuss, as interpreted by recent authors, and more properly, of Cyrtoceratites Goldfuss. This generic name will then become available for the generic unit for which these names have been employed.

The basing of Cyrtoceratites upon Orthoceratites flexuosus Schlotheim will involve the problem of the genus Archiacoceras Foerste. In a work now in progress, the living chamber of Archiacoceras subventricosum, the type species of the genus, is being described. This permits an emended description of Archiacoceras. In searching the literature, it was found that Foord (1888) considered Phragmoceratites subventricosum d'Archiac and de Verneuil a synonym of Orthoceratites flexuosus. From the available figures and descriptions of the type species, this conclusion seems to the writer unlikely, unless one assumes that Schlotheim employed excessive latitude in regard to the proportions of his type specimen in his drawing. Nevertheless, it seems highly probable that the two species, both from the Middle Devonian of the Eifel region, are congenic. From this conclusion, it should automatically follow that Archiacoceras should be suppressed as a subjective synonym of Cyrtoceratites Goldfuss. This step is not recommended at the present time, because, while the genus Archiacoceras is very well known, we know only that Cyrtoceratites agrees with it in being a rapidly expanding compressed cyrtocone with the siphuncle on the concave side of the shell. We know nothing of the structure of the siphuncle, or of the living chamber. Theoretically, Cyrtoceratites might instead be closer to Alpenoceras Foerste. Therefore it seems wisest to regard Cyrtoceratites as a legally valid genus based upon Orthoceratites flexuosus Schlotheim, but this species is not well enough known at the present time that any other species can be assigned to the genus with certainty or that the affinities of the genus can be understood.

One complication still remains. As a synonym of Cyrtocera depressa Goldfuss, 1832 (a species which we note does not become available under the rules as of that author and date but was only validated by Bronn in 1837) Foord listed Orthoceratites nautiloides Steininger, 1833, Socié. Geol. France, Mem. vol. 1, p. 80, pl. 23, figs. 1, 1a. Not only does this publication have priority over Bronn's validation of C. depressa in 1837, but in a still earlier work, that of the same paper published in German without plates, at Tréves, in 1831, the same species is listed and described. The species, therefore, is available as of that date. It is uncertain from Steininger's figure whether or not his species is identical with Cyrtoceratites depressus. I think there is a possibility that it may be different. However, if it becomes possible to study the type specimen, and the two species are found to be
identical, this name must clearly be given priority. If so Orthoceratites nautiloides will take precedence over Cyrtoceras depressa.

Concerning the two remaining spellings, no solution can be presented as simple as the ones above. Cyrtoceras is listed by Sherbourn in the Index Animalium as attributable to D'Orbigny 1840, where it was apparently used in connection with ammonoids of the Cretaceous of France. I have not seen the work. However, Teichert has found that Sowerby used it in 1837.26

Cyrtoceras Conrad, 1838, appears without description or definition. Under it is described one new species, Cyrtoceras maximum. Hall identified with this species the forms which he later described as Nautilus maximum, now referred to the genus Nephriticeras. It may be pointed out that it is uncertain whether Cyrtoceras maximum of Conrad and Nautilus maximum of Hall are identical. Internal evidence suggests that Conrad's material was not available to Hall. Conrad's description is inadequate and lacks even a locality. Even supposing that Cyrtoceras Conrad should be construed as falling within the law of priority, it is not strictly possible to recognize the genus or species. Further, Conrad's use of a neuter adjectival specific name with a masculine generic ending suggests strongly that the use of Cyrtoceras is a lapsus calami.

The sole purpose of these designations is to prevent the revival of these generic names in connection with valid generic groups. Such a course has been followed in respect to Orthoceras and its variants, with most unfortunate results, which are still of dubious merit and legality. It is hoped that these designations will prevent a similar misuse of the variations on the general theme of what has been known for the last hundred years as Cyrtoceras.

Genus STEREOTOCERAS Flower, n. gen.

Genotype Stereotoceras oppletum, n. sp.

Couch gyroceraconic, section strongly depressed, the dorsum much more flattened than the venter. The sutures are typically marked by conspicuous lobes on the mid-dorsal region, ventrally they are normally straight and transverse. The siphuncle lies close to the ventral margin of the shell. Its segments are nummuloidal, being rounded and elongate in outline in the simpler forms or in the early stages, and abruptly contracted at the septal foramen in more advanced types, being essentially parallel-sided throughout most of the length of the camera. Within the siphuncle are discrete deposits concentrated at the septal foramina, from which may project irregular processes, indicating that this is a degenerate type of actiniosiphonate structure.

The shell surface is without spires or nodes but bears only transverse lines of growth. These lines swing apicad on the venter outlining a well-developed hypomonic sinus. In the only species for which the mature aperture is known, the shell is strongly contracted laterally over the adoral part of the living chamber. Cameral deposits are developed in the phragmocone.

Discussion. — This genus may be characterized and easily recognized by the smooth shell, the broadly depressed section and the dorsal lobes that readily distinguish it from all other gyroceracones. Coiling and cross section vary exceedingly among the species, the shells ranging from one species which was probably a cyrtocone, S. citheron, to S. vetustum in which the coiling was close enough that the whorls were essentially in contact, while in the genotype the whorls were free and widely separated up to the end of the second volution where they
Stereotoceras cithcron rounded better canadense iniprec.\^snii. slightly produced vetustnm iiiipreciim oppcitim 2.
comparison transverse, oppcitnm prevalent is the the
nearly similar foot verteal figures vetustum me sp.
the slightly 2; Plate the is contact applets The
made is canadense. condition low oppcitnm distinctly
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the a keel.

This is a large gyrocercone which, when complete, consisted of two and a half to three whorls, with a coil reaching nearly a foot across. The shell is smooth, with only lines of growth, which slope apicad on the venter forming a hyponomic sinus. The whorls are free, broadly separated initially, but probably in contact at the completion of the second volution. The cross section is transverse, the dorsum faintly convex, but becoming increasingly flattened; the venter, rounded initially, develops a keel so that the section becomes subtriangular. The ventral siphuncle is made up of segments, at first nummuloidal, then parallel-sided within the camera, abruptly contracted at the septal foramen, the interior with deposits consisting of annuli at the septal foramina which send out very irregular actino-
siphonate processes. The camera are occupied by extensive organic deposits.

This species is known to me from two specimens. The holotype shows the
greater part of the phragmocone illustrating such remarkable changes in proportion that I describe it in detail. The paratype (Plate 3, fig. 2) consists only of one side of a portion of a phragmocone from a relatively late growth stage.

The holotype consists of two portions of a phragmocone, the first describing one and one quarter volutions, with perhaps a quarter of a volution missing apically, while the second represents slightly less than a quarter of a volution. The two portions cannot be connected, a small piece, probably of not more than four camerae being missing. The earlier portion attains a whorl of 130 mm.; with the second piece in place the whorl attains 160 mm. The apex of the specimen is blunt, and probably about a quarter of a volution is missing here. In the ventral length of 9 mm., the height becomes 11 mm., the width is estimated at 14 mm. Here the venter is rounded, the dorsum strongly flattened. The specimen shows the following measurements:

<table>
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<th>Interval on venter</th>
<th>Volutions</th>
<th>Height and width</th>
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<tr>
<td>74 mm. from apparent apex</td>
<td>⅓</td>
<td>22 x 38</td>
</tr>
<tr>
<td>135 mm. from above</td>
<td>1</td>
<td>38 x 68</td>
</tr>
<tr>
<td>85 mm. from above</td>
<td>1¼</td>
<td>48 x 82</td>
</tr>
<tr>
<td>(interval lost, not one sixth of volution)</td>
<td></td>
<td>49 x 77</td>
</tr>
<tr>
<td>130 mm. (from above)</td>
<td>2½</td>
<td>56 x 104</td>
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At the completion of the first volution the venter becomes subtriangular and faintly keeled, a condition which is reduced a half volution farther. The dorsum becomes gradually and progressively flattened throughout.

Sutures are straight and transverse in the first half volution, after which broad low ventral saddles develop, and the sutures become faintly oblique. The dorsal portion of the suture remains straight to the end of the first half volution, where a vestige of a median saddle appears between a pair of dorsal lobes (Plate 1, fig. 4), a condition which persists into the adult.

Septa are very shallow in their curvature throughout the shell, the depth varying from 3 mm. where the shell height is 17 mm., to 7 mm. where the shell height is 38 mm. The camerae are shallow, ranging from four in a length equal to an adoral shell height of 22 mm., to five and one half at 27 mm., seven at 38 mm. Owing to the decrease in the rate of expansion in the last quarter volution, the camerae are proportionately deeper there as customarily measured, occurring five in a length equal to an adoral shell height of 56 mm.

The siphuncle is ventral in position. In the first half volution, it is separated by more than its own diameter from the shell wall, but moves closer to the venter in the later portions. Where the height of the shell is 48 mm., the siphuncle is 3 mm. in diameter and 3 mm. from the venter. In the last quarter volution of the type the siphuncle is 2 mm. from the venter, and is 6 mm. high and 4 mm. broad at its passage through the septum.

A portion of the ventral surface was ground away to expose the siphuncle (Plate 2, figs. 1, 2). Where the shell height is 38 mm., the segment is 5.5 mm. in length. The segment increases in diameter from 3 mm. to 4.5 mm. The segment is subcylindrical throughout the greater part of the length of the camera, contracting abruptly at either end. The septal neck is recurved, brim equalling the length of the neck. The adapical part of the ring joins the adapical septum with an area of adnation equal to the brim.
The siphuncle is occupied by rather irregular organic deposits (Plate 2, fig. 1). They are largely, but not completely, confined to the area of the septal foramen and appear in longitudinal section as rather irregular annulosiphonate structures. However, they can be seen continuing irregularly over the length of the segment, where they appear to be irregular thickenings of the connecting ring. Also, there are irregular processes which extend apicad and orad from the main mass of the deposit which appear as irregular actinosiphonate rays. The several cross sections at the septal foramen fail, without exception, to show the regular actinosiphonate structure which is found in so many cyrtocoanitic genera.

The most remarkable feature of the species is the clarity with which the cameral deposits are displayed on the internal mold of the shell. These are shown in the adoral part in Plate 2, figure 2, again in section in Plate 2, figure 1; while they are seen in their more advanced condition in the region of the shell directly apicad of that in which the siphuncle was studied in detail, as shown in Plate 3, figure 1. The deposits are obscure in the early part of the shell, being best developed at a region extending from one half to one and one half volutions from the apex of the type.

The paratype increases vertically from 70 mm. to 102 mm. and agrees closely with the holotype. It is chiefly of interest in that its origin is more accurately known.

Fragments of the shell show indications of growth lines which slope apicad on the venter forming a hyponomic sinus.

Discussion — This species, the most adequately known of the genus, shows a number of very unusual growth features which justify the detailed description set forth above. Most remarkable is the marked change which occurs early in the second whorl, the sudden decrease in the rate of expansion accompanied by the development of a subtriangular section and the movement of the siphuncle to a position adjacent to the ventral wall of the shell. The apparent increase in the depth of the camera at this point is purely relative. The camera increase gradually and uniformly in depth orad, but where the rate of expansion of the shell decreases abruptly, the apparent change in septation results when the camera are measured, as is customary, in relation to the width or height of the shell.

The two fragments which constitute the holotype at first seemed to belong to different individuals; indeed, the differences shown between them are equivalent to some which have been taken as the criteria of different species. However, it was evident that such changes were the result of the examination of different growth stages. Irritatingly, the two pieces did not fit. However, the later fragment would fit, its dorsum resting on the impression of an outer whorl preserved on the initial portion, on the assumption that a portion of the phragmocone consisting of about four camera had been lost. This, however, requires that the whorls at this point should lie in contact with one another, an assumption which at first seemed such a departure from the usual condition in coiled cephalopods, that I was tempted to reject it. However, some support for this interpretation was found in S. impressum which develops an impressed zone or at least a concavity of the dorsum very suggestive of one. Another singular feature shown in this species, which I at first thought was a mistake in my own measurement, was the failure of the adoral part of the shell to increase in height. S. impressum again shows that this is not accidental, for in that species the height of the whorl decreases slightly over
the adoral part of the phragmocone. This indicates that in the types of *S. oppletum* we are dealing with a portion of the phragmocone which is approaching maturity. Nothing is known of the living chamber. By all analogy with related species, the living chamber was relatively short.

The most amazing feature of the type is the presence of actinosiphonate and cameral deposits. When this specimen, the first representative of the genus I had encountered, came into my hands, much time was devoted, in vain, to an attempt to correlate the form in some way with the spinous Devonian gyroceracoids which possessed nummuloidal siphuncles. Not until much later, and after I had come upon several other species of this genus, did its relationship with the brevicones and trochoceroids of the Brevicoceratidae become apparent.

There is some doubt in my mind as to the origin of the holotype. It came to me bearing a label “Devonian of Ohio.” Its lithology was completely foreign to any Devonian formation known to me from Ohio. I showed the specimen to Dr. G. A. Cooper and asked his opinion of its origin. He was also puzzled but stated that if the label were correct, the specimen could only have come from Delaware limestone of northern Ohio. Later, in material from the U. S. National Museum, a second specimen was found among material from the Alpena limestone of Michigan. Unfortunately the type was too singular and too complete to be set aside in favor of the second and more fragmentary specimen, which was not sufficient to give any concept of more than a small portion of the shell of this species. I am inclined to suspect that the holotype may also have come from the Alpena limestone of Michigan. The lithology of the specimen is reminiscent of only two formations, the other being the Middle Devonian of the Eifel region of Germany which has as yet yielded nothing resembling this singular species.


*Occurrence.* — As noted above in the discussion, the holotype is labeled “Devonian of Ohio.” If correct, it is probably from the Delaware limestone of northern Ohio. The paratype is from the Alpena limestone.

*Stereoceras halli* Flower, n. sp.

*Plate 1, figure 5.*

*Streptoceras compressum* Hall, 1879. Paleontology of New York, vol. 5, pt. 2, p. 432 (pars) pl. 161, fig. 51; not pl. 58, fig. 6.

The holotype is a portion of a small gyroceracon, the preserved part encompassing slightly less than half a volutions, only the dorsum well preserved, and the whole specimen slightly flattened. The cross section is depressed, the venter relatively high arched; the dorsum flatter, but still slightly convex. At the base the type is 11.5 mm. high and 19 mm. wide. The width increases to 34 mm. in a length of 28 mm. dorsally. Six cameral are preserved, occupying 1.4 mm. of the dorsal length. These average 2 mm. in length, except the last which is 1 mm. in length, indicating that the type represents an essentially mature shell. The sutures develop broad shallow mid-dorsal lobes separated by low saddles, which are more pronounced adorally than adapically. Apparently, the suture is straight ventrally. The siphuncle lies close to the ventral wall of the shell. Its structure has not been observed. The extent portion of the living chamber, 17 mm. in length, increases in width from 28 mm. to 34 mm. No surface features are shown.
Discussion — Hall (1876) figured a specimen as Trochoceras obliquatum which he later made one of the two illustrated specimens accompanying his description of Trochoceras expansum. This specimen (American Museum of Natural History, No. 2888, original of Trochoceras obliquatum Hall, 1876, Illustration of Devonian Fossils, Cephalopoda, pl. 48, fig. 6, and of Trochoceras expansum Hall, 1878, Pal. New York, vol. 5, pt 2, pl. 58, fig. 6) seems to be the one upon which the greater part of Hall’s description is based, and is therefore selected as the lectotype of that species. The other specimen, the original of Hall, 1878, pl. 111, fig. 5, is a very different species, being more rapidly expanding and gyroconic and not trochoceroid. It is the type of the new species S. halli, and is re-illustrated in the present work. Several additional representatives were found in the collection of the New York State Museum, but all were poorer specimens and failed to add to the knowledge of this form.

S. halli appears to be a relatively rapidly expanding species, though the rate of expansion has evidently been increased somewhat in all available specimens by vertical crushing. From the lack of distortion of the basal septum of the type, however, it is evident that at that point the cross section of the specimen has not been altered materially. The species is characterized readily by the combination of dorsal lobes of the sutures which are well developed and a cross section in which the dorsum is still markedly convex, although much more flattened than the venter. All of the known specimens are flattened individuals showing the dorsum. Probably fragments showing the ventral side exist, but have been confused with badly flattened fragments of Nectyloceras. Probably the complete shell described a little more than a single volute, with the whorls rather widely separated.

Holotype. — New York State Museum No. 12565/1.

Occurrence. — In the Schoharie grit of Schoharie and Albany counties. The type is from Schoharie, N. Y. I have collected the species at Wolf Hill, Albany County, N. Y.

Stereotoceras canadense Flower, n. sp.

Plate 5, figures 1-3.

Holotype a portion of a phragmocone with a portion of the living chamber, increasing from a height of 13 mm. and a width of 16 mm. to 25 mm. and 35 mm. in the basal 75 mm. as measured on the venter, with a ventral radius of curvature of 60 mm. in the early portion, increasing slightly over the incomplete living chamber which is 35 mm. in length. The cross section is depressed, the dorsum more flattened than the venter, but faintly convex. The venter is well arched, nearly semicircular, with a faint trace of a median keel. The sutures describe broad lobes on the flattened dorsum, are transverse laterally, and form low subangular saddles on the venter which shows only a trace of a median angulation in cross section. Five camere occupy a length equal to the adoral height of 24 mm. and are uniformly spaced throughout except that the last camera is slightly shorter than the others, indicating that the type is approaching maturity. The siphuncle is close to the venter and is exposed by weathering on the type. The segments are expanded within the camera abruptly at the ends, but are nearly parallel-sided throughout the greater extent of their length within the camera. Faint traces of organic deposits can be seen in the siphuncle and are concentrated at the septal foramina. They fail to show definite actinosiphonate structure. Faint traces
of cameral deposits can be seen on the ventral side of the shell. The mature living chamber has a basal width of 35 mm., a height of 25 mm. and a maximum (lateral) length of 34 mm.

The complete shell could hardly have consisted of more than three fourths of a volutions.

Discussion. — This is a relatively slender and gently curved species. It differs markedly from S. citheron in the more rounded condition of the dorsum in cross section. The section is much less specialized than that of the genotype, which it resembles in the form and structure of the siphuncle and in the presence of cameral deposits. The species which is most closely allied is S. halli of the Schobarie grit. That form is more rapidly expanding. The shell is more strongly curved, and the dorsal lobes of the sutures are narrower and less pronounced. The spacing of the camera is also somewhat closer. Differences in the cross section may be more apparent than real, but S. halli appears to have a cross section in which the dorsum is more convex and the venter is flatter. Further, S. halli shows no trace of any tendency toward the development of an obscure keel on the mid-ventral part of the shell.


Occurrence. — From the Onondaga limestone, Walpole township, Ontario.

Stereosaccus citheron Flower, n. sp.

Plate 6, figures 1-3.

Shell very gently curved and slowly enlarging, with a radius of curvature of 15 cm. for the known portion, which expands from 34 mm. to 34 mm. with estimated widths of 56 mm. and 70 mm. in 70 mm. The type is 125 mm. long, but the venter is lost adoral by weathering, and the adapical portion is laterally crushed. Cross section depressed, the dorsum more flattened than the venter but still convex. The venter is rounded with no trace of a median angle. Sutures bear a broad, inconspicuous ventral and a more prominent dorsal lobe. Camera occur between five and six in a length equal to the adoral height of the conch. Siphuncle and septa not observed. The surface bears numerous transverse strie of variable strength and spacing which slope apicad on the venter to form a hyponeomic sinus.

Discussion. — The type consists of a portion of a curved phragmocone which represents a shell of such gradual curvature that it must have been essentially gyroconic rather than gyroconic unless curvature was much greater in the adapical portions. The slight curvature and very gradual expansion serve as the best criteria of the species, but it also differs from its congeners in suture and cross section. In other species the sutures are transverse ventrally; in this one they slope slightly apicad forming broad obscure lobes. The dorsal lobe of the suture is broad and shallow, deeper than that of S. lentioexpansum, a species which differs materially in cross section, for the dorsum there is much more rounded. In S. gibbosum the curvature is greater, the sutures tend to swing slightly forward on the venter, and the septa are relatively closely spaced.

The shell was probably mature, as indicated by a slight shortening of the last camera.

Holotype. — Buffalo Museum of Science.

Occurrence. — From the Stafford limestone of the Hamilton group, South Buffalo, N. Y.
Stereotoceras lentiepum Flower, n. sp.

Plate 3, figure 4; Plate 4, figure 1; Plate 6, figures 4-5.

The type, and only known specimen, consists of somewhat less than a fifth of a volvation representing a portion of a phragmocone of a very large gyroceracine. The fragment has a ventral radius of curvature of 13 cm. The cross section is depressed, but with the dorsum nearly as convex as the venter, (Plate 4, fig. 1) both well rounded and lacking the ventral angulation and the dorsal flattening found in most other members of the genus. The cross section at the base of the specimen is 50 mm. high and 70 mm. wide. The width of the shell increases from 70 mm. to 78 mm. in the basal 50 mm., while the height does not increase. Beyond this point the weathering of the left side of the specimen and the venter makes accurate reconstruction of the proportions impossible. The shell height apparently does not increase beyond 50 mm. to the adoral end, though the width continues to increase apparently at the uniform rate indicated in the basal portion, and probably attained there a width of about 90 mm.

Sutures are straight and transverse over the venter but develop faint broad lobes on the dorsum. The basal septum is evenly curved, with a depth of 10 mm., one fifth the height of the shell at this point. The siphuncle is located close to the venter. Its structure in section has not been observed. The camera is closely spaced, eight occurring in a length equal to the adoral shell height of 50 mm. The entire specimen is septate, but the septa are not preserved throughout, and on the adoral end even the sutures are faint. The basal camera is only 5 mm. deep, but at the adoral end a camera 10 mm. deep is shown. The adoral increase in depth is rapid adapically, but the depth of the camera is nearly uniform over the greater part of the length of the shell. No trace of the shell or surface markings remains.

Discussion. — This species is at once distinguished by the nearly equal rounding of dorsum and venter in cross section. In spite of this, there is still a trace of the dorsal lobes of the sutures which distinguish other members of the genus and which are generally associated there with a more flattened dorsum. In section this species is approached only by S. gibbosum of the lthaca shale. In that species, the sutures are more strongly modified, the camera are much more closely spaced, and probably the dorsum there was actually much more strongly flattened in section than was the venter. In section S. lentiepum is the most generalized of our species, upon the dangerous assumption that a simple cross section is generalized. However, it was apparently not primitive, for the flattened dorsum appears to be a primitive character. It is interesting to note that, although the flattening of the dorsum has been lost in this species, the dorsal lobe of the sutures, a normal result of such a condition in a cross section, has nevertheless, been retained.

The shell, when complete, must have been a gyroceracine of very appreciable proportions. Even assuming that the part of the phragmocone represented by the type was near to a very short living chamber, the shell must have encompassed about two volutions, describing a disc at least ten inches across. This would be greater were the actual radius of curvature of the venter considered as original, but there is clear evidence that apparent curvature of the shell has been somewhat decreased by flattening.
The type, in spite of its badly weathered condition, shows the characters of the species very clearly. As can be seen from the illustration, a portion had been removed from the base of the specimen by making two cuts with a saw. I have restored this section in place with plasticine before photographing the type. This section shows that the septa are very incompletely preserved, and adds insult to injury by just missing the siphuncle. It should be clearly understood that this sectioning was done before the specimen came into my hands, and that I had nothing to do with it. I did not attempt to grind further to expose the siphuncle. The poor preservation of the septa made it seem very dubious whether the siphuncle was preserved, and to reach the siphuncle about 4 mm. of the larger part of the specimen would have been lost. The apparent siphuncle shown in Plate 3, figure 4 is adventitious.


_Occurrence._ — Hamilton beds, Bosanquet township, Ontario. Probably from the Hungry Hollow formation, the equivalent of the Centerfield limestone of New York.

*Stereocteras gibbosum* Flower, n. sp.

_Plate 2, figure 3; Plate 4, figure 3._

The holotype, and only known specimen, consists of a vertically crushed portion of a gyroceracocone, 160 mm. in length, consisting of ten camere and a complete mature living chamber. The shell is curved, the venter convex, with a radius of curvature of 15 mm. for the apical half of the specimen, the adoral half becoming straighter. The dorsum is correspondingly concave. In its present condition the shell expands from 40 mm. and 85 mm. to 35 mm. and 120 mm. in the basal 90 mm. In the next 70 mm., it contracts to 40 mm. and 105 mm. at the aperture. The venter expands uniformly to the aperture vertically, but laterally the sides become convex over the mature living chamber and approach each other in the adoral half so that the aperture is constricted laterally.

The cross section of the shell has been distorted by vertical flattening. However, it is evident that the dorsum, though slightly flattened, was broadly convex, while the venter was more highly arched. It was apparently devoid of a ventral keel, though flattened slightly ventrolaterally and more strongly curved in the central portion.

The sutures form low broad saddles over the venter, lateral lobes, and a dorsal saddle which is strongly flattened in the greater part of its course over the dorsum. No trace of the siphuncle remains.

The surface markings are strongly impressed upon the internal mold. They consist of rugose lines of growth which are transverse dorsally, but slope apicad on the venter surface to a broad but prominent V-shaped hypomonic sinus.

_Discussion._ — The cross section showing the rounded venter with an obscure vestige of a keel, the flattened dorsum, and flattening of the dorsal sutures, together with the very broad form, indicate that this is a typical *Stereocteras*. The most amazing feature of the species is the gibbous living chamber and the laterally contracted aperture. Unfortunately, this is the only species of *Stereocteras* of which a mature aperture is known. This leaves to conjecture the question whether in other species the living chamber may be slightly
gibbous laterally as well. This tendency is not completely unexpected in the genus, for it is obviously allied to the breviconic genus *Brevicoceras*, which is essentially a greatly shortened edition of *Stereotoceras* with the curvature much reduced. Whatever the habit of the genus may have been as to the living chamber, probably the contracted aperture was not universally shared. *S. impressum* shows in the adoral part of the phragmocone a vertical contraction of the shell which presumably continued over the living chamber.

*S. gibbosum* is another of those irritatingly rare species which is known only from the holotype. From *S. lentiepansa* of the Hamilton of Ontario, it differs materially in the suture pattern and also in the much closer spacing of the septa on the dorsum. It was probably a much more strongly curved species, and evidently the dorsum was much more prominently flattened in its original state.

**Holotype.** — Cornell University, No. 5548.

**Occurrence.** — Ithaca shale, Upper Devonian, from the old University quarries, now filled in, in the middle part of the Ithaca formation, located below McGraw Hall on the Cornell University campus.

*Stereotoceras impressum* Flower, n. sp.

Plate 3, figure 3: Plate 4, figure 2; Plate 5, figures 4-5.

The holotype is a portion of an internal mold of the outer whorl of a large gyroceracon, retaining the extreme base of a living chamber. The cross section is strongly triangular at the base, the dorsum being very faintly concave, the umbilical shoulders strongly rounded, the greatest width being attained two-fifths of the distance from the dorsum to the venter. Ventrad of this point the curvature of the sides is reduced as they converge to a rounded, but well-defined, ventral keel. The height is 57 mm., the width 62 mm. In the length of the specimen, 125 mm. on the venter, 123 mm. on the dorsum, the dorsum has become broader and flatter, the trace of the concavity in its center lost. The point of greatest width is one-third the distance from the dorsum to the venter. Here the height has decreased to 50 mm., while the width has increased to 64 mm.

The shell is only very gently curved, the average radius of curvature being 20 mm. for the ventral profile.

The sutures are straight and transverse to the curving axis of the shell on the ventral surface. On the dorsum a median rounded lobe is flanked by a pair of low rounded saddles. The 12 camere of the type vary rather erratically from 9 mm. to 12 mm. in depth on the midventral region. Six camere occupy a length equal to an adoral shell width of 62 mm., and five and a half in a length equal to the corresponding height of 57 mm.

Only an obscure trace of the siphuncle can be seen at the base of the specimen. It lies close to the venter. No trace of the shell is preserved. The internal mold bears evidence of obscure longitudinal markings which were probably a feature of the interior of the shell rather than the exterior and might even represent the slightest vestiges of cameral deposits.

**Discussion.** — The species is a singular one in that, in a portion of a shell so slightly curved as to appear cyrtocoic rather than gyroconic, there is a concavity of the dorsum. Such a dorsal concavity is a feature ordinarily associated with coiling tight enough to result in an impressed zone. For this reason, the presence of an impressed zone has often been inferred from such a concavity alone, when only a portion of an outer whorl is available for study.
In certain of the Rutoceratidhe, notably in *Homodelphoceras* and *Tetraodonoceras*, the concave dorsum is clearly developed in shells in which the whorls are free throughout life. This appears to be true also of *S. impressum*.

The species, when complete, must have attained rather large proportions and must have represented a coil of better than a foot and a half across. We have no indication whether the early portion of the shell was so tightly coiled as to develop an impressed zone or not; in general, such impressed zones on the dorsum of a mature whorl indicate impression in the earlier stages. If so, this species was probably one which was initially gyroceraconic, possibly with the whorls later coming into contact for a short distance and then becoming free. *S. vetustum* of Bohemia has the whorls in contact from an early stage. However, in *S. oppletim*, the whorls are only approaching contact at the completion of the second whorl, and are separated, indeed, widely separated, well beyond the completion of the first whorl as can be seen from our photograph (Plate 1, figure 1).

Nothing resembling this amazing species has been found in the Upper Devonian anywhere in the world so far as I am aware. The species is evidently a rare one, for the holotype is the only known specimen. In spite of the extensive collections which have been made from the Naples beds, not another fragment referable to the species, or indeed at all similar to it, has yet come to my attention.

Holotype. — New York State Museum, No. 10519.

Occurrence. — From the Cashaqua shale, Naples, N. Y.

**Stereotoceras vetustum** (Barrande)

*Nautilus vetustus* Barrande, 1865, Système Silurien du centre de la Bohême, vol. 2, text I, p. 125, pl. 35, 1866-67, fig. 2-5.


