

MIDDLE DEVONIAN BIVALVIA  
FROM THE SOLSVILLE MEMBER  
(MARCELLUS FORMATION),  
CENTRAL NEW YORK STATE

J. BOWMAN BAILEY

BULLETIN  
OF THE  
AMERICAN MUSEUM OF NATURAL HISTORY  
VOLUME 174 : ARTICLE 3  
NEW YORK : 1983







MIDDLE DEVONIAN BIVALVIA  
FROM THE SOLSVILLE MEMBER  
(MARCELLUS FORMATION),  
CENTRAL NEW YORK STATE

J. BOWMAN BAILEY

*Assistant Professor, Department of Geology,  
Western Illinois University, Macomb*

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 174, article 3, pages 193–326, figures 1–51, tables 1–12

Issued April 29, 1983

Price: \$10.20 a copy



# CONTENTS

Abstract .....	196
Introduction .....	196
Evaluation of Previous Studies .....	198
Notation .....	199
Classification .....	200
Shell Orientation .....	200
Measurements .....	202
Preparation and Photography .....	202
Acknowledgments .....	202
Stratigraphy and Paleoenvironment .....	203
General Stratigraphy .....	203
Paleoecology .....	204
Paleobiogeography .....	209
Systematic Paleontology .....	214
Order Pterioidea Newell, 1965 .....	214
Family Pterineidae Miller, 1877 .....	214
Genus <i>Ptychopteria</i> Hall, 1883 .....	214
<i>Ptychopteria fasciculata</i> (Goldfuss), 1836 .....	214
Family Ambonychiidae Miller, 1877 .....	224
Genus <i>Gosseletia</i> Barrois, 1882 .....	224
<i>Gosseletia triquetra</i> (Conrad), 1838 .....	226
Order Arcoidea Stoliczka, 1871 .....	236
Family Cyrtodontidae Ulrich, 1894 .....	236
Genus <i>Ptychodesma</i> Hall and Whitfield, 1872 .....	236
<i>Ptychodesma knappianum</i> Hall and Whitfield, 1872 .....	236
Order Nuculoida Dall, 1889 .....	245
Family Nuculidae Gray, 1824 .....	245
Genus <i>Nuculoidea</i> Williams and Breger, 1916 .....	245
<i>Nuculoidea deceptiformis</i> , New Species .....	247
Family Malletiidae Adams and Adams, 1858 .....	258
Genus <i>Nuculites</i> Conrad, 1841 .....	258
<i>Nuculites oblongatus</i> Conrad, 1841 .....	260
<i>Nuculites triqueter</i> Conrad, 1841 .....	267
Genus <i>Palaeoneilo</i> Hall and Whitfield, 1869 .....	271
<i>Palaeoneilo constricta</i> (Conrad), 1842 .....	271
<i>Palaeoneilo filosa</i> (Conrad), 1842 .....	276
Order Pholadomyoida Newell, 1965 .....	284
Family Grammysiidae Miller, 1877 .....	284
Genus <i>Grammysioidea</i> Williams and Breger, 1916 .....	284
<i>Grammysioidea alveata</i> (Conrad), 1841 .....	285
<i>Grammysioidea</i> cf. <i>elliptica</i> (Hall and Whitfield), 1869 .....	290
Order Modiomorphoida Newell, 1969 .....	292
Family Modiomorphidae Miller, 1877 .....	292
Genus <i>Modiomorpha</i> Hall and Whitfield, 1869 .....	292
<i>Modiomorpha concentrica</i> (Conrad), 1838 .....	292
<i>Modiomorpha mytiloides</i> (Conrad), 1841 .....	295



Order Unionoida Stoliczka, 1871 .....	300
Family Palaeomutelidae Weir, 1967 .....	300
Genus <i>Nyassa</i> Hall and Whitfield, 1869 .....	300
<i>Nyassa dorsata</i> (Goldfuss), 1840 .....	300
Order Veneroida Adams and Adams, 1856 .....	304
Family Mactromyidae Cox, 1929 .....	304
Genus <i>Paracyclas</i> Hall, 1843 .....	304
<i>Paracyclas rugosa</i> (Goldfuss), 1837 .....	305
Literature Cited .....	312



## ABSTRACT

A remarkably well-preserved molluscan fauna in the Solsville Member (Marcellus Formation) of the Chenango Valley, New York, provides a rare opportunity to explore the functional morphology, paleoecology, and systematic relationships of several poorly understood Devonian bivalve taxa.

Over 350 recrystallized shells and internal molds from several localities in Madison County, New York, were collected and prepared for this study. The majority of these provide valuable new data on hinge, ligament, adductor and byssal/pedal musculature, and pallial morphology. Ten genera and 14 species are represented. Only one new taxon is recognized, *Nuculoidea deceptiformis*, new species.