This species, referred to *Nedyceras* by Hyatt, possesses several characteristics which bar it from the genus. The section, flattened on the dorsum and rounded on the venter and faintly subtriangular, is correct for that genus, but also for *Stereotoceras*. The rate of enlargement is typical of *Stereotoceras* but too great for any typical *Nedyceras*. Most important, there is no trace of trochoeroid curvature, but the shell is that of a gyroceracon in which the whorls were barely in contact. It shows all the features of a *Stereotoceras* in an early stage of evolution, for the dorsal sutures have not yet developed the faint lobes which are characteristic of advanced members of the genus.

The shell is coiled, apparently with the whorls either very narrowly separated or barely in contact. No impressed zone is developed. The type consists of slightly more than one volution, but I should concur with Barrande in believing that the complete shell probably consisted of two or three whorls.

The cross section at the base of the specimen is broadly depressed, the dorsum scarcely convex, the sides strongly rounded, the venter broadly arched. At this stage the section is broader in proportion to the height than the observed stages of *S. lenticepsum*, where the dorsum is more convex, However, in the growth of the shell the height apparently increases much more rapidly than the width, so that in half a volution the width of the shell is scarcely greater than the height. If this were to continue in later parts of the shell, although I have no reason to believe that it does, the complete conch would have more the aspect of a *Nephriticeras* than that of a *Stereotoceras*. However, the relationships are made evident not only by the cross
section and sutures of the known stages, but also by the marginal position of the siphuncle, which is never ventral in the Rhadinoceratidae and normally lies dorsal of the center of the shell.

The siphuncle is illustrated as composed of segments that are slender but nummuloidal, evidently with gyrocoanic necks, though the expansion of the segment within the camera is more gradual than that of either *S. opuletum* or *S. canadense*. No trace of organic deposits has been found in the species. This is not conclusive, for evidently neither of the specimens which Barrande figured represents a mature shell.

No trace of the shell is preserved. The internal mold is smooth and gives no indication of the surface features.

This species is typical of *Stereotoceras* in form, cross section, and siphuncle. In cross section, it is intermediate between those species with a convex dorsum, *S. halli*, *S. gibbosum*, *S. lentiepansum*, *S. canadense*, and those with the dorsum definitely flattened or concave, *S. opuletum* and *S. impressum*. The cross section of the early part is probably most closely approached by *S. canadense*, but that species differs in that the curvature is much less marked, and the rate of vertical expansion of the shell is much greater. Further, *S. vetustus* is essentially a tarphycotic shell, while *S. canadense* was gyroconic or, at the most, gyroconic.

I have had opportunity to study a specimen in the collections of the Museum of Comparative Zoology (No. 5026) labeled by Hyatt "*N. sp. Group of (N.) vetustus* sp. of Barrande. A nautilian? form allied to *vetustus* but with torticone form." This is an undescribed species belonging to *Nedyoceras*, and probably accounts for Hyatt's attribution of *Nautilus vetustus* to that genus (Hyatt, 1864).

**Occurrence.**—From the calcareous band G3, Middle Devonian, Hlubocep, Bohemia.

*Stereotoceras* (?) *cruciferum* (Hall)

Plate 2, figure 4.

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*Gomphoceras* (?) *cruciferum* Hyatt, 1898, Palaeont. Amer. vol. 2, No. 9, p. 70.


This species is known only from the single specimen upon which Hall based his description of the species. It is a badly crushed shell, the most conspicuous feature of which is the convex surface of the septum, showing a siphuncle and a cruciform pattern on the septal surface. In addition, below the septal surface, as the specimen is oriented both by Hall and on our own plates, there are faint traces of the shell showing that this was a curved and not a straight species. On this basis, the shell appears to be a gyroceracone or a gyrococone. Further, the preserved portion of the shell wall shows faint traces of several sutures.

The septal surface is 44 mm. high and 40 mm. wide, the siphuncle is located 9 mm. from the venter and is 2 mm. in diameter at the septal foramen. Dorsal of the siphuncle is a long, raised area; a shorter one lies to the venter, while fainter lateral markings join these to form the cruciform pattern which gave the species its name. These markings are clearly the molds of cameral deposits. On this basis, I tentatively refer this species to *Stereotoceras*. It is atypical of the genus in the narrow condition of the whorl and in the
distance from which the siphuncle is removed from the venter. However, no other curved genus is as yet known to possess cameral deposits in the Devonian. The cross section is typical in that the dorsum is somewhat flattened, the venter more arched and narrowly rounded. The section does not, however, recall that of Gyrodocyceras, which it typically a much more strongly compressed shell, in which the siphuncle, as in typical Stereotoceras, is close to the venter, and which is known to contain actinosiphanate deposits.

The generic position of this species is still a perplexing matter. I have removed it to Stereotoceras because it seems to fit here better than in any other described genus. It has no apparent affinities with any breviconic shell, and it is difficult to see why Kindle and Miller attempted to place the species in the genus Brevicoceras, which was some improvement over leaving it in Gomphoceras, but not much.

In spite of the large amount of material that has been collected from the Schoharie grit, no additional forms have been found that can be recognized as conspecific with Hall's type of S. cruciferum.

Holotype — New York State Museum, No. 12185/1.

Occurrence. — In the Schoharie grit, Schoharie, N. Y.

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PLATES

The cost of plates has been met by the New York State Museum.
Except where otherwise indicated, all figures are natural size.

PLATE 1 (34)
### EXPLANATION OF PLATE I (34)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-4.</td>
<td><em>Stereotoceras appletum</em> Flower, n. sp.</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>(2) Septal (3) lateral and (4) dorsal views of adoral part of phragmocone.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A small portion, probably not more than four camera, is missing between</td>
<td></td>
</tr>
<tr>
<td></td>
<td>these two portions.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&quot;Devonian of Ohio&quot; probably Delaware limestone.</td>
<td></td>
</tr>
<tr>
<td>5.</td>
<td><em>Stereotoceras halli</em> Flower, n. sp.</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>Holotype, New York State Museum, No. 13565/1. Original of</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Trochoceras expansum</em> Hall, 1878, Paleontology of New York, vol. 5, pt. 2,</td>
<td></td>
</tr>
<tr>
<td></td>
<td>pl. 111, fig. 5. Dorsal aspect. Schoharie grit.</td>
<td></td>
</tr>
</tbody>
</table>
### EXPLANATION OF PLATE 2 (35)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-2. Stereotoceras oppletu Flower, n. sp.</td>
<td>13</td>
</tr>
<tr>
<td>Holotype. (1) Enlargement of section of ventral face, showing siphuncle, also traces of mural deposits in section. (2) Ventral view of same specimen, × 1, consisting of the adoral camera shown in pl. 1, fig. 1.</td>
<td></td>
</tr>
</tbody>
</table>

| 3. Stereotoceras gibbosum Flower, n. sp. | 20 |
| Holotype, ventral view, × ½. Cornell University, No. 5548. Ithaca shale, Cornell University Quarries, Ithaca, N. Y. See also pl. 4, fig. 3. |

| 4. Stereotoceras (?) cruciferum (Hall) | 23 |
| Holotype, septal view. New York State Museum, No. 12185/1. Schoharie grit, Schoharie, N. Y. |
EXPLANATION OF PLATE 3 (36)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-2.</td>
<td><em>Stereotoceras oppticum</em> Flower, n. sp.</td>
</tr>
<tr>
<td>(1)</td>
<td>Holotype, ventral view of region immediately preceding that shown in Pt. S, fig. 2, showing molds of cameral deposits.</td>
</tr>
<tr>
<td>(2)</td>
<td>Paratype, U. S. N. M. lateral view × ½. From the Alpena limestone, Galesite, Michigan, Michigan Limestone and Chemical Company, two miles east of Roger’s City, Mich.</td>
</tr>
<tr>
<td>3.</td>
<td><em>Stereotoceras impressum</em> Flower, n. sp.</td>
</tr>
<tr>
<td>4.</td>
<td><em>Stereotoceras lenticelansum</em> Flower, n. sp.</td>
</tr>
</tbody>
</table>
EXPLANATION OF PLATE 4 (37)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Stereotoceras lentiepansum Flower, n. sp.</td>
<td>19</td>
</tr>
<tr>
<td>2. Stereotoceras impressum Flower, n. sp.</td>
<td>21</td>
</tr>
<tr>
<td>Holotype, seen from the adoral end. New York State Museum, No. 10,519. Cashaqua shale, Naples, N. Y. Venter at top.</td>
<td></td>
</tr>
<tr>
<td>3. Stereotoceras gibbosum Flower, n. sp.</td>
<td>20</td>
</tr>
<tr>
<td>Dorsal view of holotype, X 1. Cornell University, No. 5548. Ithaca shale, Upper Devonian, University Quarries, Ithaca, N. Y.</td>
<td></td>
</tr>
</tbody>
</table>
### EXPLANATION OF PLATE 5 (38)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-3. <em>Stereotoceras canadense</em> Flower, n. sp.</td>
<td>17</td>
</tr>
<tr>
<td>Holotype. (1) Ventral (2) lateral and (3) dorsal views. Canada Geological Survey, Victoria Memorial Museum, Onondaga limestone, Walpole, Ontario.</td>
<td></td>
</tr>
<tr>
<td>4-5. <em>Stereotoceras impressum</em> Flower, n. sp.</td>
<td>21</td>
</tr>
</tbody>
</table>
EXPLANATION OF PLATE 6 (39)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-3. Stereotoceras eicheri Flower, n. sp.</td>
<td>18</td>
<td>Holotype. (1) Dorsal (2) lateral and (3) ventral views. The ventral surface is badly weathered. Buffalo Museum of Science, Stafford limestone, South Buffalo, N. Y.</td>
</tr>
</tbody>
</table>
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No. 25: THE PELECYPOD GENUS VENERICARDIA IN THE PALEOCENE AND EOCENE OF WESTERN NORTH AMERICA

By
Pedro Verástegui
Stanford University

September 7, 1953

Paleontological Research Institution
Ithaca, New York, U.S.A.
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# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abstract</td>
<td>5</td>
</tr>
<tr>
<td>Acknowledgments</td>
<td>5</td>
</tr>
<tr>
<td>Introduction</td>
<td>6</td>
</tr>
<tr>
<td>Material</td>
<td>11</td>
</tr>
<tr>
<td>Dental notation for <em>Venericardia</em></td>
<td>11</td>
</tr>
<tr>
<td>Hinge anomalies</td>
<td>12</td>
</tr>
<tr>
<td>Conclusion</td>
<td>13</td>
</tr>
<tr>
<td>Systematic descriptions</td>
<td>16</td>
</tr>
<tr>
<td><em>Venericardia</em></td>
<td>16</td>
</tr>
<tr>
<td>Subgenus <em>Pacificor</em>, n. subgenus</td>
<td>17</td>
</tr>
<tr>
<td>V. (Pacificor) <em>mulleri</em>, n. sp.</td>
<td>20</td>
</tr>
<tr>
<td>V. (P.) <em>nelsoni</em>, n. sp.</td>
<td>21</td>
</tr>
<tr>
<td>V. (P.) <em>susanaensis</em>, n. sp.</td>
<td>22</td>
</tr>
<tr>
<td>V. (P.) <em>durhami</em>, n. sp.</td>
<td>23</td>
</tr>
<tr>
<td>V. (P.) <em>hertleini</em>, n. sp.</td>
<td>24</td>
</tr>
<tr>
<td>V. (P.) <em>oregonensis</em>, n. sp.</td>
<td>25</td>
</tr>
<tr>
<td>V. (P.) <em>argentea</em>, n. sp.</td>
<td>25</td>
</tr>
<tr>
<td>V. (P.) <em>lutmani</em> Turner</td>
<td>26</td>
</tr>
<tr>
<td>V. (P.) <em>diabloensis</em>, n. sp.</td>
<td>27</td>
</tr>
<tr>
<td>V. (P.) <em>calafia</em> Stewart</td>
<td>28</td>
</tr>
<tr>
<td>V. (P.) <em>gabbi</em>, n. sp.</td>
<td>29</td>
</tr>
<tr>
<td>V. (P.) <em>weaveri</em>, n. sp.</td>
<td>30</td>
</tr>
<tr>
<td>V. (P.) <em>clarki</em> Weaver &amp; Palmer</td>
<td>32</td>
</tr>
<tr>
<td>V. (P.) <em>hornii</em> (Gabb)</td>
<td>33</td>
</tr>
<tr>
<td>V. (P.) <em>vallecitosensis</em> (Vokes)</td>
<td>35</td>
</tr>
<tr>
<td>V. (P.) <em>carlosensis</em> (Vokes)</td>
<td>36</td>
</tr>
<tr>
<td>V. (P.) <em>transversaria</em>, n. sp.</td>
<td>37</td>
</tr>
<tr>
<td>V. (P.) <em>taliferroi</em>, n. sp.</td>
<td>38</td>
</tr>
<tr>
<td>V. (P.) <em>lisa</em>, n. sp.</td>
<td>39</td>
</tr>
<tr>
<td>Subgenus <em>Glyptoactis</em></td>
<td>40</td>
</tr>
<tr>
<td>V. (Glyptoactis) <em>keenae</em>, n. sp.</td>
<td>41</td>
</tr>
<tr>
<td>V. (G.) <em>memastersi</em>, n. sp.</td>
<td>42</td>
</tr>
<tr>
<td>V. (G.) <em>domenuginica</em> Vokes</td>
<td>43</td>
</tr>
<tr>
<td>V. (G.) <em>marksi</em>, n. sp.</td>
<td>44</td>
</tr>
<tr>
<td>Subgenus <em>Venericor</em></td>
<td>45</td>
</tr>
<tr>
<td>V. (Venericor) <em>venturensis</em> Waring</td>
<td>45</td>
</tr>
<tr>
<td>V. (V.) <em>simiana</em>, n. sp.</td>
<td>47</td>
</tr>
<tr>
<td>Subgenus <em>Leuroactis</em></td>
<td>48</td>
</tr>
<tr>
<td>V. (Leuroactis) <em>schencki</em>, n. sp.</td>
<td>50</td>
</tr>
</tbody>
</table>
V. (L.) crescentensis Weaver & Palmer ............................................. 51
V. (L.) alisoensis, n. sp. ................................................................. 52
V. (L.) merriami Dickerson ............................................................. 53
V. (L.) smileyi (Vokes) ................................................................. 55
V. (L.) aragonia Arnold & Hannibal ............................................... 56
V. (L.) joaquinensis (Vokes) .......................................................... 60
V. (L.) vokesi, n. sp. ................................................................. 61
V. (L.) popenoei, n. sp. ................................................................. 62
Bibliography .................................................................................. 64

ILLUSTRATIONS

Plates 1-22 West Coast Paleocene and Eocene Jenericardia .......... 74-112
Chart 1 Diagram of interior of Jenericardia imbricata Lamarck .... facing 10
2 Possible phylogenetic relationship of the West Coast Paleocene and Eocene Jenericardia ................................................ facing 12
3 Subgenera and species of Jenericardia from Paleocene and Eocene of western North America ................................. 15
THE PELECYPOD GENUS VENERICARDIA
IN THE PALEOCENE AND EOCENE
OF WESTERN NORTH AMERICA

By

PEDRO VERASTEGUI

ABSTRACT

This paper presents the results of a systematic study of the pelecypod genus Venericardia from the Paleocene and Eocene of western North America. An attempt is made to establish the relation of the western American Venericardia to the species of that genus in other American provinces. In order to clarify the taxonomy of the genus, it has been necessary to introduce a new subgenus, Pacificor, which includes a group of species characteristic of and almost restricted to the North Pacific side of the Americas.

The venericard fossils of western North America belong to the subgenera Glypsoactis, Venericardia, Leuroactis, and the newly proposed Pacificor. It may be noted that Venericardia, s.l., does not occur in this area. Twelve species have been previously described from this area. Twenty-one new species are now added, and the previously suppressed V. (Leuroactis) merriami Dickerson is reinstated. Each species is described and illustrated together with a diagram of the hinge structure. Keys are given for the subgenera and species. The possible phylogenetic relationship among the species of the western American Venericardia, s.l., is shown in a chart.

All the species studied appear to have restricted geologic ranges. The purpose of this paper is to furnish aid for their identification and thus make them of more use as age indicators. It is hoped that the results presented will enable field workers to interpret more precisely the biostratigraphic significance of the associated molluscan assemblages which, in turn, may aid in making local or regional correlations.

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Financial assistance for this work was provided chiefly by separate fellowships granted me by the United States Geological Survey, by the Empresa Petrolera Fiscal del del Peru, and by the Honolulu Oil Corporation. I am grateful to those organizations and to their personnel who were instrumental in providing me with these grants, namely: Dr. D. W. Johnston of the United States Geological Survey, Ing. A. Gábrera La Rosa and Dr. C. Petersen of the Empresa Petrolera Fiscal del Peru, and Messrs. A. C. Mattei, E. W. Adams, and J. H. McMasters of the Honolulu Oil Corporation. Additional financial assistance came from research grants administered by Stanford University and contributed by Messrs. W. W. Valentine, the late E. R. Hall, and A. N. Dusenbury, Jr. I appreciate the kindness of the donors and the help of Dr. A. I. Levorsen, Dean, and of the rest of the faculty of the School of Mineral Sciences of Stanford University in obtaining these grants.

The drafting of the phylogenetic chart and the typing and assembling of this manuscript were made possible through the assistance of the Shell Grant for Fundamental Research which is here gratefully acknowledged.

The drawings illustrating the morphology of Venericardia shells were made by Mr. Walter Zawoisky of Stanford University.

INTRODUCTION

During the century since the first paper appeared on Tertiary Paleontology of western North America, the literature has become voluminous. Many of the earlier works, with their brief descriptions and poor illustrations, now seem inadequate for proper understanding of the fauna. The present study of the genus Venericardia has been undertaken as a step toward remedying these defects and clarifying some of the erroneous conclusions.

Venericardia, erected by Lamarck in 1801, has been an important genus to stratigraphers because of the narrow range in time of many of the species. Even more use might have been made of it had authors recognized the significance of seemingly slight differences in form and sculpture. A survey of the geographic distribution of the genus and of the morphology of subgenera into which it has been divided may yield information useful for the solution of certain problems in Paleocene and Eocene biostratigraphy.

A thorough study of the genus Venericardia has demonstrated clearly that some subgenera are not only of biological importance but are also of biostratigraphic significance. For example, referring to V. (Venericor) planicosta and its relatives, Olsson (1929) pointed out that it is "the most characteristic and reliable guide fossil for the marine American Eocene." A decade later, Gardner and Bowles said even more impressively: "As guide fossils the members of the planicosta group are . . . among the most significant of the Mollusca." These are modern paraphrases of Conrad's classical statement "finger-post of the Eocene," made by him in 1855 in the discussion of "Cardita planicosta" from the Eocene of California.

With better understanding of the complexity of the genus Venericardia, Stewart (1930) introduced three new subdivisions: subgenus Venericor for forms having
planicostate ribbing; "section" Leuroactis for those having a straight medial cardinal (3b); and subgenus Glyptuactis to include forms with a curved elongate right cardinal (3b) and a small anterior pustule or lateral. These subdivisions have been accepted by most subsequent workers, as they contributed to our understanding of the phylogenetic lineages, some of which are traceable as far back as Cretaceous time.

The "section" Leuroactis, here treated as subgenus, and the new subgenus Pacificor have as great a stratigraphic value in spacial and time relations as has the subgenus Venericor. Representatives of these subgenera are confined to the Paleocene and Eocene and have a wide geographic distribution.

In order to comprehend the complexity of the biologic and stratigraphic problem of Venericardia, one must consider the spacial and chronologic distribution of its component subgenera and species.

The first few representatives of Venericardia appeared in Africa, America, Asia, Europe, and Oceania at the close of the Cretaceous. With the dawn of the Cenozoic Era, groups of Venericardia began to flourish in restricted areas and from these centers or loci of dispersal species subsequently spread to various Paleocene and Eocene seas.

In this regard, it is interesting to note that G. G. Simpson (1940), studying the temporal pattern of mammalian distribution, quotes a postulate from Willis, "new forms of life originate in definite, limited regions from which as centers they expand slowly and steadily as time goes on." Simpson himself added, "that, as a rule with exception, at any given point in time, the area occupied by a form of life should be directly proportional to the age of that form of life." Furthermore, "The theory involves various interesting corollaries, such as the belief that endemics or isolated forms of life with narrow distribution are usually young forms that originated where they are found and are just starting on their careers of expansion." This theory may apply to the distribution of the Venericardiae. It is true that the distribution of any group of living things, and, in this particular case, of the venericards may have been unfavorably affected by such factors as change in currents, temperature and salinity of sea water, fluctuation of sea shores, closing of portals, and other geological events which may impede or completely obstruct the dispersal of marine organisms from their original loci. These unfavorable changes or obstacles may have caused scarcity or even total absence of species in a given area. Under normal conditions, however, the distribution of organisms is primarily dependent upon the latent strength or potentiality of a stock for areal expansion after it has attained its full strength in the area of its origin. The reader should keep in mind that what is attempted here is to analyze the geographic dispersal of organisms and not the evolutionary processes which are far beyond the scope of this paper.

The data bearing upon the geographic distribution of the West Coast venericards are analyzed for the subgenera Venericor, Leuroactis, and Pacificor. The subgenus Glyptuactis, which ranges from Cretaceous to Miocene and possibly higher, is world-wide in distribution and presents a more complex problem. It is, therefore, not considered at length in this report.
It may be mentioned in passing that no species of *Venericardia*, s. s., are known from the Eocene and Paleocene of the West Coast of North America.

So far two *Venericor* species have been recorded from the Pacific side of America: *Venericardia simiana*, n. sp., and *V. venturenisis*; they are closely related to *V. mediaplata* Gardner and Bowles and *V. regia* Conrad respectively, both of which are from the Gulf Coast.

More than 15 species of *Venericor* are recorded in the Gulf Coast Province of North America from rocks of Paleocene and Eocene ages. The abundance of species in this province and their relative scarcity in other provinces permits the conclusion that the Gulf Coast area is the locus or center of dispersal of *Venericor*.

Only two species of *Venericor* are reported in the European area: *Venericardia (Venericor) duponti* Cossmann and *V. (V.) planicosta* Lamarck. *V. duponti* from the Montian stage has an outline and a general aspect which most closely suggests *V. mediaplata* Gardner and Bowles (1930, p. 101). The other European *Venericor*, *V. planicosta*, type species of the subgenus, is the form to which great importance has been ascribed by American paleontologists.

No species of *Venericor* are reported from the upper Paleocene of the Paris Basin. Regarding this Rutsch (1937, p. 156) said, "The 'Planicosta Group' is strikingly missing in the higher part of the Paleocene (in the Landenian, Thanetian and Spathian Stages) of the European regions . . . although big venericards (*V. pectuncularis* Lamarck), are not missing in it." Furthermore, Rutsch clearly pointed out that *V. planicosta* Lamarck first appeared in Europe in the Ypresian stage and is not to be regarded as a direct descendant of *V. duponti* but undoubtedly as a migrant form from the West (America). Thus, it seems that in the Paris Basin there is a gap in the stratigraphic range of the Planicosta Group during late Paleocene time. It is felt now that *V. planicosta*, which Lamarck described from the Lutetian stage as "*Testa crassissima, costis plantis des. env. de Paris" is a direct descendant of that Ypresian form.

The venericards from the marine Tertiary of northwestern Peru were first reported by Woods (1922) under the heading "*Venericardia planicosta* (Group)."

A few years later Olsson (1928-1929) described eight new species from the same region. Gardner and Bowles (1930) revised almost all the Peruvian venericards. Their comments are enlightening.

*Venericardia negritensis* Olsson from the Negritos formation was correlated by Stewart (1930) with "*V. planicosta*" from the Wilcox formation, Alabama. Gardner and Bowles suggested that the species which Stewart probably had before him was *V. bashiplata* Gardner and Bowles from Woods Bluff, Alabama.

In the Stanford Paleontological Collection there are several specimens from the Tertiary of Peru, some of them labeled as being from the Negritos formation. Some of these were obtained through the kindness of G. Petersen, Zorritos, Peru. A comparative study of these specimens and of illustrations of the Gulf Coast venericards reveals that *V. negritensis* is a close relative of *V. bashiplata* Gardner and Bowles. Both forms have in common the same number of ribs and the same general pattern of the high hinge plate. *V. bashiplata*, however, is subquadrate in
outline and is more convex. Also at hand was a Peruvian specimen which can be identified with the one illustrated by Woods in Bosworth (1922). In its clean-cut ribs and rather narrow interspaces it resembles \textit{V. nauplata} Gardner and Bowles more than it does \textit{V. huijuiana}. (The new name for this Peruvian species is withheld pending further study of the \textit{Venericardias} of that region).

These two Peruvian forms, so closely related to those of the Wilcox formation, suggest a dispersal of the Gulf Coast \textit{venericards} in lower Eocene times. No other \textit{Venericor} is recorded either in the Paleocene or from higher horizons of the Eocene in the Peruvian Basin. Here again the two \textit{Venericor} species, the only ones so far known from Peru from the \textit{Venericor} Group, are regarded as migrant forms from the Gulf Coast Province, for the other species of \textit{Venericardia} in Peru belong to \textit{Leuroactis}, \textit{Pacificor}, or \textit{Glyptoactis}.

The pattern of distribution of the new subgenus \textit{Pacificor} is different from that of \textit{Venericor} in that the subgenus \textit{Pacificor} is not recorded in Europe and its center of expansion is western North America. \textit{Pacificor} ranges from the Paleocene through the end of the Eocene, as does also \textit{Venericor}.

In the Paleocene of the Gulf Coast Province there are some \textit{venericards} which probably belong to \textit{Pacificor}. Unfortunately, lack of material and adequate illustrations make impossible at this time any further comparison or positive identification. Nevertheless, it is mentioned here that \textit{V. huijuiana} Gardner and Bowles from the Midway is probably related to \textit{V. argentea}, n. sp., from the Paleocene of California. Although \textit{V. huijuiana} has fewer ribs (22-24), their tripartite character is the same as in \textit{V. argentea}. Further relationship between these two species is seen in the similarity of the hinges and in the broad inflation of the umboonal region. \textit{V. franciscae} Gardner and Bowles, from the late lower Eocene, is another form which undoubtedly may be regarded as a \textit{Pacificor}. The excellent illustration of the holotype of this species (Gardner and Bowles, 1930, pl. 41, figs. 1-2) shows the typical pseudoscutcheon of \textit{Pacificor} and the characteristic \textit{Pacificor} ribbing. The pattern of the hinge teeth, especially of the medial cardinal (3b) is strikingly similar to that of \textit{V. valleciitosensis} (Vokes) from the middle Eocene of California.

In Peru \textit{Pacificor} appears to be represented by \textit{Venericardia talara} Olsson from the Chaeca formation, middle Eocene. The sculpture of this species resembles that of \textit{V. transversaria} of California.

The sudden appearance of the subgenus \textit{Leuroactis} in the lower Eocene of America is of a particular interest, since no recognizable ancestors are found in any of the Tertiary marine basins of the Gulf Coast province, northwestern Peru, or west North America. On the West Coast of North America the stratigraphic range of the subgenus \textit{Leuroactis} is from lower Eocene to upper Eocene. In the Gulf Coast region and in northwestern Peru the group is recorded only in the lower and middle Eocene. No occurrences of \textit{Leuroactis} have been reported in the Paris Basin or elsewhere outside of America.

The earlier (lower Eocene) representatives of \textit{Leuroactis} (\textit{Venericardia pilskyi} from Alabama, \textit{V. pacifica} Olsson from Peru, and \textit{V. schencki}, n. sp., from California) in each of the separate American basins show only a superficial similarity to
each other. However, by the late lower Eocene, the affinity of some of the species 
(I. aragonia-I. horatiana; I. stewarti-I. parinensis) become strikingly manifest 
in their morphological similarities. This feature makes the subgenus Leuroactis a 
compact taxonomic unit characteristic of and restricted to (endemic of) North and 
South America.

EXPLANATION OF CHART 1

SIZE AND SHAPE OF SHELLS

Figure
1. Venericardia (Pacificor) lutmani Turner
   Size large; shape quadrate; measurements of length and height are indicated by 
   white lines.
2. Venericardia (Leuroactis) aragonia Arnold and Hannibal
   Outline obliquely ovate; size moderately large.
3. Venericardia (Glyptoactis) keenei Verastegui, n. sp.
   Medium-sized shell.
4. Venericardia (Glyptoactis) marksi Verastegui, n. sp.
   Small-sized shell.

CONVEXITY, NATURE OF BEAK AND UMBO

Figure
5. Venericardia (Leuroactis) aragonia Arnold and Hannibal
   Beak pointed. The distance between the arrows indicates the dimension of convexity.
6. Venericardia (Leuroactis) aragonia Arnold and Hannibal
   Lunular groove points backward as indicated by arrows.
7. Venericardia (Pacificor) susanaensis Verastegui, n. sp.
   Lunular groove points forward as indicated by arrows.
8. Venericardia (Pacificor) nelsoni Verastegui, n. sp.
   Umbo full or inflated.

CHARACTER OF RIBS AND INTERSPACES (see also Chart 2, figures 1-4)

Figure
9. Venericardia (Pacificor) venturensis Waring
   Ribs flat, tending to become T-shaped and constricting the U-shaped interspaces.
10. Venericardia (Pacificor) venturensis Waring
    Distinet umbonal ridge with ribs perceptibly narrower in the posterior area.
11. Venericardia (Pacificor) clarki Weaver and Palmer
    Ribs broadly rounded, fasciculate in the antero-dorsal area. This is typical 
    "PACIFICOR sculpture."

CHARACTER OF HINGES

Figure
12. Venericardia (Pacificor) oregonensis Verastegui, n. sp.
    Hinge low and short.
13. Venericardia (Leuroactis) aragonia Arnold and Hannibal
    Hinge high and short.
14. Venericardia (Leuroactis) aissensis Verastegui, n. sp.
    Ventral margin of hinge sinuous. This species also illustrates well developed 
    nymphal plate.

   All figures are slightly less than one-half natural size. 
   Illustrations by Walter Zawoisky
   Assistant Photographer
   Stanford University
Chart 1

1. Size large
2. Outline obliquely ovate
3. Size moderately large
4. Umbo full or inflated
5. Size medium
6. Size small

1. Quadrade
2. Convexity
3. Beak pointed
4. Backward lanual groove pointing
5. Forward

9. Ribs flat, tending to become T-shaped and constricting the U-shaped interspaces
10. Distinct umboonal ridge narrow ribs in the posterior area
11. Ribs broadly rounded, fasciculate in the antero-dorsal area

12. Hinge low and short
13. Hinge high and short
14. Sinuous ventral margin of hinge

Typical "PACIFICOR sculpture"

Well developed nymphal plate
The species of *Leuroactis* are abundant in northwestern America but are relatively scarce in the Gulf Coast region of America and in Peru. So far, nine species are recognized as belonging to *Leuroactis* in California, Oregon and Washington, three species in eastern North America, and three in Peru. Western North America with the greatest number of species (9) may be regarded as the locus or the center of dispersal of the subgenus.

**MATERIAL**

During the year that was devoted to this investigation, use was made of the large Stanford University Paleontological Collection. In addition, access was had to the extensive collections of the University of California and of the California Academy of Sciences, from which valuable holotypes were loaned to me for study. An additional advantage was the loan of material from the University of California at Los Angeles and from the United States National Museum.

In general the state of preservation of the material at hand was different from that of other provinces, such as the Gulf Coast. Since the study of the hinge plate is essential, careful preparation by use of diamond saw and small electric drill tool was necessary. These mechanical instruments proved to be useful in splitting attached valves thus exposing hinges and other internal characters of shells.

This investigation was greatly facilitated by such previous papers as those of Stewart (1930), Rutsch (1930), and Gardner and Bowles (1939), to which the reader is referred for further discussion of the genera and subgenera and the world distribution of *Venericardia*.

**DENTAL NOTATION AND MORPHOLOGIC TERMINOLOGY OF VENERICARDIA**

The system of notation of *Venericardia* hinge teeth which is followed in this report was devised by Munier-Chalmas. The teeth on the hinge plate are represented as laminae and are numbered from the center of the hinge toward the anterior and posterior margins. Odd numbers apply to the teeth in the right valve, even numbers to those of the left valve. The innermost lamina gives rise to a single cardinal pivotal tooth; the outer laminae each give rise to two teeth arranged in a series of inverted V's over the pivotal tooth.

In *Venericardia* which has a special (diagenodont) type of an heterodont dentition, the pivotal tooth is the anterior left cardinal and is number 2, the others 3a, 3b, etc., "a" standing for anterior and "b" for posterior. The corresponding sockets are indicated by a prime mark ('). Thus, the complete formula for the dentition of *Venericardia*, as shown on Chart 2, figures 5 and 6, is:

right valve 3a 2' 3b 4b' 5b
left valve 3a' 2 3b' 4b 5b'

The morphologic terms which are used in this report in the description of species are illustrated in the following two charts. All drawings are about one-half
natural size. Reference to these sketches removes the possible ambiguity from such expressions as "shell is large" or "shell is small" and also furnishes a standard of reference for such statements as "hinge is high" or "hinge is low and long."

HINGE ANOMALIES

Gardner and Bowles (1939) recorded hinge inversions in Venericardiae of the Gulf Coast of America. In the present study no sinistral *Venericardia* has been found except the one illustrated by Hanna (1925). This specimen, which was identified as "belonging to the low beak variety of *Venericardia hornii*" from San

EXPLANATION OF CHART 2

CHARACTER OF RIBS AND INTERSPACES. (see also Chart 1, figures 9-11)

Figure
1. *Venericardia* (Leuroactis) aragonia Arnold and Hannibal
   Narrow U-shaped inter-spaces near the beak, linear at adolescence, obsolete at maturity.
2. *Venericardia* (Pacificor) transversaria Verastegui, n. sp.
   Ribs with transverse wrinkles.
3. *Venericardia* (Leuroactis) crescentensis Weaver and Palmer
   Ribs obsolete.
4. *Venericardia* (Glyptonactis) keenae Verastegui, n. sp.
   Ribs fasciculate.

HINGE TEETH

Figure
5. Diagram of left valve of *Venericardia*.
   2. — Anterior (pivotal) cardinal tooth.
   3a' — Socket for right anterior cardinal tooth.
   3b' — Socket for right median cardinal tooth.
   4b. — Left posterior cardinal tooth.
   5b' — Socket for right posterior cardinal tooth.

6. Diagram of right valve of *Venericardia*.
   a' — Socket for left anterior (pivotal) cardinal tooth.
   3a. — Right anterior cardinal tooth.
   3b. — Right median cardinal tooth.
   4b'. — Socket for left posterior cardinal tooth.
   5b. — Right posterior cardinal tooth.

SHAPES OF ANTERIOR CARDINAL TOOTH (2)

Figure
7. *Venericardia* (Pacificor) calafia Stewart
   Anterior cardinal (2) cuneate, curved.
   Anterior cardinal (2) blunt.
9. *Venericardia* (Pacificor) hornii (Gabb)
   Anterior cardinal (2) cuneate elongate.
10. *Venericardia* (Pacificor) calafia Stewart
    Median cardinal (3b) scimitar-shaped.
11. *Venericardia* (Leuroactis) joquinensis (Vokes)
    Median cardinal (3b) large trigonal.
12. *Venericardia* (Pacificor) hornii (Gabb)
    Median cardinal (3b) oblique, pointing forward.

All figures are slightly less than one-half natural size. Illustrations by Walter Zawoisky
Assistant Photographer
Stanford University
interspaces U-shaped linear at adolescence obsolete at maturity

ribs fasciculate

ribs obsolete

Anterior Cardinal (2)

cuneate curved

blunt

cuneate elongate

Medial Cardinal (3b)

scimitar-shaped

large trigonal

oblique pointing forward

posterolateral scar

ligamentous pit

pedal muscle scar

anterior angular scar

posterior angular scar

nymph

escutcheon

cord

rigimental groove

5b 4b 3b' 2b 3a 2a 3b 4b 5b
Diego, California, is here identified as *V. (Leuroactis) sp. aff. V*. (*L.*) *vokesi*, n. sp. Although the right valve of this specimen is badly preserved, it nevertheless shows the presence of the esutcheonal cord which is characteristic of *Leuroactis*. Besides the rather straight medial socket (*gh*'), it has the typical sculpture of *Leuroactis* (round ribs and wavy incrementals in the adult stage). This specimen is not conspecific with *V. vokesi* as it has only 18 ribs, an unusually small number of ribs for a normal *Leuroactis* of the middle Eocene of western North America.

A curious development of the dentition was observed (Plate 13, figures 8, 9) in two valves, a right and a left one of different individuals, of *Venericardia (Pacificor) carlosensis* (Vokes). Although these hinges have the normal basic pattern of the species, there are notable anomalies in the dentition. The medial cardinal (*gh*) is distinctly terraced and has the appearance of being tripartite. The elevated central portion is twice as wide as the adjacent lateral portions and is separated from them by deep incisions, indicating that they are supernumerary as teeth. The left valve has its anterior (2) and posterior (4b) cardinals also incised to make room for these adventitious lateral teeth of the abnormal right medial cardinal. The abnormality of this individual specimen is also shown in a peculiar development of sculpture. The front ribs of the right valve are terraced, but only on the posterior side, an abnormal character for venericards. No other venericards possess such an ornamentation. Normally, whenever terracing is developed on the ribs it is in the anterior part of the shell, and the terracing is present on both sides of the rib.

It is inferred that these abnormalities are connected with a change of environment. Vokes mentions *Pelecyora aequilateralis* (Gabb), *Ostrea idriaensis* Gabb, *Loxotrema turrita* Gabb, and *Potamides carbonicola* Cooper as occurring in the same faunule with *V. carlosensis*. All these associated forms suggest water of less than normal salinity. This brackish water environment may also explain the unusual thinness and variability of shape of the *V. carlosensis* shell. Except for these peculiarities, normal individuals of *V. carlosensis* are somewhat similar to *V. vallecitosensis* and may be regarded as a variant of *V. vallecitosensis*, brought about by a change in ecologic condition.

CONCLUSION

The descriptions of species of the genus *Venericardia* from the Paleocene and Eocene of the Pacific Coast of North America are widely scattered in the geologic literature and in many cases are not sufficiently comprehensive or complete to meet the present day standards of taxonomic work. All specific descriptions are here assembled in a single report and many original descriptions have been augmented to provide an adequate basis for a comparative scrutiny of species.

In the course of the present investigation it was also discovered that many specimens in the various collections, as well as in the material collected by the writer, represented undescribed species. These new species have been compared with the previously known species and are here described and illustrated.
All species of *Venericardia* have been reviewed and comments are offered on their stratigraphic and paleogeographic significance.

The main points worthy of emphasis are as follows:

1. A new subgenus, *Pacificor*, is introduced for species possessing rounded ribs and characterized by the absence of the escutcheonal cord. Of the 19 species included in this subgenus, 13 are new.

2. The new subgenus *Pacificor* is characteristic of the Pacific region, as only a few species reached the Gulf Coast of America during both the Paleocene and Eocene.

3. Heretofore, only 12 species of *Venericardia* have been described from western North America. To this number are now added 21 new species. In addition, the suppressed synonym *V. merriami* Dickerson is reinstated as a valid species.

In all, 34 species of *Venericardia* are considered in this paper. Nineteen are assigned to the subgenus *Pacificor*, nine to *Leuroactis*, four to *Glyptoactis*, and two to *Venericardia*. No *Venericardia*, s.s., was recognized in this western North American region.

4. The species of *Venericardia* treated in this report are grouped into several phylogenetic stocks and lineages. The criterion used for the differentiation of a given stock and of the lineages within it is the constancy of the morphologic characters through geologic time. These morphologic characters are: the shape and convexity of the umbonal region, the pattern of the sculpture, and the armature of the hinge plate. In Chart 1 an attempt is made to arrange all the venericards from the Paleocene and Eocene of western North America according to their supposed phylogenetic relationship.

5. Two phylogenetic stocks are recognized in the subgenus *Pacificor*: the *mulleri* stock and the *argentae* stock. These stocks are respectively traceable from Paleocene to middle Eocene, and from Paleocene to upper Eocene.

The species of the *mulleri* stock are characterized by a low, pointed beak and a low hinge plate. Within this stock is distinguished the *susanaensis* lineage, the species of which are characterized by a trapezoidal-pyramidal shape of the anterior left cardinal (2).

The species of the *argentae* stock are distinguished by a full umbo and a somewhat high hinge plate. Within this stock is recognized the *calafia* lineage which includes the forms with the scimitar-like shape of the medial cardinal (3b). This lineage runs from the lower to the upper Eocene.

6. The subgenus *Leuroactis* also comprises two stocks, the *crescentensis* and the *aragonia*. The forms of the *crescentensis* stock can be distinguished from other members of the subgenus *Leuroactis* by the concavity at the posterior end of the ventral margin of the hinge plate and the large nymphal plate. In the *aragonia* stock, two forms, *V. joaquinesis* and *V. popenewi* represent a distinct lineage as they are characterized by an unusually trigonal cardinal (3b).

7. The species of *Glyptoactis* are not numerous, but it should be pointed out here that there are several forms which have not been described due to the poor
Subgenera and species of Venericardia from Paleocene and Eocene of Western N.A.
preservation of the material. The phylogenetic continuity of species of Glyptothecis is suggested by the fact that the upper Eocene species, *I. marksi*, is more closely related to the Miocene forms than to the species from lower horizons.

(8) The subgenus *Venericardia*, of which a large number of species are found in the Gulf Coast area, is represented on the Pacific Coast of North America by only two species, both of which occur in the Paleocene.

(9) Several authors have pointed out that one or more Paleocene or Eocene venericards from the Pacific region are closely related to forms of the Gulf Coast Province. The refinement in the classification of venericards attempted in the present study brings out even more forcefully the existence of such affinities between the forms on the Atlantic and the Pacific sides of North America. These closely related forms are useful for stratigraphic correlation between the two provinces, particularly when it is realized that the Paleocene and Eocene species of *Venericardia* have short stratigraphic ranges.

The following is a list of some of the North Pacific venericards and their closely related Gulf Coast analogues:

<table>
<thead>
<tr>
<th>Pacific Coast</th>
<th>Gulf Coast</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Eocene:</td>
<td>None</td>
</tr>
<tr>
<td>Middle Eocene:</td>
<td>(?) <em>V. mcmasteri</em> and <em>V. natchitoches</em></td>
</tr>
<tr>
<td>Lower Eocene (late):</td>
<td><em>V. aragonia</em> and <em>V. horatiana</em></td>
</tr>
<tr>
<td>Paleocene:</td>
<td><em>V. argentea</em> and <em>V. hijuana</em></td>
</tr>
<tr>
<td></td>
<td><em>V. simiana</em> and <em>V. mediaplata</em></td>
</tr>
<tr>
<td></td>
<td><em>V. transversaria</em> and <em>V. francescae</em></td>
</tr>
</tbody>
</table>

The number of analogues and the close resemblance of the species suggest a connection between the two provinces during Paleocene time which was broken during early Eocene. The connection was re-established in the late early Eocene time as is witnessed by the occurrence of the remarkably similar forms (*V. aragonia* and *V. horatiana*) on the two coasts of North America. From middle Eocene time onward, the existence of close relationship of species and of geographic connection becomes less evident.

(10) Admittedly, the results of the present study have no claim to finality. Much remains to be learned from the available data, especially, towards a better understanding of biostratigraphic aspects of the Paleocene and Eocene of western North America. It is hoped, however, that the factual data and reasoning presented here will contribute to the knowledge of the systematics and the geographic distribution of the genus *Venericardia* and will stimulate further studies and application of the results to field problems.

**SYSTEMATIC DESCRIPTIONS**

*Genus VENERICARDIA* Lamark, 1801

(Lamark, Systeme des animaux sans vertébrés, p. 123.

Type species by subsequent designation: *Venericardia imbricata* Lamark, *Venus imbricata* Gmelin (Schmidt, C. F., Versuch über die beste Einrichtung zur Aufstellung, Behandlung und
Shell of moderate dimensions, from 25 to 40 millimeters high and slightly wider; diameter more than two-thirds the height; shell not very heavy, evenly but not strongly inflated. Umbones anterior, not conspicuously prominent, but well rounded to their tips, which are turned inward and forward and are almost in contact, the rightumbo slightly higher than the left. Lunule exceedingly small, sub-umbonal, slightly less narrow in the right valve than in the left. Escutcheon not defined. Anterior extremity short, rounding smoothly into the areolate base line. Posterior extremity obtusely truncate. Posterior area indicated only by the obscure truncation, a slight flattening of the shell, and a slightly closer spacing of the radials. Sculpture of 30 to 33 narrow X-shaped radials, sharply crenate near the tips of the umbones, outlined on the adolescent and adult stages by a heavy, sharply noded cord. Ligament opisthodetic, deeply inset, produced for more than half the length of the dorsal margin. A short thin laminar anterior cardinal, an obliquely produced cuneate medial, and a much-produced laminar posterior cardinal in the right valve; a moderately heavy anterior cardinal and a produced laminar posterior cardinal in the left valve; a faint grooving barely perceptible on the lateral surfaces of the heavier teeth; no true laterals developed but a slight pucker in the shell at the extremity of the lunular groove possibly analogous to an anterior lateral. Pedal scar small but deeply impressed, close to the margin just above the dorsal extremity of the deeply impressed puriform anterior adductor scar. Posterior adductor less deeply impressed, semicircular. Pallial line obscure, simple. Inner margins deeply crenate.—[(Gardner and Bowles, 1919, p. 167.)]

KEY TO WEST COAST PALEOCENE AND EOCENE SUBGENERA OF VENERICARDIA

1 With escutcheonal cord
   Without escutcheonal cord PACIFICOR

2 Ribs fasciculate with nodes along crests GLYPTOACTIS
   Ribs flattened with U-shaped interspaces planicostate 3

3 Ribs planicostate throughout VENERICOR
   Ribs obsolete in adult stage LEUROACTIS

Subgenus PACIFICOR, new subgenus

Type species: Venericardia mulleri Verastegui, n. sp., from base of Lodo formation. Paleocene, California.

Description.—Shell medium to large in size, thick, outline round to subsquare. Umbo full, convex; umbonal ridge inconspicuous. Ribs always rounded in the adult stage; in young specimens generally tripartite with a beaded central crest in the anterior and dorsal part of the medial areas. Interradials linear, occasionally channeled on the area of tripartite ribbing. Lines of growth fine at the early stages, become coarse in the adult, sometimes completely overshadowing radials and interradials. Escutcheon wanting, replaced by a smooth area between the hinge plate and postero-dorsal margin which is designated the pseudoscutcheon. The cord, which in other venericards forms the inner boundary of this area, not present in this subgenus. Hinge plate rather low, with a sinuous ventral margin. Nympar long. Ligamental pit varies from deeply incised to shallow and long. Dentition of the right valve composed of a small, laminar anterior cardinal (3a), an anteriorly elongated cardinal (3b), and a thin posterior cardinal (3b). Left valve with a triangular or trapezoidal anterior cardinal (2) and a high, thin posterior cardinal (4b). Pedal and muscle scars well incised and pallial line not remote from the margin. Inner margins crenulate.

Discussion.—The subgenus Pacificor has several distinctive features, the most
conspicuous being the lack of the escutcheonal cord. This cord is present in all other subgenera of *Eenericardia*. Another feature of this subgenus is the characteristic sculpture, consisting of round ribs and terraced ribs. These secondary ribs are present in the anterior and early part of medial area of the shell, bounded by a line starting at approximately the mid-point of the anterior margin and swinging in a broad curve to a point near and slightly posterior to the beak. In other words, the terrace-like ribs appear to recede progressively as they are followed from the anterior end of the shell posteriorly towards the beak. This apparently uneven recession of riblets actually means their progressively stronger persistence from the posterior side of the beak anteriorly, culminating in most species with frontal ribs which show distinct tripartite ribbing extending to the margin of the shell. This distinctive pattern of primary ribs and secondary riblets will be referred to herein as typical *Pacificor* ornamentation.

There are two main phylogenetetic stocks in this subgenus: The *mulleri* stock and the *argenta* stock. The *mulleri* stock ranges from the Paleocene through the middle Eocene. The Eocene members of this stock are characterized by the low hinge plate with a trapezoidal anterior left cardinal (2), a feature which is not present in any other stock of the genus *Eenericardia*. The *argenta* stock is far more numerous in species and ranges stratigraphically from the Paleocene through the end of the Eocene.

In the subgenus *Pacificor* an interesting relationship is observed between the number of the ribs and the position of the species in the phylogenetic series. As a general rule the number of ribs decreases with time; hence, the later the species, the fewer the ribs.

The subgenus *Pacificor* is characteristic of the Pacific region of North America, and its stratigraphic range is from Cretaceous to the end of the Eocene. Finlay and Marwick (1937) noted in the discussion of the Cretaceous species *V. fyfei* from the Wangaloan stage, New Zealand: "Indeed, the escutcheon seems to separate it (*V. fyfei*) from any other named *Eenericardia*, but a separate name is withheld pending further study." This statement refers to the character of the escutcheon (pseudoescutcheon) in the subgenus *Pacificor*. The illustration of *V. fyfei*, given by Finlay and Marwick, shows characteristic round ribs with tripartite ribs in the anterior portion. This New Zealand species resembles *V. transversaria*, n. sp., from the Paleocene of California.

Although the subgenus *Pacificor* in western North America ranges from Paleocene through the end of the Eocene, the individual species have a short stratigraphic range.

*V. fyfei* from the Cretaceous of New Zealand, *V. turneri* Gardner and Bowles, probably *V. franciscana* Gardner and Bowles and *V. bijuana* Gardner and Bowles (all from the Gulf Province), and *V. talara* Olsson from northwestern Peru are the only other representatives of *Pacificor* that are known to occur outside of western North America.
### Key to the Species of the Subgenus Pacificor from Paleocene and Eocene of Western North America

1. Ribs rounded or obsolete in the adult
   - Ribs flat in the adult
   - *vallecitosenis*

2. (1) Outline subcircular or subquadrate
   - Outline obliquely ovate or elongate
   - *vallecitosenis*

3. (2) Outline subcircular, postero-ventral margin evenly rounded
   - Outline subquadrate, postero-ventral margin truncate
   - *vallecitosenis*

4. (3) Ratio of height to length greater than 1
   - Ratio of height to length less than 1
   - *vallecitosenis*

5. (4) Ribs 32 to 34; convexity low; beak pointed
   - Ribs 22; convexity high; beak full
   - *mulleri*

6. (4) Ribs 30 to 32; interradials U-shaped in the adolescent stage
   - Ribs less than 30; interradials linear
   - *argentea*

7. (6) Beak pointed, high; anterior left cardinal (2) wide, trapezoid-pyramidal
   - Beak low; anterior left cardinal (2) narrow, elongate; ribs 25
   - *oregonensis*

8. (7) Ribs 29; persistent to the margins
   - Ribs less than 29; obsolete in the ventral area
   - *susanaensis*

9. (8) Ribs 28 in the adolescent, rounded, interradials linear
   - Ribs 25 in the adolescent, flat-topped, and interradials U-shaped
   - *durhami*

10. (3) Medial cardinal (3b) trigonal, large; incrementals fine to moderately coarse
    - Medial cardinal (3b) elongate; incrementals coarse with superimposed wrinkles; ribs 22
    - *transversaria*

11. (10) Umbo highly convex
    - Umbo moderately convex
    - *gabbi*

12. (11) Ribs 23, tripartite on the anterior portion, interradials reach ventral margin
    - Ribs 20-22, simple on the anterior portion, interradials evanesce ventrally
    - *lisa*

13. (11) Ribs persist to the ventral margin
    - Ribs obsolete in the ventral area
    - *lutmani*

14. (13) Ribs 28
    - Ribs 21
    - *weaveri*

15. (13) Ribs 26; ribs rounded, interradials linear in the adolescent
    - Ribs 25; ribs flat, interradials U-shaped in the adolescent
    - *diablolensis*

16. (2) Ribs flattened in the adolescent
    - Ribs round to inverted V-shaped in the adolescent
    - *calafia*
17 (16) Usually 21 ribs (range 18-23), simple; shell medium
large, thin carbusensis
carbusensis
Ribs 22, fasciculate; shell small, thick taliaferroi
taliaferroi
18 (16) Ribs 22 to 24; umbo moderately convex; beak pointed hornii
Ribs 20 to 22; umbo more convex; beak full clarki
Venericardia (Pacificor) mulleri Verastegui, n. sp.
Plate 1, figures 6-9

Description.—Shell of medium to large size, gently convex, rounded in outline with broadly arcuate anterior and ventral margins and obtusely truncate posterior margin; narrow pointed umbones and low prosogyrate beaks at the anterior fourth. Surface ornamentation consists of 32 to 34 well-defined ribs extending from the beak to the margin, 24 ribs on the antero-medial portion and approximately 10 on the posterior area; faint, terrace-like secondary riblets evident on both sides of the first 10 anterior ribs and receding to the posterior umbral area. Riblets one-fifth of the width of the ribs; ribs in the posterior area divisible into two groups, the three nearer the dorsal margin broaden away from the beak, and in the adolescent stage usually have one secondary riblet on the posterior side of the ribs; the remaining seven ribs narrower, crowded, and cordlike; (beak areas poorly preserved in all specimens examined). Interspaces are V-shaped at the umbo but become shallower and less sharply angular in harmony with the rib crests which are sharp near the umbo and increasingly rounded ventrally. Growth lines present throughout, more apparent in the anterior area, where they intercept the crests of ribs and give the appearance of nodes. Pseudoescutcheon present. Lunule short and deep, sloping forward, distinctly convex, outlined by an incised groove, ending ventrally in a depression in the right valve. Ligament opisthodeitc, nymph narrow and elongate; ligamental pit shallow, elongate and bordered dorsally by an extension of the nymph. Hinge plate low, short, with ventral border distinctly sinuous; dentition of the right valve with a laminar anterior cardinal (3a) barely discernible on the posterior side of the lunular body, a medial obliquely cuneate cardinal (3b), and a slender posterior cardinal (3b). Pedal and adductor muscle scars not deeply incised. Pallial line entire and relatively far from the ventral margin. Crenulations of inner margin well marked in adolescent shell but obscure on a mature form.

Dimensions of holotype.—Height, 48 mm.; length, 46 mm.; convexity, 17 mm. (Other fragmentary specimens indicate a maximum size of at least 80 mm.)

Holotype.—Right valve: Stanford Univ. Paleo. Type Coll., No. 7994; collector, S. W. Muller.

Type locality.—Stanford Univ. loc. 2075, road cut, just south of middle of section line between secs. 20 and 29, in sec. 29, T. 15 S., R. 12 E., opposite junction of Panoche and Silver creeks, Panoche Quad., Fresno Co., California.

Stratigraphic position.—Base of Lodo formation. Paleocene.

Discussion.—Venericardia mulleri represents the basal stem of the subgenus Pacificor on the West Coast of North America; it possesses many characteristics common to the whole group, namely: the low beak, the typical Pacificor sculpture,
and the pseudoescutcheon. *V. argentea*, a contemporaneous form, differs from *V. mulleri* by its pronounced umbal convexity with fuller umbones, and by the somewhat flatter ribs in the adolescent shell. *V. nelsoni*, n. sp., from Simi Hills, California, resembles *V. mulleri* in the general outline of the shell but is distinguished by having only 21 ribs. *V. susanaensis*, from Santa Susana shales, lower Eocene of Simi Valley, California, seems to be closely related to *V. mulleri*. These appear to be no close analogues of *V. mulleri* in the Gulf Coast Province.

This species is named in honor of Professor Siemon W. Muller at Stanford University in acknowledgment of his advice and encouragement in the present study.

**Venericardia (Pacificor) nelsoni** Verastegui, n. sp.

Plate 2, figures 1-5; Plate 3, figure 5


**Description.**—Shell large, heavy, ovate; outline smoothly rounded, umbo inflated, prosogyrate; the medial area defined by a sudden change of slopes on the anterior and posterior sides. Sculpture not well preserved in holotype; radials consisting of 22 rounded ribs which become obsolete toward the ventral border; umbal sculpture in holotype lost by weathering; posterior area set off by five thin, crowded radials succeeded by two outermost ribs which are conspicuously wider; interradials linear; incrementals moderately strong, crowded in small stage and producing a conspicuous thickening of the borders. Lunule of the left valve narrow, pointing downward and backward; pseudoescutcheon present, slightly concave, wide, bordered by a narrow ligamental groove; nymph long and narrow; ligamental pit large, excavated in a prolongation of the nymph. Hinge plate heavy, low and short with a sinuous ventral margin; left anterior cardinal (2) long trigonal, obliquely set, posterior cardinal (4b) relatively thin, slightly broadening ventrally. Interior of holotype filled with matrix concealing the pedal and adductor muscle scars; crenulations on the inner margin not distinct.

**Dimensions of holotype.**—Height, 98 mm.; length, 91 mm.; convexity, 35 mm.


Type locality.—Univ. Cal. loc. 3765, NW ¼ SW ¼ sec. 24, T. 2 N., R. 18 W., 6,800 feet 16°E. of Hill 2150, Simi Hills, Camulos Quad., Ventura Co., California.

**Stratigraphic position.**—“Martinez marine member” of Nelson, Martinez “group.” Paleocene.

**Discussion.**—*V. nelsoni* is known from one specimen, the holotype, which was originally listed by Nelson in 1925 as *Venericardia planicosta var. venturensis* Waring. *V. nelsoni* can be readily separated from *V. (V.) venturensis* by the fewer and more rounded ribs, by the more nearly circular outline and, above all, by possessing the pseudoescutcheon, which is a diagnostic character of all species of *Pacificor*.

Unfortunately, in the type the umbal area is badly weathered and no sculpture
is visible; hence it cannot be ascertained whether the ribs are beaded or tripartite as in *V. mulleri*. Nevertheless, the outlines of both species are comparatively similar and they may be closely related, although they differ in that *V. mulleri* has about 12 more ribs and in that its hinge points downward and forward.

Of the eastern American venericards already described, none is closely related to *V. nelsoni* nor is any relative of it found in South America.

**Venericardia (Pacific) susanaensis** Verastegui, n. sp.

**Plate 5, figures 1-4**


**Description.**—Shell, large, thin, outline rounded to subquadrat, not known in detail due to the fragmentary nature of the material; umbonal area narrow, slightly inflated; beaks prosogyrate, distinctly low and pointing forward. Sculpture of holotype well preserved; 22 ribs, persisting to the margins, in the antero-medial portion and 8 in the posterior area; earliest ribs worn away but that which remains shows that they are tripartite and faintly beaded, at least in the anterior part of the shell; in the mature stage, the ribs of the antero-medial area rounded, those on the posterior area thin and crowded; the interradials V-shaped, reaching the ventral margin. Incrementals rough throughout the shell. Pseudoescutcheon narrow, concave, showing oblique lines of growth. Ligamental groove narrow; nymph thin and large, embracing anteriorly a linear ligamental pit. Hinge plate short and low with a sinusous basal margin, the sinuosity more pronounced in the right valve; dentition of holotype well preserved; a nearly vertical right anterior laminar (3b), a curved arcuate-cuneate middle cardinal (5b), slightly concave on the wide basal margin, and a cordate posterior cardinal (5b) on the inner border of the nymph body; the left valve with a trapezoido-pyramidal, strong anterior cardinal (2), and a thin posterior left cardinal (4b), slightly thickened toward the ventral end. Interior of the holotype badly preserved; pedal muscle scars small and shallow, part of the shallowly incised posterior adductor muscle scar visible, posterior adductor scar placed unusually far from the hinge plate. Inner margin strongly crenulate.

**Dimensions of holotype.**—Height, 77 mm.; length (estimated), 77 mm.; convexity, 44 mm.

**Holotype.**—Right and left valves of a single individual: Stanford Univ. Paleo. Type Coll., No. 8004; collector, R. Willis.

**Type locality.**—Stanford Univ. loc. Ca-33, McCray Oil Wells, Oil Canyon, Camulos Quad., Ventura Co., California.

**Stratigraphic position.**—Santa Susana shale. Lower Eocene.

**Discussion.**—*Venericardia susanaensis* is probably the earliest representative on the Pacific Coast of what will be called here the *susanaensis* lineage within the *mulleri* stock. (See Chart 3, page 15.) The main characteristic of this lineage is the pattern of the hinge plate and the thinness of the nymph body—features which are not present in other lineages. Unfortunately, the sculpture in the holotype is not in so good a state of preservation, but there is enough of the specimen to show the shape and outline of the ribs and that the total number of ribs is 29.
The most distinctive character of *V. susanaensis* is the left anterior cardinal (2) which is truncate, trapezoido-pyramidal, slightly asymmetrical. This shape of tooth is found in other representatives of the *susanaensis* lineage.

In addition to the type material from the Santa Susana shale, *V. susanaensis*, associated with *V. durhami*, is also recognized in the Juncal beds in the Santa Inez Mountains which establishes the Meganos (lower Eocene) age of at least a part of that formation.

**Venericardia (Pacificor) durhami Verastegui, n. sp.**

*Description.*—Shell large, thick, distinctly round in outline; umbones inflated with the anterior slope more sharply curved than the posterior; beaks low, proso- 
gyrate, situated at about the anterior one-third. Sculpture of 28 narrow, rounded ribs separated by characteristic linear interradials, faintly represented over the main part of the disk; (sculpture on tips of beaks of holotype worn and not showing whether ribs are headed or fasciculate); the antero-medial portion with 19 ribs and the posterior area with only 9, the 4 nearest to the dorsal margin being wider than the others. Lines of growth conspicuous over the greater part of the shell. Incrementals faint and smooth up to 25 mm. diameter becoming gradually coarser; dominating over obsolete radial sculpture; a distinctive feature of the species. Lamule not well preserved, apparently small and deeply incised. Pseudoescutcheon narrow and concave. Hinge plate low and short; dentition in holotype poorly preserved, traces of the cardinal (2) of the left valve, and the anterior cardinal (3a) of the right valve resemble those of *Venericardia susanaensis*, n. sp. Interior of holotype concealed by matrix.

*Dimensions of holotype.*—Height, 85 mm.; length, 92 mm.; convexity, 45 mm.

*Holotype.*—Right and left valves of a single individual: Stanford Univ. Paleo.

Type Coll., No. 8005; collector, S. W. Muller.

*Type locality.*—Stanford Univ. loc. 829, 1 V’2 miles W. of Vickers Hot Springs, Ventura Co., California.

*Stratigraphic position.*—Juncal formation. Lower Eocene.

*Discussion.*—*Venericardia durhami* appears to be closely related to *V. susanaen-
sis*, n. sp. Unfortunately the holotype is so poorly preserved that it is difficult to make a thorough comparison. In outline the shell more closely resembles *V. hertleini* but differs in the number of ribs, having 29 as opposed to 25 in *V. hertleini*. Furthermore, the interradials in *V. durhami* are narrow or linear whereas in *V. hertleini* they are open and U-shaped. *V. hertleini* also has a somewhat higher hinge plate and a considerably wider medial cardinal tooth. It is interesting to note that *V. durhami* and related forms belong to a definite group of species which is charac-
terized by a round outline and a distinctive dentition. This group, characteristic of the Pacific region of North America, has not been reported from other American provinces.
Palaeontographica Americana (III, 25) 418

Venericardia (Pacificor) hertleinii Verastegui, n. sp.

Plate 15, figures 1, 2, 6


Description.—Shell large, thick, broadly rounded, not strongly inflated; antero-ventral margin broadly rounded, the posterior slightly truncated. Umbo curved forward; beak placed at about the anterior one-third; posterior area flattened, somewhat concave and defined by a sudden change from coarse to fine ribs. Sculpture consists of 25 ribs which become obsolete near the margins. The 18 ribs in the antero-medial portion sharply angular on the beak, gradually become slightly flattened to the second annual ring then flatly rounded; the four or five ribs on the anterior area slightly terraced; those on the posterior area angular in the early stage become rounded later, the three ribs next to the gentle umbal ridge thinner and crowded, and the last four near the posterior margin are much wider. Interradials U-shaped to the second annual ring, after which they become well-defined lines; interradials obsolete on the medial portion. Incrementals, fine on the umbal area, coarse on the anterior, posterior, and on the marginal portions. Lunule of holotype small, trending downward and forward. Pseudoescutcheon present. Hinge plate low and long, with a conspicuous sinuous basal line; nympha thin and long; ligamental pit deeply incised and long. Dentition well preserved on the holotype, consists of an anterior left cardinal (2a), trapezoidal with a blunted upper end, and a posterior cardinal (4b), thin anteriorly but slightly broadening ventrally. Interior of holotype with normally incised pedal and adductor muscle scars; pallial line entire; inner margins crenulated.

Dimensions of holotype.—Height, 85 mm.; length, 91 mm.; convexity, 25 mm.


Type locality.—Univ. Cal. loc. 3090, just north of junction of San Clemente and Rose canyons, San Diego Co., California.

Stratigraphic position.—Rose Canyon formation. Middle Eocene.

Discussion.—The holotype of Venericardia hertleinii is fairly well preserved. This venericard was considered by Hanna (1925) as a variety of V. hornii (Gabb), and he suggested at the same time that it “exhibits characters which may be worthy of specific rank.” The characters by which it differs from V. hornii are the weaker inflation of the umbo and the much flatter ribs. Besides these characteristics of specific value, the shape of the anterior left cardinal (2) is also distinctive in this form and is not found in other stocks, except in that of V. susanaensis. The shape of this tooth, as was mentioned above, is subtrapezoidal with a blunted upper end. This same shape, with but slight variation, characterizes the anterior left cardinal of V. susanaensis, indicating a close relationship between these two species. V. durhami appears to be an intermediate form, although the hinge of this form is so badly crushed that it is difficult to see the real pattern of it.

This species is named after Dr. Leo G. Hertlein, Curator of Paleontology at
the California Academy of Sciences, in appreciation of his courtesy in making available the facilities of the Academy.

**Venericardia (Pacificor) oregonensis** Verastegui, n. sp.

*Plate 9, figures 7-9*

**Description.**—Shell of medium size, thick, outline nearly circular; anterior, ventral and posterior margins evenly rounded, the postero-dorsal more gently curved. Shell moderately convex, with wide umbo, greatest convexity a little above the medial point of the disk; beak prosogyrate, distinctly low, placed at about the anterior one-third. Sculpture of 24 well-rounded ribs, (poorly preserved at the beak on the holotype), consisting of 16 wide, simple ribs in the antero-medial area becoming nearly obsolete below the middle of the disk, and 8 ribs on the posterior area—3 on the weak umbonal ridge, well defined and wide, 5 at the postero-dorsal margin thin, crowded, becoming obsolete 15 mm. beyond the beak; interradials present throughout except in the medial one-third of the marginal part of the shell; incrementals faint and crowded, but fairly strong ventrally; periodic growth stages (annual rings) marked by deep incisions. Lunule small, convex, deeply inset. Pseudescutcheon and nympha not well preserved in the holotype. Hinge low and short with a distinctly sinuous ventral margin; denticulation consisting of a small, laminar right anterior cardinal (3a), a sharply triangular, curved medial cardinal (3b), and a thin right posterior cardinal (3b), not well preserved. Muscle scars and pallial line slightly incised; pedal scar somewhat more strongly defined; pallial line entire, relatively far away from the ventral margin. Inner margin with unusually deep crenulations.

**Dimensions of holotype.**—Height, 56 mm.; length, 60 mm.; convexity, 18 mm.

**Holotype.**—Right valve; Stanford Univ. Paleo. Type Coll., No. 8006.

**Type locality.**—Bluffs along Little River at junction with North Umpqua River, Glide, Roseburg Quad., Douglas Co., Oregon.

**Stratigraphic position.**—Upper Umpqua formation. Lower Eocene.

**Discussion.**—*Venericardia oregonensis* occurs in the same faunule as *V. argonii* Arnold and Hannibal and *V. merriani* Dickerson. The almost circular outline makes it a distinctive form. A possible relationship with *V. duchani*, n. sp., from the Juncal formation, California, is shown by the same pattern of sculpture, *i.e.*, in the rounded ribs, linear interradials, and crowded incrementals. Because of the bad state of preservation of the beak on the holotype, it is impossible to ascertain the details of the sculpture in this particular area; no traces of terracing or noding can be seen, but a somewhat V-shaped pattern of the ribs is to be expected. Below the middle of the disk the well-defined, round ribs become obsolete.

**Venericardia (Pacificor) argentella** Verastegui, n. sp.

*Plate 1, figures 10-14*

**Description.**—Shell of medium size, inflated-ovate in outline with the ventral margin broadly rounded, umbones prominent, greatest inflation a little above the center of the disk the surface rounds off broadly in all directions, except toward the
posterior slightly concave dorsal slope; beak prosogyrate, low and compact, placed at about the anterior one-third. Ribs 30 to 32; typical Pacificor sculpture (as described in the diagnosis of the subgenus). Posterior area with 10 ribs: the 5 nearest the dorsal margin wide, with one posterior riblet; the other 5 thin, crowded, V-shaped, with corresponding V-shaped interspaces. Interspaces in the medial portion square channeled, one-third the width of the ribs. Frontal rib crests show a beadlike appearance as in I. mulleri. Lunule small, convex, sloping forward, (not well preserved in the holotype). Pseudocutheoon present. Ligamental groove deeply incised; nympha long and wide; ligamental pit shallowly incised. Hinge plate low and short; dentition of the left valve with a strongly developed, scimitar-like anterior cardinal (2), projected over the medial plane, and a thin posterior cardinal (jb) which thickens gradually toward the ventral end. Pedal muscle scars normally incised. Adductor muscle scars and pallial line concealed by matrix.

**Dimensions of holotype (estimated).—**Height, 49 mm.; length, 51 mm.; convexity, 20 mm.

**Paratype.**—Height, 31 mm.; length, 34 mm.; convexity, 12 mm.

**Holotype.**—Left valve: Stanford Univ. Paleo. Type Coll., No. 7995; collector, P. Verastegui.

**Paratype.**—Univ. Cal. Invert. Type Coll., No. 33001.

**Type locality.**—Stanford Univ. loc. 2073, road cut, just south of middle of section line between secs. 20 and 29, in sec. 29, T. 15 S., R. 12 E., opposite junction of Panoche and Silver creeks, Panoche Quad., Fresno Co., California.

**Stratigraphic position.**—Base of Lodo formation, Paleocene.

**Discussion.**—Venericardia argentea can be distinguished from I. mulleri by the highly tumid and broadly convex umbro, by the beadlike crenulation of the frontal tripartite ribs, and by the channeled interspaces and somewhat flattened ribs in the mediol part of the shell.

I. (Pacificor), sp., obtained from a well (Capay formation?) near Marysville Buttes, Sacramento Valley, California, is closely related to I. argentea but differs from it in having only 24 ribs.

I. argentea may be related to I. hijijana Gardner and Bowles from the lower Midway of Tennessee. The resemblance is in the broad inflation of the umbonal region and the fasciculated ribs in the adolescent stage.

**Venericardia (Pacificor) lutmani Turner, 1938**

Plate 7, figures 3-5; Plate 8, figure 8


1933. *Venericardia hornii* (Gabb) subsp. *lutmani* Turner, Weaver, Univ. Washington Publ. Geol., vol. 5, p. 135, pl. 28, fig. 1, pl. 32, fig. 1.

Shell heavy, subquadrate; beaks small; 27 ribs, the posterior 9 or 10 narrower and higher than the remainder, which are nearly obsolete with the exception of the anterior three or four; lunules very short, deep; ligamental groove long, narrow.

The new subspecies differs from I. hornii calafla Stewart in having three or four additional ribs. Specimens of the new subspecies from the Santa Susana shale of the Simi Valley region have 28 or 29 ribs and may be the initial form from which the later varieties or subspecies of I. hornii evolved by progressive elimination of ribs.—[Turner, 1938, p. 90.]
Supplementary description.—Shell large, heavy, subquadrate in outline, anterior end evenly rounded, ventral gently curved, posterior truncate; umbones inflated, with low, pointed beaks situated at about the anterior one-fourth. Sculpture in holotype not well preserved; 20 ribs in the antero-medial portion; only 6 ribs preserved on anterior area, these show riblets which do not reach the anterior margin; the visible intercostals linear; increamentals coarse and over-ride ribs in the anterior area but fine on the obsolete ribs of the ventral area. Lunule small, convex, deeply inset, sloping downward and slightly forward, the right lunule three times as large as the left one. Pseudescutcheon present, flat and wide (not well preserved). Nymph thin and large ligamental pit deeply incised. Hinge plate high and long, with a sinuous ventral margin. Dentition strong, consists of a laminar, long, nearly vertical anterior right cardinal (3a), pointed downward and slightly backward; a flat, scimitar-like, ventrally sinuous medial right cardinal (3b); a cordlike posterior right cardinal (5b) placed on a wide flat nymphal body; the left valve with a low, cuneate anterior cardinal (2), the upper end touches the lunular plate, and a thin, low posterior left cardinal (4b), not well preserved in the holotype. Pedal muscle scars shallowly incised; the rest of the interior of the shell concealed by the matrix.

Dimensions of holotype.—Height, 96 mm.; length, 103 mm.; convexity, 31 mm.


Type Locality.—Univ. Cal. loc. A-1233, W. of Roseburg, Oregon.

Stratigraphic position.—Umpqua formation; Santa Susana shale. Lower Eocene.

Discussion.—The additional description of *Venericardia lutmani* is based on a restudy of the holotype. To complete the description, it was necessary to open the shell in order to expose the hinge plate.

*I. lutmani* was originally proposed as a subspecies of *I. hornii*. A careful scrutiny of the specific scope of *I. hornii* and the revision of the concept of that species shows that *I. lutmani* is sufficiently different from *I. hornii* to be regarded as a distinct species.

*I. lutmani*, together with *I. calafia* and *I. gabbi*, n. sp., form a compact group of species which will be designated here as a *calafia* lineage of the *argentea* stock. The features which are common to all these species and which may be regarded as important phylogenetic (static) characters are: the rounded to subquadrate outline with a prominent postero-ventral truncation and the large scimitar-like medial cardinal.

It should be pointed out that these characters are not present in a true *I. hornii* as this species is delimited today.

In addition to the occurrence in the Umpqua formation, *I. lutmani* is also known from the Santa Susana shale in Llajas Canyon, California.

*Venericardia* (Pacificor) *diabloensis* Verastegui, n. sp.

Plate 5, figures 5-7, 7a


Description.—Shell large, slightly subquadrate, with inflated umbo and flattened
ventral area; anterior margin broadly rounded, the ventral gently curved, and the posterior slightly truncate; beaks massive and curved forward, placed at about the anterior one-third. Umbonal sculpture consisting of 20 finely beaded and in the anterior median area laterally terraced ribs; on the posterior portion ribs cordlike, crowded and less distinct; adult sculpture characterized by 20 gently rounded, almost flat ribs separated by linear intercostals, ribs and intercostals gradually disappear with growth about 50 mm. from the beak, giving place to thick incrementals. Lunule convex, deeply inset, with lunular margin sloping almost vertically and ending in a pustule (in the left valve). Ligamental groove shallow. Hinge plate moderately high and long with a slightly sinuous ventral margin; nymph narrow but long; ligamental pit triangular, deeply incised. Dentition of the left valve consists of a scimitar-like, cuneate anterior cardinal (2), pointing toward and touching the lunular plate, with the inner face sloping uniformly toward the ventral margin of the hinge, and a thin posterior cardinal (4b), also sloping. Interior of the type filled with matrix, concealing the pedal and adductor muscle scars. Inner margins crenulate.

Dimensions of holotype.—Height, 72 mm.; length, 72 mm.; convexity, 24 mm.

Paratype.—Height, 80 mm.; length, 92 mm.; convexity, 30 mm.

Holotype.—Left valve, Stanford Univ. Paleo. Type Coll., No. 411.


Locality.—Marsh Creek, Brentwood, Contra Costa Co., California.

Stratigraphic position.—’D’ member of Meganos formation. Lower Eocene.

Discussion.—I. diabloensis closely resembles I. lutmani Turner from Oregon in outline but differs in having two less ribs than the latter. In spite of this slight difference, I. diabloensis appears to be a near descendant of I. lutmani. The affinity of I. diabloensis with other members of the calafia lineage is not clearly marked, and for that reason it is preferable to regard I. diabloensis as an off-shoot of that lineage in the late lower Eocene.

Venericardia (Pacificor) calafia Stewart, 1930

Plate 15, figures 3-5, 7; Plate 16, figures 1-3; Plate 17, figures 1, 2


1943. Venericardia hornii (Grabb) subsp. calafia Stewart, Weaver, Univ. Washington Publ. Geol., vol. 5, p. 134, pl. 28, figs. 6-7, pl. 31, figs. 4-5.

Shell large, heavy, almost circular, with small beaks; 24 radiating ribs on each valve, decorticated at the beaks, but a few of the anterior ribs still showing the lateral ridges and two of the posterior ribs of the left valve distinctly noded but apparently not ridged; on the central region, the ribs flatten and disappear when the shell is about 42 mm. long, as shown by the growth lines, the central area being quite smooth; the anterior ribs gradually give way to prominent growth lines while the posterior ribs remain more or less distinct, but not prominent, to the posterior margin; hinge of type specimen not exposed. Length, 95 mm.; height, 86 mm.; thickness of both valves, 53.5 mm.; no. 31450, Museum of Paleontology.—[Stewart, 1930, p. 168.]

Supplementary description.—(based on topotype): Lunule convex, deeply inset, the right twice as large as the left; lunular groove trending downward and back-
ward. Pseudescutcheon well defined by a wide plate delimiting by a grooved line on the dorsal side. Nymph long and narrow, somewhat alate at its posterior end, at

the anterior it embraces a shallowly incised groovelike ligamental pit. Hinge plate high with a sinuous basal margin; dentition of the right valve consists of a strong plate-shaped, anteriorly slightly convex anterior cardinal (3a); a scimitar-like, strongly curved medial cardinal (3b), showing an incised groove in the upper part of the anterior face; and a long, thin, cordlike posterior cardinal (5b), the left

valve has a high, curved, cucate anterior cardinal (2), with an oblique cord in the upper part of the posterior face to correspond to the groove in 3b; and a thin, curved posterior cardinal (4b) which slopes slightly at the ventral end. Pedal and adductor muscle scars shallowly incised, the posterior scar remote from the hinge; pallial line entire, rather near the margins. Inner margin faintly crenulated.

**Dimensions of hypotype.**—Height, 102 mm.; length, 108 mm.; convexity, 63 mm.

**Holotype.**—Right and left valves of a single individual; Univ. Cal. Invert. Pal. Type Coll., No. 31450.

**Hypotype.**—Right and left valves of a single individual, Stanford Univ. Paleo. Type Coll., No. 8017; collector, T. F. Stipp; left valve, Cal. Acad. Sci. Type Coll. No. 1828, from one mile southeast of Oil City, Fresno Co., California. Domengine

formation.

**Type locality.**—Univ. Cal. loc. 7004, Llajas Canyon, Simi Valley, Ventura Co., California.

**Stratigraphic position.**—Llajas formation, California; Tyee formation, Oregon. Middle Eocene.

**Discussion.**—Venericardia calafia Stewart from the Llajas formation, California, seems to be a representative of a well-defined group in the North Pacific Coast. It is characterized by a circular to subquadrate outline, narrow umbos and prosogyrate pointed beaks. Unfortunately, both the holotype and the topotype here described show a badly preserved sculpture, especially at the beaks. However, a specimen from the Avenal sandstone, Coalinga area, California, shows the sculpture of the beaks. The ribs are tripartite on the antero-medial area and noded on the frontal portion; the first four or five anterior ribs show a riblet on their posterior sides for only the first 15 to 20 mm. of growth. Intercostals are V-shaped at the beaks, changing to U-shaped, and finally, when the shell is 40 mm. high, abruptly narrow to a linear pattern. This general pattern of sculpture is present in V. argentea, n. sp., and other relatives that belong to the same stock.

Stewart (1930) mentioned the possibility that V. calafia is a close relative of V. pacifica Olson from northwestern Peru. Gardner and Bowles (1939) quoted Stewart on this relationship but made no further comments. After a close study of the specimen cited by Gardner and Bowles (1939, p. 179), which appears to be V. pacifica, it is concluded that V. pacifica and V. calafia are not closely related and belong to two subgenera, Lutroactis and Pacificor respectively.

V. lutmani Turner from the lower part of the Umpqua formation appears to be ancestor of V. calafia. These two species differ somewhat in outline, V. lutmani
being more subquadrate, but the pattern of the hinge is almost identical in both. Among the later forms, \textit{V. gabbii}, n. sp., is probably a descendant of and falls in line with \textit{V. calafia}, even though there are some morphological differences.

\textit{V. calafia} is important as a key marker of the middle Eocene because of its wide distribution along the North Pacific Coast. Besides occurring in southern and central California, it is found also in Oregon. There appear to be no close relatives of \textit{V. calafia} in the Gulf Province or in South America.

\textbf{Venericardia (Pacificor) gabbii Verastegui, n. sp.}

Plate 19, figures 1, 5, 6


1925. \textit{Venericardia hornii} (Gabb), Anderson and Hanna, California Acad. Sci., Oce. Papers, vol. 11, p. 174, pl. 4, fig. 1.

\textbf{Description.}—Shell large, thick, subquadrate in outline, the anterior margin broadly rounded, the ventral gently curved, the postero-ventral truncate, the postero-dorsal slightly arched. Umbo inflated, broadly convex, umbonal ridge inconspicuous but defined by a sudden change from coarse to fine ribs; beak prosogyrate, low, full, placed at about the anterior one-fourth. Sculpture consists of 23 ribs, 8 in the anterior area, wide, terraced and beaded in typical \textit{Pacificor} manner; in the medial portion 6 ribs widen ventrally away from the umbo; in the posterior portion 9 narrow ribs, the 4 nearest the cardinal margin less distinct but wider; interradials on the beak channeled, becoming linear, and persisting to the margin except in the medial-ventral area; incrementals fine in the umbonal area and coarse in the anterior and posterior portions. Lunule cordate, convex, anteriorly trending downward and slightly backward. Pseudoescutcheon distinct, wide. Hinge plate low and long; nymph triangular, long; ligamental pit elongate, deeply incised; dentition consists of a laminar anterior right cardinal (3a); a scimitar-like medial cardinal (3b) with a wide base, elongate anteriorly; and a cordlike, short posterior right cardinal (5b) on a wide nymphal body. Interior of the holotype concealed by matrix.

\textbf{Dimension of holotype.}—Height, 105 mm.; length, 106 mm.; convexity, 40 mm.

\textbf{Holotype.}—Right valve, Cal. Acad. Sci. Type Coll., No. 686; collector, M. Hanna.

\textbf{Type locality.}—Grapevine Canyon, Kern Co., California.

\textbf{Stratigraphic position.}—Tejon formation. Upper Eocene.

\textbf{Discussion.}—\textit{Venericardia gabbi} is characterized by its subquadrate outline and by its strongly convex umbo. It differs from \textit{V. hornii} (Gabb) in its outline, as the original Gabb specimen is elongate and obliquely ovate and \textit{V. gabbii} has a subquadrate outline accentuated by a sharp truncation on the posterior ventral margin. This subquadrate outline is related to other internal characters. Thus, in the study of \textit{V. hornii}, it was found that its obliquely ovate outline is correlated with the shape of the anterior medial cardinal (3b) which is elongate anteriorly, with a short basal margin. There is also a difference in that a shell with higher convexity (\textit{V. gabbi}) has wider ribs in the medial portion of the valve.

Phylogenetically, \textit{V. gabbi} is related to \textit{V. intunni} Turner and \textit{V. calafia}
Stewart. The relationship is shown by the close similarity of the shape of the 
medial cardinal (3b). In these three species this tooth has a strikingly scimitar-like 
shape. It is believed that the correlation of hinge armature with the subquadrate 
outline, which persists in a number of species through the Eocene, is not a mere 
coincidence but is a result of functional interrelation and is peculiar to a limited 
number of species. It is, therefore, to be regarded as a static phylogenetic character.

This fossil is named in honor of W. M. Gabb, in recognition of his invaluable 
work in the paleontology of western North America.

Venericardia (Pacificor) weaveri Verastegui, n. sp.  
Plate 21, figures 3, 4

fig. 1, 12.
fig. 1.

Description.—Shell large, thick, outline round to subquadrate, the anterior and 
ventral margins evenly rounded, the postero-ventral somewhat attenuate and the 
posterior margin slightly truncate. Umbo convex, inflated; umbal ridge weak, 
ribs narrower on posterior slope; beak distinctly low, at about the anterior two-fifths. 
Sculpture, characteristic of Pacificor, consisting of 21 rounded ribs relatively less 
perceptible in the ventral portion of the medial area; 14 ribs in the antero-medial 
area typically fasciculate—tripartitely ribbed—showing a distinct nodose ornamentation 
neat the beak and on rib crests; 7 ribs in the posterior area less prominent, thin 
and crowded. Interradials persistent to the margins, V-shaped on the beaks, become 
linear in the rest of the shell. Incrementals fine on the disk, coarse on the anterior 
portion. Lunule cordate, deeply inset; lunular groove wide, vertical. Pseudoco 
escutcheon well defined; hinge plate long and low with a sinuous basal margin; 
ligament groove and ligamental pit deep, the latter deeply excavated. Dentition of 
the right valve of the holotype consists of a small, laminar anterior cardinal (3a); 
a strong, cuneiform scimitar-like medial cardinal (3b); left valve of the paratype 
with a triangular, pyramidal anterior cardinal (2), and a thin, curved posterior 
cardinal (3b). Pedal and adductor muscle scars well incised; pallial line at a 
moderate distance from the margins. Inner margin with wide crenulations.

Discussion.—Venericardia weaveri is a new species which has had a confused 
taxonomic history. This species was originally identified by Arnold in 1907 as 
V. planicosta Lamarck. Subsequent workers, however, called it V. clarki Weaver 
and Palmer and regarded it as belonging to the hornii-clarki complex of species.

In the light of our present knowledge of venericards from western North 
America it can be readily shown that V. weaveri is a distinct species and that it falls 
into the phylogenetic lineage of V. gabbi. 

The diagnostic features of V. weaveri are the rounded to subquadrate outline, 
rounded ribs, and the subcuneate shape of the medial cardinal (3b). 

V. weaveri is closely related to V. gabbi, n. sp., which is a typical representative 
of the calafia lineage. The relationship can be seen in the round to subquadrate 
outline, in the general character of the ribbing, in the wide and strong nymphal body,
Palaeontographica Americana (III, 25)

and furthermore, in the convexity of the shell. *V. weaveri* is made a separate species because it has fewer ribs (by two or three) and because the basal margin of its medial cardinal (3b) is narrower. The latter difference may be due to the smaller size of the compared holotype.

A specimen that may be *V. weaveri* was obtained from the "Coldwater" formation, Ventura County, California.

**Dimension of holotype.**—Height, 71 mm.; length, 80 mm.; convexity, 29 mm.

**Holotype.**—Right valve: Stanford Univ. Paleo. Type Coll., No. 8024.

**Type locality.**—Southeast bank of Stillwater Creek, 1/4 miles NW. of Vader, Wash.

**Stratigraphic position.**—Cowlitz formation of Oregon and Washington. Gaviota formation and, questionably, "Coldwater" of California.

This species is dedicated to Dr. Charles E. Weaver.

**Venericardia (Pacificor) clarki** Weaver and Palmer, 1922

*Plate 20, figures 1-6*


1922. *Venericardia clarki* Weaver and Palmer, Univ. Washington Publ. Geol., vol. 1, No. 2, p. 19, pl. 9, figs. 4, 5; pl. 10, fig. 8.

1925. *Venericardia clarkii* Weaver and Palmer, Hanna, M. A., Univ. California Publ. Dept. Geol. Sci., Bull. 25, No. 8, p. 287-288, pl. 36, figs. 3-5; pl. 37, figs. 2, 3; pl. 43, fig. 2, (only); pl. 44, fig. 2 (only).


**Original description.**—Shell small and ovate; umbones small; anterior end slightly produced, sloping from the beaks at an angle of 20°, rounding into the ventral margin; ventral margin regularly rounded; posterior end rounded, passing from the ventral margin at about the same degree of convexity as the anterior end; posterior dorsal margin nearly straight or slightly curving to the posterior end; surface ornamented with 18 to 20 very well developed radiating ribs with rounded intercostes about half the width of the rib; the median portion of the ribs is raised and rounded, the base forming a lower ridge on each side of the ribs, giving them a tripartite character; the median, raised portion of the ribs is ornamented by fine nodes or pustules which occur on all the ribs on very young shells, and on the umbonal region and the anterior end of most of the shells; the ribs on the posterior end of the older specimens become broader and the pustulate condition obliterated; inner margin fluted. Dimensions: length, 17 mm.; height, 15 mm.; thickness, 14 mm.—[Weaver and Palmer, 1922, p. 19-13.]

**Supplementary description.** Shell large, thick, posterior cardinal margin regularly and broadly curving, ventral margin broadly rounded, joining the posterior cardinal margin in a much smaller arc, which tends to give shell a subtriangular outline; anterior margin moderately rounded but straightening out into a broad curve anterior to the small, well-defined lunule, which is circumscribed by a lateral groove anterior to the surface of the lunule, and not visible from the front of the shell; beaks prominent, anterior, and moderately high. The surface ornamentation consists of growth lines and twenty-one radial ribs (pl. 43, fig. 2), which are very well rounded on the umbone but broadly rounded near middle of shell, and flattened or nearly obsolete near margin, due to increased prominence of growth lines. Radial ribs may be separated into two groups. Posterior six to eight are much narrower, closer, and less distinct than other ribs of shell. Line of demarcation extends from beak to posterior dorso-ventral point. Hinge massive but only moderately wide. Anterior cardinal left valve slightly bifid, a character found in many of the valves of this species; large socket nearly straight on the anterior side but broadly curving on the posterior forming an angle of about forty degrees with the hinge line. Inner margin crenulate.

**Dimensions of the pleurostomes figured:** left valve: 110 mm.; altitude, 100 mm.; thickness, 37 mm.; right valve: length, 100 mm. (broken); altitude, 92 mm. (broken); thickness, 35 mm. —[Hanna, 1925, p. 288.]
Hypotype.—Both valves of an individual, Stanford Univ. Paleo. Type Coll., No. 8022, from bluffs along Cowlitz River below the mouth of Driew Creek, east of Olequa, sec. 34, T. 11 N., R. 2 W., Little Falls, Lewis County, Washington.


Discussion.—Unfortunately the holotype of Venericardia clarki is not a good representative of the species; it is a young form of only 18 mm. in height, while mature specimens reach more than 100 mm.

Numerous specimens have been available for the present study and the published illustrations have helped in the evaluation and restriction of the concept of V. clarki.

Hanna (1925) has noted the wide variation in the specific characters of the immature specimens and has also indicated that several species or variants might be described from that complex. Hanna's recognition of forms belonging to potentially different species among V. clarki was correct.

In the present study, a critical evaluation of the morphologic characters of venericards from the upper Eocene has shown the existence of definite phylogenetic lineages evolving from ancestral stocks in lower horizons.

In the present work, thus far, two phylogenetic lineages, the hornii and the calafia are recognized in the upper Eocene. As it was pointed out, in the discussion of V. hornii (Gabb), these two phylogenetic lineages are characterized by distinct morphological features related to the outline of the shell. The hornii lineage is characterized by having an obliquely ovate outline which is the same as that of V. clarki. The close relationship of V. clarki to V. hornii, s.s., is also seen in the similarity of the general pattern of the hinge plate.

V. clarki, having an obliquely ovate outline and the characteristic oblique median cardinal, falls into the phylogenetic lineage of V. hornii.

Notwithstanding the close relationship of V. clarki to V. hornii, specific differences can be recognized. V. clarki has relatively greater convexity associated with a more prominent umbo, fewer ribs (two or three), and the less elongate triangular-pyramidal left anterior cardinal (2). All of these characteristics are constant and have sufficient value for the separation of V. clarki from other species.

V. clarki is widely spread in the upper Eocene of Washington and Oregon and is questionably recorded in California from the Markley formation.

Venericardia (Pacificor) hornii (Gabb)

Plate 18, figures 1-7; Plate 19, figure 7


*Original description.*—Shell large, thick, convex, subquadrate, oblique; beaks prominent, anterior, subterminal; cardinal margin broadly arched, sloping slightly, and uniting with the posterior end with a regular curve; base broadly rounded, most prominent in the middle, from which point it runs upwards rapidly towards the anterior end, which is broadly and regularly curved; posterior end obliquely subtruncate, angular below. Surface marked by twenty-two broad rounded ribs, a little the smallest posterior to the umbonal angle [sic]: these ribs are somewhat flattened above, especially towards the base, have acute interspaces, and are crossed by numerous coarse, irregular lines of growth. Hinge very thick, robust, and resembling that of *C. planicosta* of the Eocene.

Figure, natural size.

*Localities.*—Abundant near Fort Tejon; also found at Martinez, and near Clayton.

I dedicate this magnificent species to my friend, Dr. Horn, U.S.A., in recognition of the valuable assistance he has rendered me, in collecting Cretaceous fossils in the vicinity of Fort Tejon.

It is not so surprising as might appear at first glance, that Mr. Conrad should have referred this shell to Lamarck’s species. The form figured is probably an extremely oblique one, although all of the adult specimens show more or less of an approach to this shape. The young shells, of which I have examined a large number, approach much more nearly to *C. planicosta* in outline. Add to this the fact that whenever the shell is weathered so as to lose the outside layer, the ribs become quite flat, angular on the sides, and with broad, flat interspaces. Wherever the surface is preserved intact, however, the roundness of the ribs, and the narrow, acute interspaces, show a character entirely incompatible with the other form. A further resemblance is in the hinge, which, as well as my memory serves me, is nearly, if not quite, undistinguishable from that of *C. planicosta* — [Gabb, 1864, p. 174.]


*Hypotype.*—Left valve, No. 8019, from same as 8018.

*Hypotype.*—Hinge of a right valve, No. 8020, from same locality as 8018.

*Hypotype.*—Right valve, Cal. Acad. Sci. Type Coll. No. 7728, from east bank of Live Oak Creek, about three-quarters of a mile from the mouth.

*Venericardia hornii* (Gabb), in Gabb's words (1869, p. 168) "Fingerpost of the Tejon group," has definite characters to differentiate it from other contemporaneous forms. Stewart (1930) established and figured the lectotype of the species which serves as a standard on which to base the concept of the species. With this lectotype for reference, it is possible to clear up "the problem of variation," indicated by previous authors including Gabb himself.

In 1864, pp. 149-150, describing this species, Gabb indicated that the outline of *V. hornii* is "subquadrate, oblique." Afterward in the comments he wrote, "The form is probably an extremely oblique one, although all the adult specimens show more or less of an approach to this shape." After subsequent work on the Eocene fauna of California, Gabb in 1899, p. 188, revised the description of *V. hornii* and modified his previous description of the outline as follows: "Shell variable in shape, subtrigonal to subquadrate." This change in the original concept was occasioned by his having seen specimens from other localities, for he said, "Since then (1864) it has been found in several localities, and fine specimens had been
obtained near New Idria, and West of Griswold’s on the road from the latter place to San Juan.” Today these localities are regarded as of middle Eocene age, and it is evident that the Venericardia forms Gabb then had before him were quite different from the true V. hornii.

Hanna (1925, p. 286), evaluating the morphologic characters of V. hornii, concluded that the general outline of this species varies from rounded to subquadrate, and that in some specimens the truncation of the postero-ventral margin makes a greater angle with the posterior cardinal margin than in others. In the latter the outline will be nearly quadrate and in the former broadly rounded posteriorly.

The variability of the outline of V. hornii does not appear to be so great as Hanna stated. Upon closer study of the specimens and illustrations at hand it seems that the concepts of V. hornii and of one or more forms, including V. clarki Weaver and Palmer, have been confused by different authors. The oblique outline is present in shells which have little or no truncation of the postero-ventral margin. This is only one of the several interrelated morphological characters of the shell. Thus, a specimen having a roundish or a subquadrate outline in the adult stage, differs from one with obliquely ovate outline by having different hinge teeth and, to some extent, a different umbonal convexity.

In V. hornii, which has an obliquely ovate outline, the medial cardinal (3b) is elongated anteriorly with a short marginal base. In V. gabbii, with subquadrate outline, the same tooth is scimitar-like and although similarly curved anteriorly, it has a wider marginal base.

In addition to the California occurrences, the true V. hornii is found also in Oregon. Turner (1938) had stated that some Oregon specimens, especially from Cape Arago, resemble in outline V. hornii more than V. clarki. The illustration of V. hornii subsp. clarki on pl. 14, fig. 1 (Turner, 1938) (refigured by Weaver, 1942) shows a species which has all the characters of V. hornii. Furthermore, two specimens in the California Academy of Sciences Collection, from Cape Arago region, Oregon, also belong to V. hornii, as is manifested by their obliquely ovate outline and by the pattern of the hinge.

Venericardia (Pacificor) valletiosensis (Vokes), 1939

Plate 12, figures 1-3


Holotype 15614; loc. A-1022; length 65.0 mm., altitude 63.0 mm.
Paratype 15615; loc. A-1022; length 32.5 mm., altitude 31.5 mm.

Description.—Shell large, heavy, almost circular in outline; umbos moderately inflated; surface with 23 radiating ribs, those on the central portion of the valve being planicostate and separated by flat-bottomed interspaces about two-thirds as wide as the ribs; valve slightly angulate at the sixth rib from the posterior margin, the posterior ribs narrow, somewhat ridged and closer together, the anterior 5 or 6 ribs so interrupted by the growth-lines as to appear to be noded, and separated by interspaces wider than the ribs; growth lines elsewhere on the shell not prominent; humle small and inconspicuous; hinge plate small, the central cardinal of the left valve comparatively small, trigonal in shape and somewhat posterior to the umbo; socket large, curved on both the anterior and the posterior sides; posterior cardinal long, thin, and high; nymph plate thin, high, so close to the posterior cardinal as to suggest a deeply grooved tooth.
Comparison.—M. vallecitosensis may be readily separated from all previously described West American species by the flat-topped ribbing, which more nearly approaches the type characteristic of M. planicosta than is the case in any other recognized species from this region.—[Vokes, 1939, p. 67.]


Discussion.—Venericardia vallecitosensis is characterized mainly by flat ribbing, a feature which would suggest the affinity to the subgenus Venericor, but the presence of the pseudoscutcheon and the low hinge plate indicate that this species should be assigned to the subgenus Pacificor.

The similarities in morphological characters between V. carlosensis and V. vallecitosensis (Vokes) indicate a very close relationship between them. These two species with low hinge and oblique medial cardinal stand isolated from the rest of the Pacificor species and are considered as belonging to an off-shoot with no indication as to their immediate ancestry.

Venericardia (Pacificor) carlosensis (Vokes), 1939
Plate 13, figures 4-9
Holotype 15619; loc. A-1017; length 73.0 mm.; altitude 57.5 mm.
Paratype 15620; loc. A-1017; length (incomplete), 67.0 mm.; altitude 63.0 mm.
Paratype 15621; loc. A-1017; length (incomplete), 51.0 mm.; altitude 45.5 mm.
Paratype 15622; loc. A-1017; length (incomplete), 30.5 mm.; altitude (incomplete) 23.0 mm.

Description.—Shell moderately large, thin for the genus, variable in shape, quadrate to subtriangular; umbos small, anterior; lunule minute, deeply impressed; escutcheon narrowly rounded, elongate; posterior end of shell obliquely angulate; surface with 21 radial ribs, the posterior 5 ribs small, rounded and weakly developed, separated by interspaces of equal width; the 3 ribs anterior to these strongly developed, persistently flat-topped, angulate at the edges, and separated by V-shaped interspaces of equal width; the 5 anterior ribs nodose in appearance due to the strength of the growth-lines and separated by interspaces of equal width; the 8 ribs on the center of the valve minutely nodose in the early stages of development, flat-topped during adolescence, and rounded in the adult; hinge-plate small, the right cardinal curved, narrow and elongate, the nymph-plate long and grooved, the right socket narrow and obliquely set with a small tubercle on the anterior side; the left anterior cardinal small and subtriangular; the posterior cardinal long, thin and curved, the nymph-plate long, low, and so closely set against the posterior cardinal as to appear to be a part of that tooth.

Comparison.—The small umbo and general outline is very suggestive of Gabb's original figure of M. hornii, but the small hinge-plate with the narrow elongate right cardinal and the character of the ribbing are distinctive. The shape and the character of the ribbing is sufficient to distinguish the new subspecies from all other described species of Megacardita.

Additional notes.—The number of ribs is constant: of 40 specimens examined 4 had 20 ribs, 27 had 21, 8 had 22, and 1 had 23. This form occurs at but one locality in the Vallecitos (U.C. loc. A-1017), where it is associated with Plevyora acclilateralis (Gabb), Ostrea libraensis Gabb, Loxotema turrita Gabb, Putamides carbonicola Cooper, and Calyptraea diegana (Conrad). These species suggest that the water was of less than normal salinity, which may be a possible explanation for the thin shell and the great variation in shape.—[Vokes, 1939, p. 68.]

Holotype.—A right and left valve of the one individual. Univ. Cal. Invert. Pal.
Type Coll., No. 15619 from Univ. Cal. loc A-1017, top of a small ridge 800' SW. of Hill 2,200 near centre of south edge of sec. 16, T. 17 S., R. 12 E.

Discussion.—A cursory examination of the more or less flat ribs in V. carlosensis would suggest a relationship to Venericor (="planicosta") group. A more comprehensive study, however, reveals that V. carlosensis has a pseudoescutcheon, a characteristically low hinge and an obliquely inclined medial cardinal (3b). These morphological characters are not found in the subgenus Venericor but are present in the group of species which form an offshoot from the main stocks of Pacificor and which include V. carlosensis and V. valleicosensis.

The thinness of the shell of V. carlosensis was first noticed by Vokes (1939). This was mentioned anew by White (1940). As has been pointed out earlier it would seem that the brackish water environment could also account for other abnormalities which were observed in the hinge of V. carlosensis (see Pl. 13, figs. 8 and 9). It can be seen how the medial cardinal (3b) of the right valve and the anterior (2) and the posterior (4b) left cardinals are split as if they were tripartite. No other explanation for such abnormality can be presented at this time.

On the East Coast, V. (Pacificor) turneri Gardner and Bowles appears to be closely related to V. carlosensis. The striking similarity of the hinges as well as of the outline, which in itself is unusual for venericards, suggest a direct relationship.

Venericardia (Pacificor) transversaria Verastegui, n. sp.

Plate 2, figures 2-4


Shell large, thick, inflated, outline subquadrate. Umbo prominent, strongly curved forward (unfortunately beak, lunule, and part of the hinge are broken in the holotype); anterior margin broadly rounded, ventral margin gently curved, turning abruptly about 90° to the straight posterior margin. With typical Pacificor sculpture modified by superimposed wrinkled laminations consisting of 22 ribs; the 6 anterior radials characterized by having lateral riblets not reaching the anterior margin; 4 of the 6 ribs on the posterior area thin, 2 marginal ribs wider. Interradials linear in the antero-medial portion, becoming gradually wider and U-shaped in the posterior area. Pseudoescutcheon wide, concave, and distinct. Ligamental groove well developed. Hinge heavy, high, and short with a sinuous basal line; dentition not well preserved in the holotype, except the base of the massive and curved middle right cardinal (3b). Pedal muscle scar deep and large; adductor muscle scars deeply impressed. Shell conspicuously thickened at the postero-ventral point of the posterior scar; pallial line irregular, rather far removed from the margin; inner marginal creulations very coarse.

Dimensions of holotype.—Height, 70 mm.; length, 76 mm.; convexity, 29 mm.


Type locality.—Univ. Cal. loc. 3705, NW 1/4 SW 1/4 sec. 24, T. 2 N., R.
18 W., 6,800 feet N. 10° E. of Hill 2150, Simi Hills, Camulos Quad., Ventura Co., California.

Stratigraphic position.—“Martínez marine member” of Nelson, Martínez “group.” Paleocene.

Discussion.—Unfortunately, Venericardia transversaria is based on one specimen, the holotype, which is not well preserved, the beak, the lunule, and part of the hinge being broken off. In spite of this, the rest of the shell shows enough features to justify the establishment of this interesting new species, which is different from any other contemporaneous form of western North America.

V. talara Olsson from the middle Eocene Chacra formation of northwestern Peru is closely related to V. transversaria. The peculiar ribbing consisting of transverse wrinkles is observed in both forms. Although Olsson (1929) related his species to V. rotunda Harris, the ornamentation of the shell suggests that V. talara is a species of Pacificor, and not related to V. rotunda, which probably belongs to the subgenus Glyptoactis.

V. transversaria and V. nelsoni, n. sp., which bear the same locality number, must have come from the same stratigraphic horizon, the “Martínez marine member” of the “Martínez group” of Nelson (1925), Simi Valley, California.

The striking similarity in the external appearance (wrinkled ribs) of V. transversaria to that of the Cretaceous species V. fyfei from New Zealand suggests that V. fyfei or a V. fyfei-like form was probably a radical of the transversaria lineage in the subgenus Pacificor.

Venericardia (Pacificor) taliaferroi Verastegui, n. sp.

Plate 1, figures 15, 16


Shell small, convex, outline obliquely cordate, anterior and ventral margins broadly rounded, the posterior obtusely truncate, the postero-dorsal somewhat arched; umbonal area convex; beak prosogyrate, curved forward, low, at about the anterior one-fourth. Posterior area depressed, slightly concave, characterized by finer ribbing. Sculpture (well preserved in the holotype) consisting of 20 to 22 ribs; the anterior-most 3 ribs V-shaped, the next 11 ribs tripartite with lateral terraces about one-fifth the width of the radials; ribs separated by U-shaped channels; the posterior 7 ribs V-shaped, the second from the last a little higher than the rest; interradials apparently obtusely V-shaped; with fine incrementals on the umbonal area, anteriorly coarsened to give the radials the appearance of being crenulated; periodic constrictions of growth (annual rings) well marked. Lunule impressed, slopes downward and forward. Hinge and interior of the types concealed by coarse matrix.

Dimensions of holotype.—Height, 20.5 mm.; length, 22 mm.; convexity, 9 mm.

Holotype.—Left valve: Stanford Univ. Paleo. Type Coll., No. 7996; collector, H. G. Schenck.

Type locality.—NW ¼ NE ¼ sec. 30, T. 25 S., R. 10 E., ¼ mile SSW of Bench Mark 719, south of Williams Ranch on the Nacimiento River, Adelaida Quad., San Luis Obispo Co., California.

Stratigraphic position.—Dip Creek formation. Paleocene?

Discussion.—Venericardia taliaferroi is a new species which was originally misidentified as V. venturensis Waring. The round ribs and the typical Pacificor distribution of fasciculate (terraced) ribs show that it is unrelated to V. venturensis which belongs to the subgenus Venericor (the "planicosta" group). Unfortunately, the poor state of preservation of V. taliaferroi makes it impossible to determine the suspected presence of the peculiar type of escutcheon (pseudoescutcheon) which is so characteristic of all species of the subgenus Pacificor.

On the basis of ribbing alone, V. taliaferroi appears to be closely related to V. argentea, n. sp., but it can be easily distinguished from that species by having a smaller number of ribs (22) and by the wider interradials.

There is some doubt about the geologic age of V. taliaferroi, and for that reason it is indicated here as questionably Paleocene. It should be pointed out that by its size, general shape, and its smaller number of ribs, V. taliaferroi resembles more closely the Cretaceous than the Paleocene forms. The fossils which were found associated with V. taliaferroi, as reported by Taliaferro (1944), seem to indicate a mixture of Cretaceous and Paleocene elements. The state of preservation leaves much to be desired and until better material is obtained from the Deep Creek formation, no precise dating of the rocks can be made with any degree of certainty.

Venericardia (Pacificor) lisa Verastegui, n. sp.
Plate 21, figures 1, 2

Shell large, outline subquadrate to ovate, the anterior margin passing into the ventral in an evenly rounded arc, the postero-ventral margin attenuate, the posterior slightly curved; umbonal region inflated; beaks low, placed at the anterior one-third. Sculpture (not well preserved in the holotype) consists of 20 to 22 simple, rounded ribs. Ribs almost obsolete in the ventral part of the medial portion of the shell, but distinct to the margin in the anterior and posterior areas. Interradials linear, evanescent in the medial portion and near the ventral area. Incrementals fine, threadlike. Lunule cordate, small; lunular groove wide, trending downward and slightly forward. Pseudoescutcheon present. Hinge plate low and long. Nymph long; ligamental pit in front of the nymph deeply incised; anterior right cardinal (3a), laminar, small; a medial (3b) strong, curved forward, with a long basal margin; a posterior cardinal (5b) thin, cordlike; the left valve with a small, trigonal, elongate anterior cardinal (2) and a thin, curved posterior cardinal (4b). Pedal and adductor muscle scars small and shallowly incised. Inner margin crenulate.

Dimensions of holotype.—Height, 77 mm.; length, 80 mm.; convexity, 27 mm.

Holotype.—Two valves originally in attached position: Stanford Univ. Paleo. Type Coll., No. 8023.
Type locality.—Bluffs along Olequa Creek at Old Ainslee Mill, T. 11 N., R. 2 W., Lewis Co., Washington.

Stratigraphic position.—Cowlitz formation. Upper Eocene.

Discussion.—*Venericardia lisa* is closely related to *I. weaveri*. The relationship is seen in the inflation of the umbonal region and in the low beak. The two species differ in the pattern of the ribbing, which in *I. lisa* is simple and in the ventral part of the medial portion is almost obsolete and smooth after the shell has reached the height of 40 mm. Another difference is that in *I. lisa* the medial cardinal (3b) is not high and scimitar-like but has a long basal margin and the tooth is elongated anteriorly.

Forms found in the Gaviota formation, Santa Inez Mountains, Santa Barbara Co., California, appear to be closely related to *I. lisa*.

Subgenus **Glyptoactis** Stewart, 1930


Type species by original designation: *Venericardia hadra* Dall. Lower Miocene (Chipola formation) of Florida.

The American Miocene *Venericardia* are not so high as the typical or *Venericor* or *Leuroactis*. For this group the new subgeneric name *Glyptoactis* is proposed with *I. hadra* Dall as the type species (Dall, 1903, p. 1429, pl. 53, figs. 11, 13, Chipola). The species differ from the typical in having a curved elevate right cardinal and a small anterior pustule or lateral. The right hinge of a closely related species has been figured by Dall (1903, p. 1430, pl. 53, fig. 12) and his figures of both species have been reproduced by Gardner (U.S. Geol. Survey Prof. Paper 142-B, 1926, p. 90, pl. 17, figs. 11-13). The group is known from the Eocene *I. alticostata* (Harris, Bull. Am. Paleontology, vol. 6, 1919, p. 82, pl. 39, figs. 1-5, Claiborne) — and is still living on the West Central American coast as *V. ewiei* Broderip (Reeve, Conch. Iconica, vol. 1, 1843, pl. 5, fig. 24, Cardita). Judging from the figures, *I. alticostata* from the French Eocene is another member of this group (Cossman and Pisarro, 1906, pl. 31, figs. 97-7, Lutetien-Bartonien). *Cardita* sandiegosensis (from the Eocene of California may also be a *Glyptoactis* (Hanna, Univ. California Bull. Geology, vol. 16, 1927, p. 283, pl. 37, figs. 1-2, 8-9).

The hinge of *Glyptoactis* suggests the minute Mediterranean *Glans* Megerle 1811 (Becquoy, Dautzenberg, and Dollius, Moll. Russillon, vol. 2, 1892, p. 221, pl. 38, figs. 21-25), which has more distinctly laterals and a shorter right cardinal elongated anteriorly. Were it not for the similarity of *Glyptoactis* with some of the species of *Venericardia* s.s., I should place *Glyptoactis* under *Glans*, but the resemblance may be fortuitous, and temporarily at least *Glyptoactis* is better left under *Venericardia*, since it is difficult if not impossible at the present time to recognize the two groups among immature Eocene specimens. These specimens may actually show the development of a subgenus, but such an interesting conclusion could only be accepted after a much more exhaustive study of them has been made. —[Stewart, 1930, p. 151.]

To this original description of *Glyptoactis* one may add that all species included in this subgenus possess the escutcheon cord and fasciculate (tripartite) ribs. The fasciculate ribs are especially well developed in Cretaceous and Paleocene species such as *Venericardia* (*Glyptoactis*) beauvonti Archang, *I. alticostata* (Conrad), *I. (G.) kennei*, n. sp., and other related forms. The species from progressively higher horizons show a gradual waning of this character. *I. (G.) marcki*, n. sp., from the upper Eocene has terraced ribs only in the mature (marginal) part of the

1 Pronounced “lecessah”; the Spanish *lisa*, meaning smooth, is chosen in reference to the smooth surface near the ventral margin.
shell, and the Miocene type of the subgenus V. (G.) hypna Dall shows only a weakly developed trace of terraced ribs in the marginal area.

It should be noted that terraced ribs may occur in other subgenera of Venericardia; but, as in Pacificor, these fasciculate ribs are always confined to the anterior part of the shell, and in a progressive phylogenetic development, become more and more restricted to the anterior area and to the area near the beak, never extending to the ventral margin in the medial part of the shell.

In Glyptoactis, as has already been pointed out, the terraced ribs in their progressive phylogenetic development become weaker in the beak area and look as though they were “pushed off” to the margin of the shell.

The “anterior pustule or lateral,” mentioned by Stewart in the original description of Glyptoactis, may be present in other subgenera and, therefore, is not a diagnostic character of Glyptoactis.

**KEY TO THE SPECIES OF THE SUBGENUS GLYPTOACTIS FROM PALEOCENE AND EOCENE OF WESTERN NORTH AMERICA**

1. Ribs terraced in the antero-medial area
   - 2. Ribs terraced in the medial area only
     - 3. Ribs 30
     - 4. Ribs 21
     - 5. Ribs 18; valve inflated, with full umbo
     - 6. Ribs 17; valve less inflated, pointed umbo

**Venericardia (Glyptoactis) keenae Verastegui, n. sp.**

Plate 1, figures 1-5

**Description.**—Shell small, cordate-subquadrate in outline, anterior and ventral margins broadly rounded, the posterior truncated and the dorsal margin slightly arcuate; umbo strongly convex with the most prominent point above and slightly anterior to the mid-point of the disk; posterior area sharply delineated by a change in sculpture and radially depressed; beak prosogyrate, low and compact. Sculpture distinct, consisting of 30 ribs persistent throughout the entire surface of the shell; of these, the 4 anterior ribs crowded, thin, faintly fasciculate, (slightly terraced); the next 14 ribs conspicuously terraced, so that they appear to be tripartite with a central crest bordered on each side by smaller riblets (the central crest beaded with light funnel-shaped tubercules not discernible upon ribs of the umbonal area); the succeeding 4 ribs with a terraced face only on the posterior side; posterior area with 4 crowded V-shaped ribs; the remaining 4 ribs a little wider, with riblets on the posterior side. Interspaces at the anterior and posterior portions V-shaped; in the medial area, with deep U-shaped channels. Incrementals fine and sharp, more noticeable on the posterior area of the adult shell. Lunule small, distinctly convex, bounded by an incised lateral groove which in the left valve ends ventrally, with the walls of the trough forming a knob (the anterior pustule of Stewart). Escutcheon slightly discernible, bordered below by a cord. Ligamental groove narrowly incised. Nymph narrow and elongate. Ligamental pit not evident. Hinge plate low and short with a straight ventral border; dentition of the left valve consists of a nearly
trigono-pyramidal anterior cardinal (2), isolated from the lunular plate; and a
thin posterior cardinal (4b) broadens toward the ventral end. Pedal muscle scar
small and shallowly incised; adductor muscle scars moderately incised, pallial line
entire and remote from the ventral margin. Inner margins crenulate.

Dimensions of holotype.—Height, 34 mm., length, 34.5 mm.; convexity, 13.5 mm.

Holotype.—Left valve: Stanford Univ. Paleol. Type Coll., No. 7993; collector,
S. W. Muller.

Type locality.—Stanford Univ. loc. 2073; road cut, just south of the middle of
section line between sec. 20 and 29, in sec. 29, T. 15 S., R. 12 E., opposite junction
of Panoche and Silver creeks, Panoche Quad., Fresno Co., California.

Stratigraphic position.—Base of Lodo formation. Paleocene.

Discussion.—Venericardia keenae is interesting for its apparent resemblance to
V. alticostata (Conrad). *V. keenae* differs from *V. alticostata* by having a few more
ribs and by the less ornate sculpture. The two species have a similar outline and
the same pattern of sculpture on the posterior portion, which is characterized by
V-shaped radials. The holotype of *V. alticostata* is described from Gosport sand,
Alabama.

The noteworthy point is that in *V. keenae* we have a representative of the
alticostata stock which occurs in the Paleocene on the West Coast of North America,
and *V. keenae* may be regarded as the stem form of the Pacific Coast species of
*Glyptoactis*.

The fossil is named in honor of Dr. Myra Keen, Curator of Paleontology at
Stanford University, in grateful recognition of the help and advice received through-
out this investigation.

*Venericardia (Glyptoactis) memastersi* Verastegui, n. sp.

Plate 13, figures 2, 3

Description.—Shell small, quadrate in outline, anterior margin evenly rounded,
the ventral slightly curved, the posterior distinctly truncated, making an angle of
90° with the ventral margin; postero-ventral and postero-dorsal ends sharply rounded
to subangular, accentuating the quadr-line outline of the shell. Umbo strongly inflated,
curved forward, prosogyrate, with beak placed at about the anterior one-fourth.
Umbonal ridge, delimiting the posterior area, defined by the change in the coarseness
of the ribs. Sculpture similar to that of *V. keenae*, n. sp., consisting of 21 well-
developed ribs; 4 simple crowded ribs on the anterior portion followed on the medial
portion by 9 ribs definitely terraced on both sides; 8 ribs on the posterior area simple,
V-shaped; the crest of the ribs bears fine nodes which are conspicuous on the ventral
area of the valve. Interradials U-shaped. Incremental sculpture fine. Lunule
small, semicordate, trending forward and downward, with deeply incised lunular
groove. Escutcheon narrow. Hinge plate low and long, with an arched ventral
margin. Nymph thin; ligamental pit inconspicuous. Dentition consisting of pustule-

2 See for example, Harris, G. D., Bull. Amer. Paleont., vol. 6, No. 31, pp. 82-84, pl. 30,
figs. 1-5, 1919.
like anterior left cardinal (2), broken off in the holotype; and a slender, long posterior cardinal (4b). Pallial line entire, closely placed to the margin. Inner margin strongly crenulate.

**Dimensions of holotype.**—Height, 17 mm.; length, 18 mm.; convexity, 8 mm.

**Holotype.**—Left valve: Stanford Univ. Paleol. Type Coll., No. 8011; collector, C. Sternberg.

**Type locality.**—San Clemente Canyon, San Diego Co., California.

**Stratigraphic position.**—La Jolla formation. Middle Eocene.

**Discussion.**—*Venericardia memastersi* is a representative of the subgenus *Glyptoactis* which has a world-wide distribution. *V. domenginica* Vokes, supposedly of the same age, is closely related to *V. memastersi*, but the latter has ribs more pronouncedly tripartite (terraced), has four more ribs, and a greater umbonal convexity. The superficial similarity of *V. natchitoches* Harris from the Weches formation (middle Eocene of Texas) with *V. memastersi* is striking. They are so closely related that by looking at the illustrations alone one would be inclined to regard them as conspecific. But upon further examination, it can be seen that *V. natchitoches* has only 14 ribs and is undoubtedly a different species.

There is a suggestion that in the well-defined phylogenetic lineage of some venericards a progressive decrease in the number of ribs takes place in the progressively higher (younger) members of the lineage. This is shown by the Paleocene *V. keenei*, with 30 ribs and the middle Eocene *V. memastersi* which has only 21 ribs. On the same basis it can be inferred that *V. domenginica* with only 17 ribs occupies a still higher position in the lineage than *V. memastersi*.

The species is named in honor of J. H. McMaster, Chief Geologist of the Honolulu Oil Corporation.

**Venericardia (Glyptoactis) domenginica** Vokes, 1939

**Plate 13, figure 1**


**Holotype** 15011; loc. A-1219; length, 24.5 mm.; altitude, 24.0 mm.

**Paratype** 15012; loc. A-1003 (Pine Canyon, Mt. Diablo); length, 19.2 mm., altitude, 19.0 mm.

**Paratype** 15013; loc. A-1003; length, 14.5 mm.; altitude, 14.1 mm.

**Original description.**—Shell small, moderately inflated, inequilateral, almost circular in outline; umbo small, high, prominent; lunule impressed; sculpture consisting of 17 radial, ridged strongly beaded ribs, separated by round-bottomed interspaces slightly more than half as wide as the ribs, the ribs being finer and closer together on the posterior portion of the valve; posterior cardinal of the hinge in the right valve long, slender, curved, the anterior cardinal in the left valve reduced to a small rugosity bounding the anterior end of the large central socket, with a well-defined anterior lateral pustule.

**Comparison.**—*V. domenginica* differs from the described western Eocene species referred to the Carditidae in size, shape, and character of the ribbing. It finds its nearest analogue in the group of *F. acutocosta* in the Lutetian-Bartonian of France.

These small species of *Venericardia* have not heretofore been studied in the California Eocene. Previous writers have apparently considered them to represent immature individuals of the larger described species, here referred to the genus Megacardita Sacco. They differ from these in possessing a well-developed anterior lateral tooth. Forms similar to *V. domenginica* have been found in the collections from the type Tejon, the Llajas formation, and the vicinity of Mount Diablo.—[Vokes, 1939, p. 66.]
Discussion.—In his original description Vokes questioned the placing of the species *V. domeniginica* in the subgenus *Glyptoactis*. The restudy of the type shows, however, that *V. domeniginica* possesses the diagnostic characters of *Glyptoactis* and, therefore, without doubt belongs to that subgenus.

No new material was available during the present study and the inclusion of the original description and illustration in this report is made for the sake of full coverage of all the venericate species of the Pacific Coast of North America.

**Venericardia (Glyptoactis) marksi** Verastegui, n. sp.

Plate 19, figures 2-4

Description.—Shell small, thin, outline subcircular, the anterior and ventral margins evenly rounded, the postero-ventral truncated, the postero-dorsal slightly arched. Umbo fairly convex, prominent, with the greater inflation in the middle of the disk; beak prosogyrate, heavy, full, placed at about the anterior two-fifths. Sculpture consists of 18 ribs strongly ornamented by fine closely spaced beads along the crests; of these, the 5 in the anterior area thin, simple, separated by wide U-shaped interspaces twice as wide as the ribs; the 8 medial ribs simple in the early umbonal area, but become terraced (tripartite) in the mature part of the shell; interspaces wide, U-shaped; the 5 ribs on the posterior area closely spaced and thin with interspaces V-shaped; increments fine, more visible on the flat-bottomed interspaces. Lunule small, convex. Escutcheon wanting. Hinge rather high for the subgenus; dentition of the right valve consists of a small anterior cardinal (3a), a cuneate long medial cardinal (5b), and a slender posterior cardinal (5b). Interior of the holotype concealed by matrix except for the inner margin, which is strongly crenulate.

Dimensions of holotype.—Height, 20 mm.; length, 18 mm.; convexity, 9 mm.

Holotype.—Right valve: Stanford Univ. Paleo. Type Coll., No. 8021; collector, J. Marks.

Type locality.—Stanford Univ. loc. 183, east side of Live Oak Canyon, Kern Co., California.

Stratigraphic position.—Live Oak member of Tejon formation, 1,760 feet above base and 210 feet below top. Upper Eocene.

Discussion.—*Venericardia marksi*, from the type locality of the Tejon formation, California, is probably a descendant of *V. domeniginica* Vokes. These two species are closely related but *V. marksi* can be readily distinguished from *V. domeniginica* by its heavier and less pointed beak, by its circular outline, and by the greater convexity of the shell.

*V. marksi* appears to be the last member of the *Glyptoactis* stock on the Pacific Coast of North America.

The advanced phylogenetic stage of this species is indicated by almost complete loss of the fasciculate ribs. Only vestiges of terraced ribs can be observed near the margins of the *V. (G.) marksi* in which respect it resembles the type species *V. (G.) hadra* Dall.

This species is dedicated to Dr. Jay Glenn Marks in recognition of his work in the type Tejon area.
Subgenus VENERICOR Stewart, 1930


Type species by original designation: Venericardia planicosta Lamarck (Eocene of the Paris Basin and of the Bracklesham beds of England).

Shell large, heavy, its apparent inflation increased by the thickness of the shell. Outline trigonocordate, strikingly cordate in the profile of the double valves. Umbones inflated, turned inward and forward, that of the right valve a little higher and fuller than the left, placed well forward. Laminae narrow, deep, slightly wider in the right valve than in the left and deeper in the left valve than in the right, delimited by a groove that strongly dents the inner margin. Escutcheon not defined. Anterior extremity short, rounding obliquely into the upcurved base; posterior lateral margin obscurely truncate. Posterior area indicated by the obuse flattening of the shell and a change in the character of the radial sculpture. Radials in 26 on the antero-medial portion of the left valve, possibly 1 more on the right and 7 on the posterior area; the earliest ribsbing very narrow, sharply crested and finely crenate, the adolescent and early adult ribs on the anteromedial portion simple, flat-topped and slightly wider than the U-shaped channels that separate them; the ribs upon the posterior area narrow, crenate, and crowded; radial sculpture overturn by the incremental toward the margins of the adult shell, most persistent anteriorly; no trace of lateral carding but a slight tendency toward an undercutting of the ribs discernible. Ligament deeply inset, marginal, notched on heavy nympha. Hinge plate high, trigonal. A short thin laminar anterior cardinal, a heavy, somewhat scimitar-shaped medial cardinal, and a laminar posterior cardinal produced along the inner margin of the nymph in the right valve; a short anterior and produced posterior cardinal, both of them moderately heavy, and separated by a deep and obliquely produced ligament pit, in the left valve. Inner surface thickened over the area of the adherent mantle. Pedal pit very deep. Anterior adductor scar also very deep and obliquely produced; posterior scar broader, not quite so deep. Palial line ragged and rather far removed from the deeply crenate inner margins.

The description is based on the subgenotype, U. S. National Museum, No. 12704 (pl. 36, figs. 1, 3, 2; pl. 36, figs. 5, 6), from Grignon, in the Paris Basin, the locality from which Lamarck received his type material for the species.

Specimens in our collection from the Bracklesham beds of Selsey, Sussex, differ from those from the Paris Basin in the higher, more anterior beaks, higher hinge plates, slightly lower rib count, and less persistent ribbing.—[Gardner and Bowles, 1939, p. 168.]

KEY TO THE SPECIES OF THE SUBGENUS VENERICOR FROM PALEOCENE AND EOCENE OF WESTERN NORTH AMERICA

1 Ratio of height to length greater than 1: postero-ventral truncate ventiurensis

Ratio of height to length less than 1: postero-ventral margin elongate simiana

Venericardia (Venericor) ventiurensis Waring, 1917

Plate 3, figures 1-4; Plate 4, figure 5

1917. Venericardia planicosta ventiurensis Waring. California Acad. Sci., Proc., ser. 4, vol. 7, No. 4, p. 80, pl. 11, figs. 6, 7, and 9 only.


1950. Venericardia ventiurensis Waring, Scheck and Keen, California Fossils for the Field Geologist, pi. 19, fig. 5. (Refigured holotype).

Shell large, thick, cordate, deeply convex; altitude greater than the length; beaks large, turned forward, nearly touching; lunule small; anterior cardinal margin deeply excavated in angle; posterior cardinal margin deeply grooved and broadly convex; posterior margin convexly truncate; surface ornamented by 25-30 large, square shouldered ribs, which are strong clear to the margins, with deep squared interspaces; posterior ribs narrow and indistinct; entire surface marked by wrinkled lines of growth. Locality 4, L. S. J. U. Pal. Coll.

This subspecies exhibits characteristics different from any of this genus previously found on the Pacific Coast. It is probably characteristic of the Martinez, or lower Eocene. It resembles very closely T. planicosta Harris from the Midway of Alabama and Georgia.

Its chief distinguishing features are the prominent truncation of the submargins, narrowness and sparseness of ribs compared with the later forms, and a nearly constant relation.
between the altitude and length, the former being slightly greater. It is readily distinguished from that in the Tejon, or Upper Eocene. A typical specimen of *V. planicosta venturcnsis* measures 73 mm. in height and 67 mm. in length, while a similarly perfect specimen of *V. planicosta hornii* measures 82 mm. in height and 100 mm. in length.—[Waring, 1917, p. 80.]

Supplementary description.—Shell large, thick, cordate, umbos highly convex and curved forward; posterior region defined by a marked change in character of sculpture, and by a distinct change in the direction of the slope; beaks at about one-fifth the length of the shell. Lunule deeply sunken, large, bordered by an incised lunulare groove in the left valve ending below in a pustule corresponding to a depression in the right valve; right part of the lunule one-third larger than the left. Sculpture consists of 26 to 28 ribs persistent to the margins; in the antero-medial area 20 ribs, V-shaped in the early stage, flat-topped and T-shaped at maturity; in the same area interradials change from V-shaped at the beaks to U-shaped with overhanging rims, tending to constrict the interradials; in the posterior area 8 to 9 ribs crowded, separated by linear interspaces, the 3 or 4 ribs nearest the posterior dorsal margin noticeably broaden away from the beaks, the others remain thin and cordlike. Incrementals faint, wrinkled, cover the whole surface, but anteriorly thicken at the intersection with radials, giving them a nodose appearance. Escutcheon present. Ligament opisthodetic. Nymph narrow and elongated. Ligamental pit shallow. Hinge plate heavy, long and low, ventral margin sinuous; dentition in the right valve a small anterior laminar cardinal (3a), a massive subcuneate middle cardinal (3b) curved forward, and a short thin laminar posterior cardinal (5b). Left valve with a small trigonal tooth (2) pointing up and forward and a high thin posterior cardinal (4b). Pedal and adductor muscle scars strongly incised. Pallial line entire, at a normal distance from the margin. Inner margin strongly crenulate.

Dimensions of holotype.—Height, 73 mm.; length, 67 mm.; convexity, 59 mm.

Holotype.—Right and left valves of a single individual: Stanford Univ. Paleo. Type Coll., No. 159; collector, B. F. Parsons.

Hypotypes.—Stanford Univ. Paleo. Type Coll., Nos. 7998, 7999, 8000.

Type locality.—Stanford Univ. loc. 2097, 3 miles ENE. of Simi Peak near head of east fork of Las Virgenes Canyon, Simi Hills, Camulos Quad., Ventura Co., California.

Stratigraphic position.—“Martinez marine member” of Nelson. Paleocene.

Discussion.—The general outline of *Ienericardia venturcnsis*, the umbonal inflation, the flattened ribs, the pattern of the hinge, and the presence of the escutcheonal cord, are the characteristics which indicate that *I. venturcnsis* belongs to the subgenus *Ienericardia*. This species and *I. simiana*, n. sp., obtained from the same assemblage, are the only members of the subgenus which are known from the Paleocene and Eocene of western North America.

*I. venturcnsis* was thought by Waring to resemble *I. planicosta* of Harris, known now as *I. mediaplata* Gardner and Bowles, but the ration of height to length in *I. venturcnsis* is reverse to that in *I. mediaplata*. On the other hand, *I. simiana*,

from the same faunule as *V. venturensis*, appears to be closely related to *V. media-plata*, and this fact probably accounts for the misinterpretation which was made of it by various authors.

*I. venturensis* may be related to *I. regia* Conrad of the Aquia formation, Maryland'. The sculpture pattern in both species is strikingly similar, although the nodose aspect on the umbo does not appear in the western form. Unfortunately specimens of *I. regia* were not available for study but the published figures suggest that the two species may belong to the same phylogenetic line.

Dickerson* mentioned that *I. venturensis* has prominent nodes with strong V-shaped ribs, but this again appears to be a misrepresentation due to the confusion of *I. venturensis* with *I. transversaria*, n. sp., a species which was contemporaneous with *I. venturensis*.

*I. venturensis* is found at Univ. Cal. loc. A-432, Lower California. This find is interesting to note, since a part of the section of the undifferentiated Paleocene-Eocene of Lower California may be correlated with the "Martínez marine member" of Nelson.

**Venericardia** (Venericor) simiana Verastegui, n. sp.

Plate 4, figures 1-4

1917. *Venericardia planicosta venturensis* Waring, California Acad. Sci., Proc., ser. 4, vol. 7, No. 4, p. 36, pl. 11, fig. 8 only.

Shell large, thick, cordate in outline, anterior margin broadly rounded, the ventral gently curved, sharply rounded at the postero-ventral end, passing into truncated posterior; umbones slightly convex; posterior area set off both by the umbonal ridge and by the difference in sculpture; beaks low, at about the anterior one-fourth. Ribs 28-30; 19 in the antero-medial area persistent, V-shaped at beaks flat-topped throughout the surface of the disk and separated by U-shaped interspaces; posterior area with 9 cordlike ribs crowded, separated by narrow U-shaped inter-radials. Lunule deeply set, convex, pointing downward and backward, bordered anteriorly by a lunular groove; in the left valve the lunular groove ends in a pustule corresponding to a small depression on the right valve. Escutcheon not defined. Wide ligamental groove and elongated nymph, with a deep triangular ligamental pit at its anterior end. Hinge heavy, low, long, with a distinctly sinuous basal margin; dentition strong and prominent; right anterior cardinal (3a) laminar, vertical, minute; a middle cardinal (3b) curved, scimitar-like, with a dorsal edge sharply grooved ventrally; posterior cardinal (5b) thin, almost undifferentiated; paratype No. 8002 with an elongate, cuneate left anterior cardinal (2) and a high, thin, posterior cardinal (4b). Pedal scars small; adductor muscle scars concealed by matrix in all specimens examined; pallial line remote from the strongly crenulate margin.

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Dimensions of holotype.—Height (estimated), 65 mm.; length, 62 mm.; convexity, 25 mm.; paratype: height, 65 mm.; length, 69 mm.; semidiameter, 27 mm.


Paratype.—Stanford Univ. Paleo Type Coll., No. 8002.

Type locality.—Stanford loc. No. 2697, Simi Hills at head of Las Virgenes Canyon, Calabasas Quad., Ventura Co., California.

Stratigraphic position.—"Martinez marine member" of Nelson, Martinez group. Paleocene.

Discussion.—I'. simiana is most closely related to I'. mediaplata from the Midway formation of Wilcox County, Alabama, but I'. mediaplata is less elongated in shape and its medial cardinal (3b) is not so wide at the base.

I'. simiana is distinct from I'. venturensis. The former is longer than high, whereas I'. venturensis is higher than long and is more convex than I'. simiana. The umbo in I'. venturensis is conspicuously high as contrasted with a low umbo in I'. simiana.

Among the original material illustrated by Waring as I'. venturensis the specimen pl. 11, fig. 8, shows all the characteristic features of I'. simiana and, therefore, should be classified as belonging to that species.

Outside of Simi Hills area I'. simiana is found in Stanford Univ. loc. No. 460, Panoche Hills, Fresno County, California.

Subgenus LEUROACTIS Stewart, 1930


Type species by original designation: Venenicorda pilbryi Stewart, lower Wilcox (Nanafalla and Tuscanoma formations) of Alabama.

The subgenus Leuroactis as a section under subgenus Venenicor was first recognized by Stewart in 1930. Gardner and Bowles in 1939 followed this arrangement but did not employ the name in the systematic description except as the heading of the chapter dealing with this systematic unit.

As neither "Section" nor "Group" have a legal status in the International Rules of Zoological Nomenclature, it is preferred to treat Leuroactis as a subgenus.

Leuroactis was introduced by Stewart in 1930 as follows:

An apparently new species is described from Yellow Bluff (Wilcox) which is believed to be related to I'. horatiana rather to I'. planicosta, and these two species are given a new section name Leuroactis.—Stewart, p. 154, 1930.

The short straight right cardinal of I'. pilbryi resembles the corresponding tooth in the hinge of I'. horatiana, and the species seem more closely related to that species than to I'. planicosta and its allies. In I'. planicosta the right cardinal curves antero-dorsally. The difference is best shown in immature specimens (25 to 30 millimeters in length), and there also the resemblance to I'. horatiana may be seen. While this difference is not very great it indicates that I'. pilbryi is off the main stem of I'. planicosta. The new section name Leuroactis is here proposed, with I'. pilbryi as type species. I'. horatiana and its Pacific relative I'. aragonia are placed in this section because they have the straight right cardinal. While all the adult specimens of I'. pilbryi have the straight cardinal, the character is not so well marked on some of the large specimens of I'. horatiana particularly when compared to the hinge of large specimens of I'. regia, which appears to belong with I'. planicosta in Venenicor. I'. pilbryi has the most unique hinge, while that of I'. horatiana approaches the hinge of Venenicor.—[Stewart, 1930, p. 160.]
On the Pacific side of North America, the subgenus *Leuroactis* is represented by nine species, whereas only two species of this subgenus are known from the Gulf province and three from Peru. The abundance of species on the West Coast furnishes ample material for a critical study of *Leuroactis* and permits a more comprehensive diagnosis of the subgeneric characters.

In the revised sense the subgenus *Leuroactis* includes species which possess the following morphological character:

Shell large, thick, moderately convex, outline subcircular to subtrigonal; anterior margin attenuate or sharply rounded passing gradually into gently curved to almost straight ventral margin; postero-ventral margin curving abruptly into broadly rounded postero-dorsal margin. Position of beak at the anterior one-fifth to one-third. Radial ribs in different species vary from 17 to 39.

The distinctive feature of the ornamentation is the progressive change in the character of individual ribs when followed from the beak to the outer margin. The ribs are sharply angular up to about 5 mm. from the beak, then become flat-topped for the next 1 to 3 cm., after which they gradually become broadly rounded. Near the margin of the shell, ribs tend to become obsolete, as for example, in the extreme case of *Venericardia merriami* Dickerson. Along with the morphological development of ribs, from the beak outward, there is a corresponding change in the interradials. In the part of the shell where the ribs are angular, the interradials are V-shaped, and where they become flat-topped, the interspaces are narrow and U-shaped. As the ribs become broadly rounded, the interradials narrow down to linear incisions and gradually become completely overshadowed by the wavy growth lines or incrementals. Lunule cordate, deeply incised. Escutcheon present, well defined by the escutcheonal cord. Hinge plate high and short. Dentition very distinctive, characterized by the straight medial cardinal (3b) which may vary in shape from narrow to broadly triangular. Inner features of the shell normal, not differing from other venericards except for the fact that the inner margins are invariably crenulate.

KEY TO THE SPECIES OF SUBGENUS *LEUROACTIS* FROM PALEOCENE AND EOCENE OF WESTERN NORTH AMERICA

1. Ribs on the anterior area tripartite; noded
   - aragonia
   - Bubs not tripartite

2. (1) Ribs persistent almost throughout (on at least 9/10 of the shell)
   - schevcki
   - Ribs obsolete almost throughout (on at least 9/10 of the shell)

3. (2) Nymphal plate alate; ventral margin of hinge concave at posterior end
   - crescentensis
   - Nymphal plate not alate; margin of the hinge not concave

4. (3) Lunule (right valve) sloping backward
   - alisoensis
   - Lunule (right valve) sloping forward or vertical

5. (4) Medial cardinal (3b) trigonal
   - merriami
   - Medial cardinal (3b) subcuneate (bluntly truncated)
6 (3) Medial (3b) trigonal with wide base, large 
Medial cardinal (3b) cuneate, elongated

7 (6) Antero-dorsal margin broadly and evenly rounded,
22 to 24 ribs
Antero-dorsal margin sharply rounded to subangular, 21 ribs

8 (6) Shell elongate postero-ventrally, 22 ribs
Shell trigono-subquadrate, 24 ribs

Venericardia (Leuroactis) sechenki Verastegui, n. sp.

Plate 4, figures 6-8

Shell large, thick, umbo narrow, convex, elongated diagonally and twisted forward; anterior margin evenly rounded, ventral margin slightly curved, posterior margin truncate; beak prosogyrate, at about the anterior one-third. Ribs 23, broadly rounded in the adult, in the young stage flat-topped, separated by narrow U-shaped interradials gradually becoming linear incisions; 16 ribs on the antero-medial portion, 7 compressed cordlike ribs on the posterior area, those nearest the posterior margin less discernible. Incrementals faint, distinctly wavy about 3 cm. from the beak become more sharply defined and threadlike near the ventral margin. Lamule deeply inset, convex, bordered by a deeply incised lunular groove. Escutcheon present. Ligamental groove well defined. Hinge plate very short and high with a straight ventral margin. Anterior cardinal (3a) broken in holotype but apparently placed vertically; socket (2') unusually deep, almost vertical, curving forward; medial cardinal (3b) very prominent, somewhat twisted forward, with a short basal margin and a knife-edged upper end; socket (4b') narrow, deep throughout its length; posterior cardinal (5b) wanting. Interior not well preserved; pedal muscle scar shallow; adductor muscle scars deeply incised; pallial line distant from the margin. Inner margin distinctly crenulate.

Dimensions of holotype.—Height, 74 mm.; length (estimated), 75 mm.; convexity, 25 mm.


Type locality.—About 2 miles northeast of Simi Peak, Simi Hills, Camulos Quad., Ventura Co., California.

Stratigraphic position.—Santa Susana shale. Lower Eocene.

Discussion.—The presence of Venericardia sechenki is perhaps the most interesting discovery among the northwestern American venericards. This species may represent the basal stem of the subgenus Leuroactis on the Pacific Coast, just as V. pilshryi Stewart appears to be the ancestor of that group in the Gulf Coast and V. pacifica Olsson in the lower Eocene of northwestern Peru. These forms are not closely related, but in the general aspect one may see certain similarities between them. They all possess a straight cardinal tooth (3b) and have similar sculpture. In the eastern and Peruvian forms, the shape of the radials and inter-radials is strikingly similar to those of V. sechenki, despite the greater number of ribs, 35 in V. pilshryi and 32 in V. pacifica.
No other *Venericardia* belonging to *Leuroactis* and related to *V. schencki* has been described from the Paleocene of America. The sudden appearance of the three forms, *V. pilsbryi*, *V. pacifica*, and *V. schencki* in the lower Eocene of the American continents remains an open problem. Gardner and Bowles (1939) said of *V. pilsbryi* that, "Apparently it arose from some ancestor common with the *mediaplata* stock but probably left the main strain prior to Midway time." The origin of the Pacific Coast form *V. schencki*, the analogue of *V. pilsbryi*, is equally uncertain although the present study reveals that *V. simiana*, the Pacific Coast analogue of *V. mediaplata*, is only distantly (if at all) related to *V. schencki*.

*V. schencki* being the earliest representative of the *Leuroactis* clan in the early lower Eocene of the Pacific Coast is probably an allochthonous form of the North Pacific fauna. It is of interest to note that *V. schencki* and *V. pilsbryi* occur approximately at the same stratigraphic position (lower Eocene) and their kinship to *V. pacifica* may bear on dating of the Salina formation of northwestern Peru.

*Venericardia (Leuroactis) crescentensis* Weaver and Palmer, 1922

Plate 6, figures 1-3


**Original description.**—Shell small and subquadrate in outline; posterior dorsal line straight, slightly obtuse; posterior margin straight, extending almost at a right angle to the dorsal margin and abruptly passing into the ventral margin which curves slightly to the anterior end; anterior moderately produced; surface ornamented with 22 wide, flat-topped, radiating ribs with interspaces about one-third of the width of the ribs; on the posterior dorsal region the ribs become narrower and the interspaces wider; an umbonal ridge extends from the beaks to the posterior ventral point.

**Dimensions.**—Length, 15 mm.; height, 12 mm.; thickness, 10 mm.

**Occurrence.**—At locality 358 (Univ. Wash. Pale. Coll.) at Joice Station, one-fourth of a mile east of Tongue Point railroad, Port Crescent, Clallam County, Section 11, Township 9 North, Range 8 West.—[Weaver and Palmer, 1922, p. 19.]

**Supplementary description.**—(Based upon hypotype Univ. Cal. No. 30196). Extremely large shell measuring about 100 mm. in height; beak placed at about the anterior one-fourth. Sculpture consisting of 22 ribs; 16 ribs on the antero-medial portion, extending to the second annual ring (approximately 30 mm.), the fine concentric incrementals override the whole surface beyond and become coarse toward the margin of the shell; in the posterior area 6 to 7 ribs discernible, reaching the ventral-posterior margin. Lunule elongate, rather convex, bordered by a distinct lunular groove. Hinge plate high and short, its ventral margin characteristically concave in the posterior end. Nymph conspicuously alate, projecting from a short and wide nymphal body. Dentition strong, in harmony with the ponderous size of the shell: laminar right anterior cardinal (3a) long, placed on the posterior border of the lunular plate; medial cardinal (3b) unusually pronounced, cuneate, sharply edged, slightly curving forward and transversely depressed on the antero-ventral margin; posterior cardinal (3b) long and narrow, placed on the anterior
border or base of the nymphal body. Pedal and adductor muscle scars, as well as pallial line, deeply incised. Inner margins smooth to faintly crenulate.

*Dimensions of hypotype.*—Right valve, Univ. Cal. Invert. Pal. Type Coll., No. 30196; height, 100 mm.; length, 112 mm.; convexity 37 mm.

Holotype.—Right valve: Univ. Wash., No. 170. (Cal. Acad. Sci. Type Coll., No. 7433.)

*Type locality.*—Univ. Wash. loc. 348, a quarter of a mile east of Tongue Point, Crescent Bay, Clallam Co., Washington, sec. 22, T. 21 N., R. 8 W.

*Stratigraphic position.*—Crescent formation. Lower Eocene.

*Discussion.*—The original description of *Venericardia crescentensis* was based upon a specimen of a young individual. The supplementary description given here is based on a very large hypotype, a specimen which was figured by Weaver in 1942. This specimen is the largest of all the venericards from the North Pacific Coast that have been examined during this investigation.

*V. crescentensis* appears to be a distinct offshoot of the main phylogenetic line of the subgenus *Leuroactis*. It is characterized by the heaviness of the hinge with deep sockets to accommodate the large teeth; by the nymphal plate which is distinctly alate and protruding on the postero-dorsal margin, and lastly, by the concavity of the postero-ventral margin of the hinge.

It is to be noted that a direct correlation appears to exist between the strength of the posterior concavity in the ventral margin of the hinge plate and the degree of alation of the nymphal plate. The stronger the concavity of the hinge, the more pronounced is the winglike structure on the nymphal plate. These morphological characters are static as they show no perceptible trend or change through the stratigraphic range of the species.

These two characters are developed to a high degree in *V. crescentensis*, *V. merriami* Dickerson, and *V. alisoensis*, n.sp., and may be justly regarded as true phylogenetic characters uniting these three West Coast species in a distinct lineage or stock. No representatives of this stock have been as yet recognized outside of western North America.

*Venericardia* (Leuroactis) *alisoensis* Verastegui, n.sp.

*Plate 10, figures 1-3*

*Description.*—Shell large, thick, subquadrate in outline, the anterior margin sharply rounded, the ventral only slightly curved, passing through an evenly rounded postero-ventral part into a truncate posterior margin. Umbo somewhat flat, with low, prosogyrate beak. Sculpture (badly preserved in the holotype) consists of 24 rounded ribs, 16 on the antero-medial portion, 8 on the posterior area; interradials linear; both ribs and interradials lose their sharpness and become obsolete at diameter of 40 mm.; fine wavy incrementals cover the disk. Lunule small, deeply inset; lunular groove almost vertical with lower end slightly pointing backward. Escutcheon not well preserved. Hinge low and short, its basal margin sinuous and concave at the posterior end. Ligamental groove and pit shallowly incised; nymphal alate as in *V. merriami* Dickerson, projecting toward the dorsal margin; dentition strong, consisting of a laminar right cardinal (3a); a medial cardinal (3b) cuneate,
trigonal, with a wide basal margin and thin upper end; and a posterior right cardinal (5b) cordlike, standing out on the anterior border of the alate nymphal plate. On the holotype only the shallowly incised pedal and anterior adductor muscle scars preserved.

*Dimension of holotype.*—Length (estimated). 99 mm.; convexity 27 mm.


*Type locality.*—Univ. Cal. loc. 7019, west side of Aliso Canyon (West) beds striking northwest and dipping west. Fossils occur in narrow lenses. Elev. 1,820 feet, Los Angeles Co., California.

*Stratigraphic position.*—Llajas formation. Middle Eocene.

*Discussion.*—The holotype of *Venericardia alisoensis* unfortunately is an incomplete specimen. The species appears to be closely related to *V. merriami* Dickerson of Oregon by having a low beak, small umbonal convexity, the same general pattern of the hinge plate and, above all, the same type of alate nymphal plate. They differ, however, in the character of ornamentation and the two species can also be separated by the fact that *V. alisoensis* has a triangular medial whereas in *V. merriami* the medial cardinal is only subcuneate with a blunt upper end. Furthermore, in *V. merriami* the radial ribs become obsolete sooner, within the first 10 mm. from the beak, and most of the shell shows only fine concentric increments. In *V. alisoensis* the radial sculpture persists to approximately 40 mm. from the beak.

*Venericardia (Leuroactis) merriami* Dickerson, 1914

Plate 8, figures 1-7


1929. *Venericardia ionensis* Waring, Clark, Stratigraphy and Faunal Horizons of the Coast Ranges of California, pl. 3, fig. 13.

1943. *Venericardia aragonia* Arnold and Hannibal, Weaver, Univ. Washington Publ. Geol., vol. 5, p. 137, pl. 32, fig. 3 and fig. 6 (only).

*Original description.*—This subspecies of *V. planicosta* is apparently the end member of an evolutionary series which begins with the typical *V. planicosta* in the Martinez, the Lower Eocene group of California. The middle member is *V. planicosta hornii* (Gabb) of the lower Tejon. This form in the adult stage lacks the marked radial ribbing of *V. planicosta hornii* (Gabb), and it is in general a higher form as well. The concentric ribbing of this form is much stronger than that of the lower Tejon subspecies. Young individuals, however, resemble the lower Tejon form so closely that one is not warranted in recognizing the subspecies upon the basis of the immature forms.

*Dimension:* Height 70 mm.; length 70 mm.

This subspecies resembles *V. potapaensis* Clark & Martin, of the Maryland Eocene in that the radial ribbing in both forms is becoming obsolete. They appear to differ in shape, however. The type, which is figured, is an extreme case of lack of radial ribbing. Other specimens associated with it at the same locality show fairly distinct ribbing in the neighborhood of the unions. This species is one of the most characteristic forms of the Siphonolida suturcensis Zone. It occurs abundantly but poorly preserved at a University of California locality eight miles south of Ione, Amador County, California, at the O'Neill Sandstone Quarry, Sec. 27, T. 5 N., R. 10 E., Mt. Diablo B. L. and M., in strata which were previously recognized as Ione. It is associated at this place with *Murexoturris hornii* Gabb, *Turritella merriami* Dickerson, and a few other species. This fauna proves the Ione to be only a facies of the Tejon Eocene.
Type.—No. 241, and eotype, No. 222, Cal. Acad. Sci. Locality 25, Roseburg Quadrangle, Oregon, near the center of Sec. 19, T. 26 S., R. 3 W., on the east bank of Little River, at its confluence with the Umpqua, underneath the bridge at that point.

Named in honor of Professor J. C. Merriam of the University of California.—[Dickerson, 1914, p. 118.]

Revised description.—Shell medium to large, trigono-cordate in outline, anterior margin sharply rounded, the ventral almost straight, the postero-ventral attenuated, and the postero-dorsal broadly rounded. Umbones flattened especially on the disk; beaks low and prosogyrate; umbonal ridge distinct, delimiting the posterior area from the medial portion, the posterior area measured opposite the pramontory in the nymphal plate making an angle or less than 90° with the axial plane of the shell. Sculpture consisting of 19 ribs less conspicuous than those of V. aragonia Arnold & Hannibal; ribs apparently noded, somewhat flat-topped and simple on the frontal area; interradials narrow, U-shaped at the beaks, and linear and disappearing on the umbones, giving place to concentric increments covering most of the shell surface in a definite wavy pattern, faint at the beginning, and becoming coarse in the adult stage. Lateral deeply inset. Escutcheon present. Nymphal plate distinct, strongly alate, projecting toward the postero-dorsal margin; ligamental pit shallowly incised as a short groove placed at the anterior end of the nympha. Hinge plate high and short, bearing a characteristic Leuropectis dentition, consisting in the right valve of a small, laminar anterior cardinal (3a); an almost straight, subcuneate medial cardinal (3b) with a wide base, and a thin short posterior cardinal (5b); left valve with a conspicuous long thin anterior cardinal (2) and a thin, long, high posterior cardinal (4b), sloping toward the ventral margin of the hinge. Pedal and adductor muscle scars deeply incised; pallial line entire, normally placed. The inner margins fairly crenulate.

Dimension of holotype.—Height, 63 mm.; length 73 mm.; convexity 47 mm.

Holotype.—Right and left valves of a single individual: Cal. Acad. Sci. Type Coll., No. 241; collector, R. Martin.

Type locality.—Cal. Acad. Sci. loc. 25, Roseburg Quad., Douglas Co., Oregon.

Stratigraphic position.—Upper Umpqua formation. Lower Eocene.

Discussion.—Ermericardia merriami was defined as a subspecies of V. planicosta by Dickerson in 1914. In 1925 Hanna concluded that V. merriami was only a member of a gradational series within the limits of the species V. ionensis Waring. Many years later, because of the priority, Stewart replaced the name ionensis by aragonia. Thus, since 1925 merriami was suppressed as a synonym first under ionensis and later under aragonia.

A critical study of Dickerson’s holotype of V. p. merriami reveals a number of important morphological characters which justify the reinstatement of V. merriami as a distinct species.

Several contrasting characters distinguish V. merriami from V. aragonia. These characters vary within certain limits in each of the species but the general pattern does not change. Specifically V. merriami lacks tripartite frontal ribs, has less prosogyrate and much lower beaks and less inflated umbos, the angle between the posterior area and the axial plane of the shell is less than 90°, and lastly, V. merriami has less conspicuous ribs and a distinctively alate nymphal plate. The differentia-
tion of these two species is even more sharply marked in the young specimens, as is shown in Plates 8 and 9. One can see from the figures the twisted and higher beak of the immature *V. aragonia* and the beaded character of its much more conspicuous tripartite early ribs. The young individual which was figured by Dickerson as a paratype of *merriami* has all these diagnostic characters and, therefore, belongs to *V. aragonia*. By contrast, the other immature specimens of *V. merriami* show much lower and less prosogyrate beaks and have a weak or obsolete sculpture.

*V. crescentensis* Weaver and Palmer, from the lower part of the Umpqua formation in Oregon, appears to be the ancestor of *V. merriami*. The relationship of the two forms is manifested by the conspicuous alation of the nymphal plate. In California, *V. alisoensis*, n. sp., from the Simi region seems to be closely related to the Oregon form, but the scarcity of material prevents an analysis of the degree of relationship.

**Venericardia (Leuroactis) smileyi** (Vokes)

*Plate 10, figures 4, 5*

1939. *Megarditida* (*Venericor*) *aragonia* (Arnold & Hannibal) *smileyi* Vokes, New York Acad. Sci., Annals, vol. 38, pp. 67-68, pl. 6, figs. 1-2 (only). (For fig. 3 see under *Venericardia* *jaquiguensis* (Vokes).)

**Original description.**—Shell large, heavy, with prominent umbo; posterior broadly rounded from umbo to posterior ventral edge where quite angulate, the ventral margin broadly rounded to the anterior cardinal edge, the shell there rounding sharply to the straight anterior cardinal margin; lunule small, deeply impressed; escutcheon elongate, well developed; surface with 31 rounded subobsolete ribs separated by narrow linear interspaces; the posterior 5 ribs narrower and less well developed than those on the rest of the valve; right valve of the hinge with a large trigonal and curved cardinal; left valve with a small elongate anterior cardinal and an elongate curved posterior cardinal, the posterior cardinal broad ventrally.

**Comparison.**—This subspecies may be distinguished from *M. aragonia* (Arnold & Hannibal) by the stronger ribbing. In specimens of size equivalent to that of the holotype of the subspecies *smileyi*, the ribbing is totally obsolete. The large trigonal cardinal in the right valve of this subspecies also differs greatly from the narrow elongate cardinal in *M. aragonia*. The size of this cardinal is quite variable in the latter species, but in none of the specimens examined does it approach the size or the trigonal outline which is characteristic of the California subspecies. The details of the outline serve to separate this form from any of the other described species from the West Coast Eocene.—[Vokes, 1939, p. 68.]

**Revised description.**—Shell large, umbo gently convex, beak low, placed at about the anterior one-third, outline trigono-subquadrate, anterior margin sharply rounded, the ventral straight, the posterior straight, forming an angle of 70° with the ventral margin. Typical *Leuroactis* sculpture, consisting of 24 apparently rounded ribs, poorly preserved in the holotype; 16 ribs on the antero-medial portion wide, subobsolete beyond 60 mm. from the beak, high, but more noticeable posteriorly; the posterior area with 8 thin, crowded cordlike ribs, the 3 near the posterodorsal margin somewhat wider; interradials linear, disappearing near the margin; incrementals with wavy pattern, crowded and becoming coarse with age. Lunule deeply inset, convex anteriorly and upward. Escutcheon narrow. Nymph thin; nymph plate weakly alate; ligamental pit deeply inset, wide and large. Hinge short, rather low, with an arched ventral margin; right cardinal (3a) thin, almost vertical; medial cardinal (3b) deltoid, curved; posterior right cardinal (5b) long, thin. Muscle scars and paliial line not exposed in holotype.
Dimension of holotype.—Height, 78 mm.; length, 86 mm.; convexity, 28.7 mm.


Type locality.—Univ. Cal. loc. 672, SE ¼ NW ¼ sec. 24, T. 18 S., R. 14 E., Coalinga Quad., Fresno Co., California; massive sandstone forming southern portion of the crest of Parson's Peak.

Stratigraphic position.—Avenal sandstone, 45 feet above the base. Middle Eocene.

Discussion.—Venericardia smileyi is here revived because it appears that at least two species were confused by Vokes. In the first place, V. smileyi is only distantly related to V. aragonia and cannot be regarded as a subspecies of the latter. (See phylogenetic chart.)

A scrutiny of the types shows that the paratype of V. smileyi actually belongs to V. joaquinensis (Vokes) as restricted in the present report. The original figure of the hinge of the holotype, (unfortunately reversed in the process of reproduction), Vokes (1939) pl. 6, fig. 2) showed a deltoid medial cardinal (3b) obliquely curved. Referring to this tooth Vokes said, "... right valve of the hinge with a large trigonal and curved cardinal." and on the same page, V. smileyi is said to have a "large trigonal cardinal." In reality, a large trigonal cardinal characterizes V. joaquinensis (Vokes) and not V. smileyi. Only the paratype of Vokes' V. smileyi has a socket (3b') wide enough to accommodate such a large trigonal cardinal. It is, therefore, concluded that this paratype should be removed from V. smileyi and assigned to V. joaquinensis.

During the course of the present investigation, permission was obtained to expose the hinge of V. joaquinensis. This hinge shows a socket large enough to accommodate the large trigonal cardinal mentioned by Vokes. A series of specimens of V. joaquinensis in the Stanford University Collection shows that the shape and the size of this tooth are constant characteristics of the species which adds further support for the restriction of the name V. smileyi to the holotype of Vokes.

No other specimens of this species were seen during the course of this study. The holotype is not well preserved and its exact relationship, therefore, must remain in doubt until more and better material becomes available.

Venericardia (Leuroactis) aragonia Arnold and Hannibal, 1914

Plate 9, figures 1-6


1914b. Venericardia planicosta merriami Dickerson (partim), California Acad. Sci. Proc., ser. 4, vol. 4, p. 118, pl. 11, fig. 1b (only) (paratype of V. merriami Dickerson).


1915. Venericardia planicosta var. ionsensis Waring in McLaughlin, California Min. Ber., Bull. 69, Folio, pl. 1, fig. 22 (name and figure).


1929. Venericardia ionsensis Waring, Clark, Stratigraphy and Faunal Horizons of the Coast Ranges of California, pl. 3, fig. 8.


1943. *Venericardia aragonia* Arnold and Hannibal. Weaver, Univ. Washington, Publ. Geol., vol. 5, p. 137, pl. 25, figs. 2, 3, 4, and 5, pl. 32, figs. 4, 5, 10, and 11 (only).

Shell large, thick, trigono-cordate in outline, anterior margin rounded, attenuate, the ventral nearly straight, the postero-ventral margin also attenuate, and the postero-dorsal broadly rounded. Umbo convex, curved forward, umbalal ridge distinct, delimiting the flattened posterior area at an angle of approximately 90° with the axial plane of the shell; beaks rather high and distinctly pointed, placed at about the anterior one-fourth. Sculpture consisting of 10-20 ribs; on the young shell the ribs well developed, beaded at the beaks, becoming flat-topped for a distance of up to 25 mm. from the beaks; the anterior 4 or 5 ribs faintly tripartite. In the adult shell ribs rounded, become gradually obsolete, especially on the disk; in the senile stage ribs faintly discernible around the posterior side of the medial portion. Interradials flat-topped and sharply linear on rounded ribs; incremental faint, wavy on the disk, becoming coarse with age and more prominent on the anterior and posterior areas of the shell. (The holotype shows some well-marked annual rings spaced about 10 mm. apart.) Lunule deeply inset, the part in the right valve about three times as large as that in the left valve; lunular groove almost vertical but sloping down and backward. Escutcheon well defined. Nymph with a flaring, broad base; ligamental groove shallowly incised; ligamental pit shallow but well defined. Hinge plate high and rather short with a straight ventral margin; dentition strong, anterior right cardinal (3a) thin, laminar; middle cardinal (3b) cuneate, long, straight, sometimes transversely grooved along the ventral margin; the posterior cardinal (5b) long, thin, cordlike; the left valve (hypotype, Univ. Cal. Pal. Type Coll., No. 30175) with an anterior cardinal (2) bluntly elongate and a posterior cardinal (4b) sloping in the ventral part to the basal margin of the hinge. Interior with deeply incised small pedal and adductor muscle scars. Pallial line entire, slightly rugose. Inner margins crenulate.

**Dimensions of neotype.**—Height, 73 mm.; length, 82.5 mm.; convexity, 20 mm.

**Neotype (Stewart, 1938).**—Right valve, Stanford Univ. Paleo. Type Coll., No. 619; collector, H. Hannibal.


**Type locality.**—Umpqua Valley, Oregon.

**Stratigraphic position.**—Umpqua formation. Lower Eocene.

**Discussion.**—Early investigators regarded *Venericardia aragonia* as an important stratigraphic marker and made use of it in the regional and even inter-continental correlation in America. For a number of years forms from central and southern California that are now recognized as distinct species were identified by most workers as *V. aragonia* or *V. ionensis*. Even the Gulf Coast form, *V. horatiana* Gardiner from the Wilcox formation, Texas, has been on several occasions treated by different authors as conspecific with *V. aragonia*. Furthermore, *V. parinensis* Olsson from Parinas formation of northwestern Peru was also considered to be related to the Oregon species.
The lack of proper discrimination of species and the general confusion which involved the species *V. aragonia, V. ionensis, V. merriami, V. horatiana, and V. parinensis,* was in all probability due to the extreme brevity of the original description of *V. aragonia* ("*V. hornii* with obsolete ribs") and the lack of adequate illustrations.

For a better understanding of the *aragonia* problem it is necessary to review the history of the case.

In June, 1914, Arnold and Hannibal proposed the name *aragonia* for the venericard from the Umpqua formation, Oregon, with the following brief description "*V. hornii* with obsolete ribs, (variety *aragonia* A.& H.)." Six months later, Waring, in a paper on "Eocene Horizons of California," mentioned a fossil which he named *V. planicosta ionensis* Waring from the east side of San Joaquin Valley. The figure of *V. p. ionensis,* published by Waring shortly thereafter in McLaughlin (1915), was of a specimen from the Umpqua formation of Oregon.

In December of the same year, Dickerson (1914), discussing the "Fauna of the Siphonalia sutterensis Zone in the Roseburg Quadrangle, Oregon," described a new subspecies, *V. planicosta merriami* Dickerson, of which one figured specimen (fig. 1b) is now recognized as *V. aragonia*.

Later, Hanna (1925), in his paper on the "Notes on the Genus *Venericardia* from the West Coast of North America," claimed that a gradational series existed within the species *V. ionensis* and that the species varied within definite, but wide limits. At one extreme of the series Hanna placed forms with a high beak and broad and heavy hinge (*aragonia*), at the other extreme were forms with a low beak and a narrower hinge (*merriami*). Hanna concluded that "his (Dickerson's) 'type' and 'cotype' of *V. p. merriami* become plesio-types of *V. ionensis* Waring." Subsequent workers have followed Hanna in this conclusion and the name *merriami* was generally suppressed as a synonym under *V. ionensis*.

In the meantime, as no holotype of *V. aragonia* could be found (it perhaps never existed) Stewart in 1930 designated as neotype of *aragonia* the specimen of *V. p. ionensis* which was figured by Waring in 1917. Stewart wrote: "... in absence of specimens from the Arago formation, the specimen figured by Waring (1917, pl. 11, fig. 1) from the Umpqua formation, Oregon, which was said to have been collected by Hannibal, is here designated the neotype of the "variety" *aragonia*, it being impossible to establish a holotype or a lectotype for this name." It will be observed that the figure of *V. p. ionensis* published by Waring in 1917 is a slightly enlarged reproduction of the picture of *V. p. ionensis* which he published in McLaughlin in 1915, at the time the "variety" *ionensis* was first established. There is little doubt that the illustration of 1917 was prepared from the same negative which was used in 1915.

Because of the priority of the name *aragonia*, Stewart had placed, and rightly so, the name *V. ionensis* as a synonym under *V. aragonia*.

Subsequent workers accepted the suppression of *V. merriami* and *V. ionensis* as synonyms of *V. aragonia* and a general belief prevailed that these names referred to the same species. The present study shows, however, that there is a good reason
for the reinstatement of *V. merriami* as a valid species, distinct from *V. aragonia*.

The examination of the *V. merriami* holotype at the California Academy of Sciences, shows that it is different from *V. aragonia*, although it is true that the figured paratype and appears to be conspecific with *V. aragonia*.

*V. merriami* is distinguished from *V. aragonia* by the absence of tripartite ribs, by the less inflated umbo, lower and less prosogyrate beak, and by having a distinctly alate nympha plate. The sum of these characters is judged to be sufficient for a specific separation of the two forms and for the reinstatement of Dickerson's name *V. merriami* as a valid species. The presence of the alate nympha plate in *V. merriami* merits a particular emphasis. This structure is regarded to be a phylogenetic character of the crescentensis stock, distinguishing it from *V. aragonia* and similar forms which constitute the aragonia stock.

Previous authors have mentioned that *V. horatiana* Gardner may be conspecific with *V. aragonia*, and Rutsch (1936) even went so far as to propose that the name *horatiana* be replaced by *aragonia*. It is true that on the basis of published figures, the two forms are almost indistinguishable and the idea of having only one name for the two at first glance appears to have a sound basis. Fortunately, good specimens of *V. horatiana* in the Stanford University Collection were available for study. They appear to be specifically identical with the hypotype of *V. horatiana* figured by Stewart in 1930 and by Gardner and Bowles in 1939. A large suite of specimens of *V. aragonia* afforded a careful comparison of these two species. On close examination, one sees dissimilarities of at least specific magnitude between the two forms. For example, in young specimens the beaks differ noticeably in shape being weakly twisted and lower in *V. horatiana*; the latter has three or four more ribs, and individual ribs are somewhat narrower than in *V. aragonia*; furthermore, *V. horatiana* is less convex and has not so thick a shell. Thus, it is concluded that although the forms have a striking superficial resemblance, the difference between them is of sufficient magnitude to justify separation. The specific difference between them may well be explained as modifications brought about by slight environmental changes at the extremes of their geographic range.

The existence of a close relationship between *V. aragonia* from the West Coast with *V. horatiana* from the Gulf Coast region is of paramount significance. This is one of few instances among the venericards where a genetic connection can be recognized in the forms occurring on the opposite coasts of the continent, and it furnishes a basis for a long range correlation. *V. horatiana* is a key fossil for the upper Wilcox in the Gulf Province and *V. aragonia* occurs in the Umpqua formation in Oregon. The affinity between these two species permits the conclusion that the beds containing them are the same or approximately the same in age.

The suggestion by several authors that *V. parinensis* Olsson of northwestern Peru could be a correlative of either *V. aragonia* or *V. horatiana* appears to be untenable. A fine specimen of *V. parinensis* in the Stanford University Collection shows no close resemblance to either *V. aragonia* or *V. horatiana*. The hinge of *V. parinensis* resembles that of *V. stewarti* Gardner and Bowles.
Venericardia (Leuroactis) joaquinensis (Vokes), 1939

Plate 11, figures 1-4; Plate 12, figures 4-6

1939. Megacardita (Venericardia) hornii (Gabb) joaquinensis Vokes, New York Acad. Sci., Annals, vol. 38, pp. 69-70, pl. 8, fig. 1 (only); pl. 9, fig. 1 (only) (for pl. 8, fig. 2 and pl. 9, fig. 2 see under Venericardia vokesii Versteegh.)

Original description.—Shell large, heavy, variable in shape; umbos prominent, inflated, anterior; posterior cardinal margin convex, rounded, ventral nearly straight, anterior broadly rounded ventrally but quite sharply rounded dorsally, straightening out to the small, deeply impressed lunule; sculpture consisting of 21 subobsolete radial ribs appearing as low rounded waves on an otherwise smooth surface; hinge-plate large; posterior cardinal on the left valve long, thin, strongly curved; anterior cardinal short, thin, small; nymph-plate strong, appressed to the posterior cardinal at the anterior end.

Comparison.—This subspecies may be distinguished from typical M. hornii (Gabb) and M. hornii elahi (Weaver and Palmer) by the obsolete character of the ribbing. It differs from M. aragoinia (Arnold & Hannibal) in being less angular at the posterior ventral margin, more sharply rounded anteriorly, and in having lower, more massive umbos. It differs from other described forms of Megacardita in both shape and character of ribbing.

The principal variation in this species is in the height-length ratio. The general features of the outline, notably the shape of the anterior and posterior ends, are constant and appear to be characteristic. The subspecies is confined to the collections from the Reef Ridge area and is notably abundant in the chert-pebble conglomerate at the base of the section in the area.—[Vokes, 1939, p. 69.]

Revised description.—Shell large, heavy, round to subquadrate in outline, anterior margin attenuate, the ventral Nearly straight, and the posterior rounded, slightly truncate, makes an angle of 80° with the ventral margin. Umbo convex, bordered posteriorly by a weak umbonal ridge separating it from the posterior area; beak prosogyrate, low, full. Sculpture consists of 22 to 24 ribs; ribbing semi-obsolete on the disk, but apparently distinct on the beaks (ornamentation poorly preserved near the beaks); 16 ribs on the antero-medial area, wide and simple; 8 thin ribs crowded on the posterior portion, the 3 nearest to the postero-dorsal margin nearly obsolete; interradials shallow, U-shaped at the beaks, becoming linear and obsolete over the main part of the shell. Incrementals faint, crowded, wavy throughout, becoming more distinct and coarse with age. Lunule small, deeply inset, convex; deep lunular groove trending downward and forward. Escutcheon well defined by a prominent escutcheon-cord. Nymph long, resting on a weakly alate nymphal plate; ligamental pit deeply incised, wide and elongate. Hinge plate rather high but short, with a straight basal margin. Dentition heavy, in the holotype (left valve) consisting of an almost vertical, straight, elongated anterior cardinal (2) and a long, large posterior cardinal (4b) broadens ventrally; in the paratype (a right valve), a long and almost vertical anterior cardinal (3a); a large, trigonal medial cardinal (3b) characteristic of this species; and a heavy, large right posterior cardinal (5b) also broadens ventrally. Inner features of holotype concealed by matrix; paratype showing pedal and adductor muscle scars well-incised, pallial line entire, normally placed. Inner margins crenulate.

Dimensions of holotype.—Height, 95 mm.; length, 108 mm.; convexity, 33 mm.


Type locality.—Univ. Cal. loc. 4170, west side of Big Tar Canyon, Reef Ridge area, Chohame Quad., Kings Co., California.

Stratigraphic position.—Avenal sandstone and Domengine formation. Middle Eocene.

Discussion.—Venericardia joaquinensis was originally established by Vokes as a subspecies of Megacardita (Venericor) horntii. A critical study of the type material shows that V. joaquinensis has the characters of the subgenus Leuroactis and is only distantly related to V. horntii which belongs to the subgenus Pacificor.

Venericardia joaquinensis was originally described by Vokes in 1939 on the basis of one holotype and two paratypes, but the hinge was only seen in one of the paratypes.

During the present studies, permission was obtained from Professor Durham of the University of California to prepare the hinge in the holotype. The exposed hinge proved to be so markedly different from that of the figured paratype that one could not escape the conclusion that the two specimens belong to two species. The hinges of these two forms have general patterns which characterize two phylogenetic lineages within the aragonia stock.

The hinge in the holotype of V. joaquinensis is characterized, mainly, by wide trigonal socket (3b') to accommodate a large trigonal medial cardinal (3b). The hinge on the paratype, on the other hand, has the general aspect of that of V. aragonia, although it is somewhat lower, and the socket (3b') is narrow to fit a cuneate medial cardinal. The paratype in question, however, cannot be regarded as conspecific with V. aragonia. It is more obliquely elongate in outline, and lacks the bundled or fasciculate ribs. For this reason it is taken to represent a distinct species which is here named V. vokesi, n. sp.

It will be noted that the other paratype of V. joaquinensis, after the preparation of the concealed hinge, proved to be conspecific with the holotype.

The true joaquinensis hinge (in the holotype) characterizes the lineage which, as far as is known, culminated with V. popenozi n. sp., in the upper Eocene, whereas the hinge of V. vokesi belongs to a group of species that appears to have left no descendants and died out at the close of the middle Eocene.

Venericardia (Leuroactis) vokesi Verastegui, n. sp.

Plate 14, figures 1-3

1939. Megacardita (Venericor) horntii (Gabb) joaquinensis Vokes, New York Acad. Sci. Annals, vol. 38, pp. 69-70, pl. 8, fig. 2 (only); plate 9, fig. 2 (only).

Description.—Shell large, thick, cordate, obliquely elongate in outline; anterior and posterior margins attenuate, ventral very gently curved, and postero-dorsal gently arched. Umbo convex and umbal ridge even less sharply defined than in V. joaquinensis; beak prominent, prosogyrate, placed at about the anterior one-fourth. Sculpture consisting of 22 broadly rounded ribs; 4 simple ribs well defined in the
upper one-third of the shell, becoming inconspicuous and giving place to fine wavy increments, which become coarse with age; on the posterior area eight weak ribs, relatively more discernible than the anterior ones and traceable to the ventral margin. Interradials linear in the early part of the shell, becoming obsolete, represented over most of the shell by weakly defined shallow furrows. Lunule deeply inset, the right part three times as large as the left; lunular groove trending downward and backward. Escutcheon well defined by the hinge-cord. Hinge rather low and short, with a straight ventral margin; nymph narrow, long; ligamental pit shallowly incised; dentition strong, consisting in the right valve of a short, small anterior cardinal (3a); a cuneate, elongate medial cardinal (3b) slightly curved forward; and a long posterior cardinal (5b); the figured holotype (left valve) with an anterior cardinal (2) curved upward and forward, elongate and truncate at the upper end, and a curved, long and high posterior cardinal (4b). Other inner characters concealed by matrix.

*Dimensions of holotype.*—Height, 84 mm.; length, 100 mm.; convexity, 30 mm.


*Paratype.*—Right valve: Stanford Univ. Paleo. Type Coll. No. 8016, from southwest corner Sec. 17, T. 17 E., R. 23 S., half a mile east of Big Tar Canyon, Cholame Quad., Reef Ridge sheet, Kings Co., Cal.

*Type locality.*—Two thousand feet east and 500 feet north of SW corner sec. 17, T. 23 S., R. 17 E., half a mile east of Big Tar Canyon, Cholame Quad., Reef Ridge sheet Kings Co. California.

*Stratigraphic position.*—Avenal sandstone, 20 feet above base. Middle Eocene.

*Discussion.*—*Venericardia vokesi* is characterized by an elongate outline and by the pattern of the hinge; it can be distinguished from its nearest relative *V. aragonia* Arnold and Hannibal, by the absence of tripartite (fasciculate) ribs in the frontal area near the beaks.

The new species *V. vokesi* is based on a specimen which was originally described by Vokes as a paratype of *V. joaquinensis*. Subsequent preparation of the holotype hinge of *V. joaquinensis* proved it to be specifically different from that of the paratype which had a much more elongate outline, less massive beak, and a lunule sloping downward and backward in contrast with the vertically sloping lunule in *V. joaquinensis*.

*Venericardia* (*Leuroactis*) *popenoei* Verastegui, n.sp.

Plate 22, figures 1-3

Shell large, thick, subquadrate in outline, with an almost horizontal antero-dorsal margin; the anterior margin evenly rounded toward the ventral margin; the antero-dorsal end sharply rounded to subangular. Umbonal convexity perceptibly flattening toward the anterior margin. Beak prosogyrate, low, placed at about the anterior one-third. Sculpture of *Leuroactis* type, consists of 21 ribs, simple, flat-topped in the early stage, then rounded until the shell is 35-40 mm. high, and finally become almost obsolete; differentiated as follows: 14 ribs on the antero-medial portion and 7 ribs in the posterior area, not so wide, but slightly more
conspicuous. Interradials U-shaped on the tip of the umbo, become linear and gradually disappear, their position still marked by the wavy pattern of increments. Growth lines or increments distinct in the holotype, fine in the young stage but become coarse with age. Lunule of holotype (left valve) narrow and high; lunular groove well incised, trending downward and forward. Escutcheon present and distinctly defined by the escutcheonal cord. Ligamental groove wide and deep. Nymph thin and short; ligamental pit long, incised and rough. Hinge plate rather short and low with an almost straight ventral margin. Dentition (left valve) consists of a bean-shaped anterior left cardinal (2) isolated from the lunular arch, a triangular socket (3b') wide to accommodate a large trigonal cardinal (3b) (a distinctive character of this species), and a thin, high posterior cardinal (4b) slightly broadened ventrally. Pedal muscle scar small, adductor muscle scars shallowly incised. Pallial line entire, distinct from margin, apparently represented by a band of transverse rugosities Inner margins crenulate.

Dimensions of holotype.—Height, 112 mm.; length, 115 mm.; convexity, 31 mm.


Type locality.—Univ. Cal. at Los Angeles loc. L-581, east side of main branch of Sespe Gorge, Ventura Co., California.

Stratigraphic position.—“Coldwater” formation “just below Eocene-Sespe contact.” Upper Eocene.

Discussion.—Venericardia popenoei, beautiful representative of the subgenus Leuroactis, unfortunately is represented by one incomplete specimen in which the postero-ventral portion is missing. The rest of the valve is in a good state of preservation showing all the features characteristic of the subgenus.

The flexuous curvature in the convexity of the shell and the striking hinge plate distinguish this species from any other Leuroactis. Its closest relative appears to be V. joaquinensis (Vokes) from the Avenal sandstone, middle Eocene of California. They can be distinguished by the slight concavity in the anterior area of the shell and by the wider trigonal socket (3b') in V. popenoei.

This species is the last known member of the subgenus Leuroactis, the group which was abundant on the Pacific side of America. Starting in lower Eocene with V. schencki, the group reached its climax with V. popenoei in the uppermost Eocene and probably died out at the close of the Eocene, as there are no further records in the Tertiary of any species of this group. However, some Recent forms such as V. megastropha (Gray) have sculpture and hinge remarkably similar to those of Leuroactis.

It is interesting to note that no representative of Leuroactis is recorded in the upper Eocene of eastern America and Peru. The restricted geographic occurrence of V. popenoei to the North Pacific of America may be taken as an additional evidence that Leuroactis, like Pacificor, had its metropolis in western America, as Venericor did in eastern America.
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Kew, W. S. W.


Kleinpell, Robert M.


Lamy, Ed.


Marks, Jay G.


Merriam, Charles W., and Turner, F. E.


Merriam, Charles W.


Nelson, Richard N.


Olsson, A. A.


Rutsch, R.


Schenck, Hubert G., and Keen, A. Myra


Schenck, Hubert G., and Kleinpell, Robert M.


Sellards, E. H., Adkins, W. S., and Plummer, F. B.

White, Robert T.


Woodring, W. P.

PLATES

PLATE I (40)
EXPLANATION OF PLATE 1 (40)

Figure 1-5. *L'enericardia* (*Glyptoactis*) *keenae* Verastegui, n. sp. .......... 41

Holotype, a left valve, (Stanford Univ. Paleo. Type Coll., No. 7993), from Stanford Univ. loc. 2073, road cut just south of the middle of section line between secs. 20 and 29, in sec. 29, T. 15 S., R. 12 E., opposite junction of Panoche and Silver Creeks, Panoche Quad., Fresno Co., California. Base of the Lodo formation. Paleocene.

1. Exterior of holotype.
2. Front view.
3. Dorsal view.
4. Posterior view.
5. Interior.
6a. Diagram of hinge of holotype.

6-9. *L'enericardia* (*Pacificor*) *mulleri* Verastegui, n. sp. ............... 20

Holotype, a right valve, (Stanford Univ. Paleo. Type Coll., No. 7994), from the same locality as of fig. 1. Base of the Lodo formation. Paleocene.

7. Interior.
7a. Diagram of hinge.
8. Posterior view.

10-14. *L'enericardia* (*Pacificor*) *argentea* Verastegui, n. sp. ............. 25

Holotype, a left valve, (part below the dotted line is reconstructed), (Stanford Univ. Paleo. Type Coll., No. 7995), from the same locality as figs. 1 and 6. Base of the Lodo formation. Paleocene.

10. Exterior of holotype.
11. Front view.
12. View of hinge.
12a. Diagram of hinge.

15, 16. *L'enericardia* (*Pacificor*) *taliferroi* Verastegui, n. sp. .......... 38


15. Exterior of holotype.
16. Hinge of paratype, a left valve, (Stanford Univ. Paleo. Type Coll. No. 7997).
PLATE 2 (41)
### EXPLANATION OF PLATE 2 (41)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1, 5. <em>Ienericardia (Pacificor) nelsoni</em> Verastegui, n. sp.</td>
<td>21</td>
</tr>
<tr>
<td>1. Interior of holotype.</td>
<td></td>
</tr>
<tr>
<td>2. Diagram of hinge of holotype.</td>
<td></td>
</tr>
<tr>
<td>5. Front view of holotype.</td>
<td></td>
</tr>
</tbody>
</table>

2-4. *Ienericardia (Pacificor) transversaria* Verastegui, n. sp. | 37 |
| Holotype, a right valve (part of beak above dotted line reconstructed), (Univ. Cal. Invert. Pal. Type Coll., No. 32804-a), from the same locality as figure 1. |
| 2. Interior of holotype. |
| 3. Diagram of hinge of holotype. |
| 4. Front view of holotype. |
PLATE 3 (42)
EXPLANATION OF PLATE 3 (42)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-3. Venericardia (Venericor) venturensis Waring</td>
<td>45</td>
</tr>
<tr>
<td>1. Front view of hypotype, two valves in attached position. (Stanford Univ. Paleo. Type Coll., No. 7998).</td>
<td></td>
</tr>
<tr>
<td>2. Exterior of left valve of hypotype.</td>
<td></td>
</tr>
<tr>
<td>3. Rear view of hypotype.</td>
<td></td>
</tr>
<tr>
<td>4. Venericardia (Venericor) venturensis Waring</td>
<td>45</td>
</tr>
<tr>
<td>4. Interior of hypotype, a right valve, (Stanford Univ. Paleo. Type Coll., No. 7999).</td>
<td></td>
</tr>
<tr>
<td>4a. Diagram of hypotype from Stanford Univ. loc. 2697.</td>
<td></td>
</tr>
<tr>
<td>5. Venericardia (Pacificor) nelsoni Verastegui, n. sp.</td>
<td>21</td>
</tr>
<tr>
<td>5. Exterior of holotype.</td>
<td></td>
</tr>
</tbody>
</table>
PLATE 4 (43)
EXPLANATION OF PLATE 4 (43)

Figure

Page

1. *Venericardia* (*Venericor*) *simiana* Verastegui, n. sp. ............... 47


1. Interior of paratype (Stanford Univ. Paleo. Type Coll., No. 8002).

2-4. *Venericardia* (*Venericor*) *simiana* Verastegui, n. sp. ............... 47

Holotype, a right valve, (Stanford Univ. Paleo. Type Coll., No. 8001), from the same locality as fig. 1. "Martinez marine member" of Nelson, Martinez "group." Paleocene.

2. Front view of holotype.
3. Interior of holotype.
4a. Diagram of hinge of holotype.
4. Exterior of holotype.

5. *Venericardia* (*Venericor*) *venturensis* Waring ................... 45

From the same locality as fig. 1. Note the greater convexity than in *V. simiana*. "Martinez marine member" of Nelson, Martinez "group." Paleocene.

5. Front view of hypotype (Stanford Univ. Paleo. Type Coll., No. 8000).

6-8. *Venericardia* (*Lenroactis*) *schencki* Verastegui, n. sp. ............... 50

Holotype, a right valve, (Stanford Univ. Paleo. Type Coll., No. 8003), from about 2 miles NE of Simi Peak, Simi Hills, Camulos Quad., Ventura Co., California. Santa Susana shale. Lower Eocene.

7. Front view.
8. Interior of holotype.
8a. Diagram of hinge of holotype.
EXPLANATION OF PLATE 5 (44)

Figure Page

1-4. Venericardia (Pacificor) susanaensis Verastegui, n. sp. ................. 22

Holotype, both valves originally in attached position, (Stanford Univ. Paleo. Type Coll., No. 8004), from McCray Oil Wells, Oil Canyon, Camulos Quad., Ventura Co., California. Santa Susana shale. Lower Eocene.

1. Interior of left valve.
2. Front view of holotype.
3. Interior of right valve.
3a. Diagram of hinge of right valve.
4. Exterior of left valve.

5-7. Venericardia (Pacificor) diabloensis Verastegui, n. sp. ................. 27

Holotype, a left valve, (Stanford Univ. Paleo. Type Coll., No. 411), from Marsh Creek, Brentwood, Contra Costa Co., California. "D" member of Meganos formation. Lower Eocene.

5. Front view of holotype.
7. Hinge of holotype.
7a. Diagram of hinge of holotype.
EXPLANATION OF PLATE 6 (45)

**Figure**

1. **Venericardia (Leuroactis) crescentensis** Weaver and Palmer ........ 51


   1. Exterior of hypotype.
   2. Interior of hypotype.
   2a. Diagram of hinge of hypotype.

3. **Venericardia (Leuroactis) crescentensis** Weaver and Palmer ........ 51

EXPLANATION OF PLATE 7 (46)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-2. <em>Ineriecardia (Pacificor) durhami</em> Verastegui, n. sp.</td>
<td>23</td>
</tr>
<tr>
<td>Holotype, both valves in attached position, (Stanford Univ. Paleo. Type Coll., No. 5005), from 1 1/2 miles W. of Vickers Hot Springs, Ventura Co., California, Juncal formation. Lower Eocene.</td>
<td></td>
</tr>
<tr>
<td>1. Exterior of right valve showing crushed ventral portion.</td>
<td></td>
</tr>
<tr>
<td>2. Dorsal view of holotype.</td>
<td></td>
</tr>
<tr>
<td>3-5. <em>Ineriecardia (Pacificor) lutmani</em> Turner</td>
<td>26</td>
</tr>
<tr>
<td>3. Hinge of left valve.</td>
<td></td>
</tr>
<tr>
<td>4. Anterior view of right valve.</td>
<td></td>
</tr>
<tr>
<td>5. Hinge of right valve.</td>
<td></td>
</tr>
<tr>
<td>5a. Diagram of hinge of right valve.</td>
<td></td>
</tr>
</tbody>
</table>
EXPLANATION OF PLATE 8 (47)

Figure

1, 4, 7. *Jenericardia* (*Leuroactis*) *merriami* Dickerson ................. 53


1. Hinge view of right valve.
1a. Diagram of hinge of right valve.
4. Interior of left valve.
7. Exterior of left valve.

2, 3. *Jenericardia* (*Leuroactis*) *merriami* Dickerson ................. 53


2. Anterior view.
3. Posterior view showing fossilized ligament.

5, 6. *Jenericardia* (*Leuroactis*) *merriami* Dickerson ................. 53

Hypotype, a right valve, (Stanford Univ. Paleo. Type Coll., No. 8007), from the same locality as figs. 2, 3. Upper Umpqua formation. Lower Eocene.

5. Anterior view showing convexity and shape of beak.
6. Exterior of right valve of the same young specimen.

8. *Jenericardia* (*Pacificor*) *lutmani* Turner ................. 26


8. Right valve showing weathered exterior.
EXPLANATION OF PLATE 9 (48)

**Figure**

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1-3. <em>Venericardia (Leuroactis) aragonia</em> Arnold and Hannibal</td>
<td>57</td>
</tr>
<tr>
<td>1. Exterior of neotype.</td>
<td></td>
</tr>
<tr>
<td>2. Hinge of neotype.</td>
<td></td>
</tr>
<tr>
<td>2a. Diagram of hinge of neotype.</td>
<td></td>
</tr>
<tr>
<td>3. Anterior view of neotype.</td>
<td></td>
</tr>
<tr>
<td>4. <em>Venericardia (Leuroactis) aragonia</em> Arnold and Hannibal</td>
<td>57</td>
</tr>
<tr>
<td>4. Interior of hypotype.</td>
<td></td>
</tr>
<tr>
<td>5, 6. <em>Venericardia (Leuroactis) aragonia</em> Arnold and Hannibal</td>
<td>57</td>
</tr>
<tr>
<td>5. Anterior view of left valve showing beaded and tripartite character in the early stages of ribs.</td>
<td></td>
</tr>
<tr>
<td>7-9. <em>Venericardia (Pacificor) oregonensis</em> Verastegui, n. sp.</td>
<td>25</td>
</tr>
<tr>
<td>7. Exterior of holotype.</td>
<td></td>
</tr>
<tr>
<td>8. Anterior view.</td>
<td></td>
</tr>
<tr>
<td>9. Interior of holotype.</td>
<td></td>
</tr>
<tr>
<td>9a. Diagram of the hinge of holotype.</td>
<td></td>
</tr>
</tbody>
</table>
EXPLANATION OF PLATE 10 (49)

Figure

1-3. *Venericardia (Leuroactis) alisoensis* Verastegui, n. sp. .................. 52
   Holotype, a right valve, (Univ. Cal. Invert. Pal. Type Coll., No. 30176), from west side of Aliso Canyon (West), beds striking NW and dipping W (Elev. 1,320 feet), Los Angeles Co., California. Llajas formation. Middle Eocene.
   1. Exterior of holotype.
   2. Dorsal view.
   3. Interior.
   3a. Diagram of hinge of holotype.

4, 5. *Venericardia (Leuroactis) smileyi* (Vokes) ....................... 55
   4. Exterior of holotype.
   5. Hinge of holotype.
PLATE 11 (50)
EXPLANATION OF PLATE 11 (50)

Figure Page

1, 3, 4. *Venericardia (Leuroactis) joaquinsis* (Vokes) ................. 60

   Holotype, a left valve, (Univ. Cal. Invert. Pal. Type Coll., No. 15616), from west side of Big Tar Canyon, Reef Ridge area, Cholame Quad., Kings Co., California. Avenal sandstone, Middle Eocene.
   1. Interior of holotype.
   1a. Diagram of hinge.
   3. Anterior view.
   4. Exterior.

2. *Venericardia (Leuroactis) joaquinsis* (Vokes) ................. 60

   Hypotype, a right valve, (Stanford Univ. Paleo. Type Coll., No. 8016), from 2,000 feet N., 500 feet E of SW corner sec. 19, T. 14 S., R. 12 E., Panoche Hills, Panoche Quad., Fresno Co., California. Domengine formation. Middle Eocene.
   2. Hinge view of hypotype.
EXPLANATION OF PLATE 12 (51)

Figure

1. 2. *Venericardia* (Pacificor) *vallecitoseis* (Vokes) .......................... 35

   1. Hinge view.
   2. Exterior of left valve.


4-6. *Venericardia* (Leuroactis) *joaquinensis* (Vokes) ........................ 60

   4. Interior.
   5. Exterior.
   6. Anterior view.
EXPLANATION OF PLATE 13 (52)

Figure

Page

1. *Venericardia (Glyptoactis) domenginica* Vokes ......................... 43


   1. Exterior of holotype × 1.5. (After Vokes).

2, 3. *Venericardia (Glyptoactis) nicmastersi* Verastegui, n. sp. .......... 42

   Holotype, a left valve, (Stanford Univ. Paleo. Type Coll., No. 8011), from San Clemente Canyon, San Diego Co., California. La Jolla formation. Middle Eocene.

   2. Interior of holotype.
   2a. Diagram of hinge, × 2.
   3. Exterior of holotype, × 1.5.

4, 5. *Venericardia (Pacificor) carlosensis* (Vokes) ....................... 36


   4. Exterior of right valve of holotype.
   5. Dorsal view of holotype.

6-9. *Venericardia (Pacificor) carlosensis* (Vokes) ....................... 36

   All from San Carlos Creek, San Benito Co., California. Domengine formation. Middle Eocene.

   6. Exterior of left valve of a hypotype, both valves in attached position, (Stanford Univ. Paleo. Type Coll., No. 8012).
   7. Interior of left valve of hypotype (Stanford Univ. Paleo. Type Coll., No. 8013).
   7a. Diagram of hinge.
   8. Abnormal hinge of right valve of hypotype, (Stanford Univ. Paleo. Type Coll., No. 8014).
   8a. Diagram of same hinge figured in 8.
EXPLANATION OF PLATE 14 (53)

Figure

<table>
<thead>
<tr>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1, 2. <em>Venericardia</em> (<em>Leuroactis</em>) <em>vokesi</em> Verastegui, n. sp. .......... 61</td>
</tr>
<tr>
<td>1. Interior.</td>
</tr>
<tr>
<td>1a. Diagram of hinge of holotype.</td>
</tr>
<tr>
<td>2. Exterior.</td>
</tr>
<tr>
<td>3. <em>Venericardia</em> (<em>Leuroactis</em>) <em>vokesi</em> Verastegui, n. sp. .......... 61</td>
</tr>
<tr>
<td>3. Interior of paratype.</td>
</tr>
<tr>
<td>3a. Diagram of hinge.</td>
</tr>
</tbody>
</table>
EXPLANATION OF PLATE 15 (54)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1, 2, 6. <em>Venericardia (Pacificor) herreini</em> Verastegui, n. sp.</td>
<td>24</td>
</tr>
<tr>
<td>1. Interior of holotype.</td>
<td></td>
</tr>
<tr>
<td>3. Diagram of hinge.</td>
<td></td>
</tr>
<tr>
<td>2. Exterior.</td>
<td></td>
</tr>
<tr>
<td>4. Anterior view.</td>
<td></td>
</tr>
<tr>
<td>5. Exterior of left valve.</td>
<td></td>
</tr>
<tr>
<td>3-5. 7. <em>Venericardia (Pacificor) calafia</em> Stewart</td>
<td>28</td>
</tr>
<tr>
<td>Hypotype, a left valve, (Cal. Acad. Sci. Type Coll., No. 1828), from one mile SE of Oil City, Fresno Co., California. Domengine formation. Middle Eocene.</td>
<td></td>
</tr>
<tr>
<td>3. View of hinge of hypotype.</td>
<td></td>
</tr>
<tr>
<td>3a. Diagram of hinge.</td>
<td></td>
</tr>
<tr>
<td>4. Anterior view.</td>
<td></td>
</tr>
<tr>
<td>5. Dorsal view.</td>
<td></td>
</tr>
<tr>
<td>7. Exterior of left valve.</td>
<td></td>
</tr>
</tbody>
</table>
EXPLANATION OF PLATE 16 (55)

Figure

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. <em>Venericardia (Pacificor) calafia</em> Stewart</td>
<td>28</td>
</tr>
<tr>
<td>2-3. <em>Venericardia (Pacificor) calafia</em> Stewart</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td>Hypotype, (topotype) both valves originally in attached position (Stanford Univ. Paleo. Type Coll. No. 8017).</td>
</tr>
<tr>
<td></td>
<td>2. Exterior of right valve.</td>
</tr>
<tr>
<td></td>
<td>3. Anterior view.</td>
</tr>
</tbody>
</table>
EXPLANATION OF PLATE 17 (56)

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1, 2. <em>Venericardia (Pacificor) calafia</em> Stewart</td>
<td>28</td>
</tr>
</tbody>
</table>

Hypotype, both valves originally in attached position, (Stanford Univ. Paleo. Type Coll. No. 8017), from Llajas Canyon, Simi Valley, Ventura Co., California. Llajas formation, Middle Eocene.

1. Interior of left valve.
1a. Diagram of hinge of left valve.
2. Interior of right valve.
2a. Diagram of hinge of right valve.
EXPLANATION OF PLATE 18 (57)

**Figure**

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1, 4.</td>
<td><em>Venericardia (Pacificor) hornii</em> (Gabb) ........................................ 33</td>
</tr>
<tr>
<td>1.</td>
<td>Exterior of right valve (after Stewart).</td>
</tr>
<tr>
<td>4.</td>
<td>Original figure of <em>F. hornii</em> (after Gabb).</td>
</tr>
<tr>
<td>2, 3.</td>
<td><em>Venericardia (Pacificor) hornii</em> (Gabb) ........................................ 33</td>
</tr>
<tr>
<td>2.</td>
<td>Exterior, × 1.5.</td>
</tr>
<tr>
<td>3.</td>
<td>Dorsal view, × 1.7.</td>
</tr>
<tr>
<td>5, 6.</td>
<td><em>Venericardia (Pacificor) hornii</em> (Gabb) ........................................ 33</td>
</tr>
<tr>
<td>5.</td>
<td>Interior of hypotype.</td>
</tr>
<tr>
<td>5a.</td>
<td>Diagram of hinge.</td>
</tr>
<tr>
<td>6.</td>
<td>Front view of hypotype, showing low convexity in contrast with Pl. 19, fig. 1.</td>
</tr>
<tr>
<td>7.</td>
<td><em>Venericardia (Pacificor) hornii</em> (Gabb) ........................................ 33</td>
</tr>
</tbody>
</table>
EXPLANATION OF PLATE 19 (58)

Figure | Page
--- | ---
1, 5, 6. *Jenricardia* (*Pacificor*) *gabbi* Verastegui, n. sp. .......................... 30


1. Anterior view.
2. View of hinge.
3. Exterior.

2, 3, 4. *Jenricardia* (*Glyptoactis*) *marks* Verastegui, n. sp. .......................... 44

Holotype, a right valve, (Stanford Univ. Paleo. Type Coll., No. 8021), from east side of Live Oak Canyon, Kern Co., California. Tejon formation (type locality). Upper Eocene.

2. Interior of holotype.
3a. Diagram of hinge.
4. Exterior of holotype.

7. *Jenricardia* (*Pacificor*) *horni* (Gabb) ................................. 33

Hypotype, a young specimen, right valve, (Calif. Acad. Sci. Type Coll., No. 7728), from east bank of Live Oak Creek, about three-fourths of a mile from the mouth. Tejon formation (type locality). Upper Eocene.
EXPLANATION OF PLATE 20 (59)

Figure | Page
--- | ---
1, 4, 5. *Jenericardia* (*Pacificor*) *clarki* Weaver and Palmer | 32


1. Anterior view of hypotype.
2. Exterior of left valve showing weathered area.
3. Exterior of right valve; dashed line shows true round outline.

2, 3. *Jenericardia* (*Pacificor*) *clarki* Weaver and Palmer | 32


2. Interior of holotype.

6. *Jenericardia* (*Pacificor*) *clarki* Weaver and Palmer | 32


EXPLANATION OF PLATE 21 (60)

Figure  

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1, 2.</td>
<td>39</td>
</tr>
<tr>
<td>3, 4.</td>
<td>31</td>
</tr>
</tbody>
</table>

1, 2. *Venericardia (Pacificor) lisa* Verastegui, n. sp.  
1. Exterior of hypotype.  
2. Interior of hypotype.  
2a. Diagram of hinge of hypotype.

3, 4. *Venericardia (Pacificor) weaveri* Verastegui, n. sp.  
Holotype, a right valve, (Stanford Univ. Paleo. Type Coll. No. 8024), from SE bank of Stillwater Creek, 1 1/4 miles NW of Vader, Washington. Cowlitz formation. Upper Eocene.
3. Exterior of hypotype.  
4. Interior.
EXPLANATION OF PLATE 22 (61)

Figure       Page

1-3. *Enericardia* (*Leuroactis*) *papenoei* Verastegui, n. sp. ................. 62


1. Interior of holotype.
2. Exterior of holotype.
3. Anterior view of holotype.
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</tr>
</tbody>
</table>
I

Hull, Quebec ........................................ 280
Hungry Hollow formation ....................... 378
Hussakof, L., and Bryant, W. L. .................. 129, 139
Huxley, T. ............................................ 61
Hyatt, A. .............................................. 27-33, 227, 350
Hydromedusae .................................... 369, 205
Hydrozoa ............................................ 63, 174, 175, 181
Hyman, L. H. ........................................ 72, 189
Hyphalmyiformes .................................. 107, 115, 17

I

Iatan formation .................................. 344
iatai, Ethelococoides ............................... 52, 343
Ichthyodoridae ..................................... 104
Igna, Bolivia ........................................ 195, 195
Ihdeirosidae ........................................ 183
idriaensis, Ostrea ................................. 407, 430
imbicatula, Venus ................................. 410
Incomediae ......................................... 410
impositus, Ohioaspis ............................... 8, 107
imposition, Ohioaspis ............................. 110, 117

Impressum, Stereoceras .......................... 370, 373, 379
incerta, Platystrophia ............................. 21, 276
incule, Buscyon .................................... 22, 247
incomplete, 249, 257, 290
Index Animalium .................................. 370
inferofacial, Platystrophia ......................... 272
insectis, Hexarhizites ............................. 195
Int. Rules Zoological Nomenclature ............. 368
Interradii ........................................... 177, 192
interstratius, Latiro fusus ......................... 325
Intra-Coastal Canal, N.C. .......................... 95
Ione formation ................................... 447
ionense, Venericardia ............................. 450, 451
ionensis, Venericardia ............................. 452, 454
ioenosis, Venericardia ............................. 447, 478, 450, 458
Irdeale, T. .......................................... 225, 230
Ichneumancusus ................................. 128
Islandicus, Cotus ................................. 289
Islandicus, Cotus ................................. 289
Islandicus, Cotus ................................. 289
Isho ................................................ 241, 212
Ithaca beds ........................................ 61, 68, 366
Ithaca formation .................................. 377

J

Jackson, Mississippi ............................ 239
Jackson's law ..................................... 80
Jefferson formation ............................... 105, 114
Jeffrey, J. G. ....................................... 236, 239
"Jellyfish" .......................................... 61, 70
Jellyfish ............................................ 173, 297
Jennings Co, Indiana .............................. 111
Johannisemis, Leuroactis .......................... 50, 51, 444, 454
Joipecoceris ................................. 466, 466, 445, 450
Venericardia ..................................... 50, 51, 444
Johansson, A. W. ................................ 400
Johnston, W. A. ................................... 311
Jongmans, Halle, and Gothan ................. 161, 169
Juncal formation ................................. 417
Junonina, Voluta ................................ 233
Jurassic, Euphyt...
Studies of Carboniferous Crinoids 319
Pt. I. A group of Pennsylvanian crinoids from the Ardmore Basin 323
Pt. II. Delocrinids of the Brownsville formation of Oklahoma 340
Pt. III. Description of two new Cremsyphonaria from the Pennsylvanian of Nebraska 342
Pt. IV. On new species of Alcmenocarida and Ulrichicrinus from the Fayetteville formation of Oklahoma 345
Strimple, Melba 340
Strohm, Oklahoma 340, 341
Studer, F. V. 374, 376
Sturany, R. 292
Subhorzochoanitis 9
Subumbrella 175
Subventricosus, Archiacoceras 369
Succoeceras 36, 47
sucker, Malacoceris 358
superbus, Lophopectus 142
sussanaensis, Pacificor 404, 416, 416
Venericardia 404, 416, 416
suterensis, Siphonella 447, 452
Swindale, J. H. 242
Sycotopus 244, 247
Symphysial teeth 141
T
Tanioglossa 231
talara, Venericardia 403, 432
taliaferroli, Pacificocor 403, 414, 416
Venericardia 404, 416, 416
suterensis, Siphonella 447, 452
Swindale, J. H. 242
Sycotopus 244, 247
Symphysial teeth 141
Tetranodonoceras 365, 380
Tetraeroceras 271
Tetraurina, Kirklandia 16, 16, 18
tetraurina, Kirklandia 19, 20 173, 175, 178
Todidae 190, 206
Nodosaria 156
thannatocoenetic 105
Theacoceras 365
Theolenia 105, 118
Thorsen, G. 329, 341, 252
Ticonderoga, New York 25, 27
Tilly Lake, South Carolina 246
Titanichthys 141
Tomlinson, C. W. 233
Tongue Point, Washington 445
Torell, O. M. 157
torley, Carboniceras 3
Toufoungian 45
tracebeatus, Leviafusus 255
Trachylium 173-175, 190
Trachymedesae 175, 199
transversaria, Pacificocor 410, 416, 416
Venericardia 410, 416
trapezium, Pasciolaria 250
Traquair, R. H. 113
Trenton Hull formation 271
trentonsenid, Platystrophia 24, 272, 276
Trenton limestones 23
Trentonianus, Pleurobrachia 271
Trematodoceras 265, 266
Trophoceras 265, 266
Tropholites 365
Trophephus 365, 266
Tropholites 365, 266
Trophoceras 365, 266
Trionycoidellidae 24, 24
trousuls, Urosalpinx 25, 259, 259
Tryon, G. W. 335, 254
tulipa, Pasciolaria 254, 257, 257
Tully pyrite bed 139
Tuloumnoeceras 294, 341
Tuloumnoeceras 294, 341
Tuloumnoeceras 294, 341
Tuloumnoeceras 294, 341
Tuloumnoeceras 294, 341
Tuloumnoeceras 294, 341
Tuloumnoeceras 294, 341
Tuloumnoeceras 294, 341
Tuloumnoeceras 294, 341
U
Ule, F. O. and 7, 9, 11, 14
Uliechicrinus 347
Ullsteinius 103
Umpqua formation 419, 439, 451
Umpqua River, Oregon 448
Umpqua Valley, Oregon 451
undatum, Bucinum "unicostata", Platystrophia 241
uniplacata, Platystrophia 374, 275
United States Geological Survey 400
United States National Museum 324-339
University of Cincinnati 62
urnaeformis, Lecythriscus 329
Urosalpinx 259, 299, 297
uxoris, Platystrophia 24, 277
V
Vader, Washington 426, 427
Vaginoceras 15, 22, 37, 47
Valcour, New York 16, 18, 28
Valentine, W. W. 409
validum, Gyronaedeus 366
vallecostenensis, Megacardita 429
Pacificor 51, 429
Venericardia 409, 413
Venericer 429, 431
Valleyville, Quebec 308
Vane, Dr. 94
variabilis, Ethelocrinus 329, 322, 323
Velella 323, 71, 74-79
velolia, Veellea frontispiece 71, 75
Velliddea 61, 65, 77
Vulpes 176, 205, 214
Venericardia 399, 457
Venericer 399, 404-409
Venice, Ohio 411, 439, 449
Vendirenas, Venericer 111
Ventrosiphonata 8, 37, 46, 48
Ventura County, California 415, 416, 423
Vicanerenaus, Venericardia 404, 428
venturesenius, Venericer 415, 431, 432, 439
Venericer 415, 431, 432, 439
venus, Holoecus 8, 107, 120
Venustuloides, Holoecus 8, 107, 120, 121
Verastegius 479
The Pelecypod genus Venericer
dina the Palco
eocene and Eocene of Western North America 390
vetrella, Sestoceratina 364, 371, 380
Naedyceras 380
Naedyceras 380
Naedyceras 380
Vickers Hot Springs, California 417
Vicksburg, Ohio 378
Vigilis series 341
vokesi, Leurometis 173, 407, 407
Venericardia 53, 407
Voolorthelia 10
Voluta 223
Volutillotia 226
Washburn Series 226
Volutospina 240
volutus, Dellicrinus 340

W
Wabanee group 341, 342
Waccanaw Pliocene 345, 348
251, 290, 295
wacawamensis, Conus 21, 218
wacoensis, Kingena 185
Wagner, Frances J. E. 399
Walcott, C. D. 61, 70, 83
158-187, 195
Walcottceras 15
Walpole township, Ontario 376
wallomensis, Fusa 293
waltonia, Hesperidina 296
Wangan Basin 411
Wanawanian 12, 45
Wanwancorceras 13
Washburn, A. 307
Watansab, Polyedemia 5, 39
Watertown, New York 41, 250
Watkis, W. T. 174, 184, 185
158, 325, 326
Watkins, K. T. 312, 323, 326, 328
Watson, M. S. 109
Watson, R. B. 226
Weaver, Charles E. 426
weaveri, Pacificor 60, 429
Venericardia 60, 409
Venericer 60, 409
Wells, J. W. 363, 368

Fish remains from the middle Devonian bone beds of the Cincinnati Arch region 186
Weso formation 158, 185
Wernsdorfer schicht, Carpathia 291
West Texas State Teachers College, Canyon Texas 174, 186
westermanskia, Podocer 336
Whitmee, L. S. 312, 323, 326, 328
Whitcomb, L. A. 226
Richards, H. G. 255
Wileco formation 402, 451
Wilderungsuka 106
wildungensuka, Clado
clusus 186, 186
Protasus 433
Proctasus 433
Pseudosclera 133
Prosobranch 289
Wilson, Druid 289
Winchester, Helen 225
Winton, W. M. 185
wisconsinense, Gyronaedyceras .......... 366
Wissenbachia ..........366, 367
Wolf Hill, New York ... 275
Wolinian ............... 45
Wolungoceratidae ..... 21, 24
Woodring, W. P. ........228, 250
Woods Bluff, Alabama .......... 239
Wright, J. .............. 346

X
Xiphosura .................. 186

Y
Yorktown Miocene ......249, 296
298
Yorktown, Virginia ....247, 249

Z
Zawolsky, Walter ......400, 404
406
zitteli, Atollites ..........195, 201
Lorenzinia ............... 195

END OF VOLUME III