Study affirms the contention of Williams (1886) and McAlester (1962a) that large numbers of specific and generic names applied to Devonian bivalves are biologically meaningless owing to taxonomic oversplitting by early authors. The nomenclatural chaos inherited from them evidently stems from (1) lack of adequate morphological data, especially on the hinge and internal features; (2) definitions too narrowly based, i.e., often on as few as one or two specimens; (3) broad variation introduced by preservational differences or different postdepositional histories; (4) the failure of early authors to stress genetic, ecophenotypic and ontogenetic shell variations; (5) parochialism among past authors resulting in few transatlantic comparisons of European and Amer-

ican species. With these observations in mind, the erection of new names has been largely avoided. Generic usages have been reviewed and, in most instances, revised. Roughly 150 evaluations and comparisons of other North American and European species have been incorporated using the improved morphologic data supplied by the Solsville collection as a basis for comparison. About 160 possible synonyms have been suggested; 73 of these are new. In several instances more familiar North American names are superseded by earlier European ones.

Paleoecologic reconstruction of the Solsville suggests two distinctive nearshore marine deltaic bivalve communities: (1) the *Gosseletia* community dominated by epifaunal and semi-infaunal byssate filter feeders associated with arenaceous sediments, and (2) the *Nuculoidea* community characterized by abundant deposit feeders in more argillaceous substrates. An autecological interpretation of each taxon is provided.

Biogeographic comparisons with several other Devonian faunas in North America and Europe are investigated. Evidence suggests that (1) the Appalachian and Midwestern North American taxa of the Middle Devonian are closely allied with the Lower to Middle Devonian taxa of central Europe; (2) the Michigan Basin fauna contains numerous North American endemics; and (3) Western North American taxa have fewer relations to Appalachian taxa than earlier authors have supposed.

## INTRODUCTION

In view of the excellent preservation of bivalves in the Solsville beds of New York, a rare opportunity to examine functional morphology of several poorly known Devonian taxa and to assess their relationships to similar European Devonian taxa is afforded. Such a clarification, which is the primary function of this study, is an essential prerequisite for proper evaluation of bivalve biogeographic and biofacies distributions as well as species autecology.

Relatively few comprehensive treatments of Devonian bivalves have been published since the classic monographs of James Hall (1884, 1885), Frech (1891), and Beushausen (1895), the first of which concerns American taxa, and the other two deal with species from the Rhineland of Germany. Although the

works of Frech and Beushausen have been largely ignored by subsequent American authors, Hall's systematics have been vigorously attacked, notably by H. S. Williams (1886), and more recently by McAlester (1962a). As Williams (p. 194) indicated, "impatience naturally becomes extreme when we look at the prodigious amount of alteration which has been made in the identification, both specific and generic, in the plates illustrating the fossils supposed to be representative types.

"... In the final work, 1885, generic and specific names are changed, in most cases with no reason given, occasionally with the note 'by error' inserted in the list of synonyms. These alterations are not a simple few, but for the plates and explanations, there is an



average of one alteration of identification for every species in the book.”

Williams concluded that these mistakes were not simple errors but occurred because taxonomic systems by which species were conceived and defined were entirely too rigid, lacking flexibility to account for either intra-specific variation or preservational differences. Consequently, specimens displaying minor phenotypic or preservational distinctions were treated as additional species. As Williams (p. 196) further indicated, “The evil of this species making habit is only aggravated by the minuteness and carefulness of the observer, and in the study of fossils it is particularly aggravated by the rarity of good specimens and the imperfection of the characters expressed. In its extreme [indicating Hall’s work] it has ceased to be a classifying of organisms, or even fossils, and has become merely a narration of the differences exhibited by specimens.”

The result of Hall’s exuberance in defining species is the splitting up of what are often morphological continua (morphoclines) into separate morphospecies, producing a system of classification with neither biological validity nor operationally pragmatic value. Again, to quote Williams, “species and genera can scarcely be called good, so long as the author himself is unable to distribute the typical specimens, twice alike, without reference to the labels.”

It would be grossly unfair, however, to blame Hall for generating all the present confusion, because oversplitting of taxa was widespread among Hall’s American and European contemporaries. Intractable taxonomic practices, for example, are evident in works of Beushausen (1895) and Frech (1891). In one instance in particular, Frech, despite reasonable arguments of Follmann (1885) to the contrary, insisted on maintaining undue specific distinction between two morphologically identical forms, “*Pterinea*” *fasciculata* Goldfuss from the Rhineland and “*P.*” *flabella* (Conrad) from eastern North America, on the basis of geographical separation alone. Frech in his time, of course, could not have realized the proximity of North America and Europe during the Devonian.

Certain later authors perpetuated the tra-

dition of nomenclatural excesses established by these pioneering works. For example, among the 108 bivalve species and varieties treated by Spriestersbach and Fuchs (1909), Fuchs (1915), and Spriestersbach (1915), 81 were new with an average of 76 percent new names per work. Williams himself, who had previously been so adamantly critical of Hall’s work, as McAlester (1962a, p. 11) stated, “later lapsed into nomenclatural abuses which make Hall’s seem harmless.” In Williams and Breger’s (1916) study of the fauna of the Lower Devonian Chapman Sandstone of Maine, for example, of the 51 species and varieties of bivalves described, 39 were new. And, a surprising number of holotypes of these are unrevealing fragments which cannot be convincingly classified even at the ordinal level. By 1917, Williams’s deteriorating taxonomic philosophy openly encouraged nomenclatural extravagance. His “metamorphic species” concept weighted biologic variation and preservational effects equally. Morphologic characters introduced by postdepositional events, he asserted (1917, p. 52), are “as clear and distinct as if they were original characters, and in description and illustration must be treated as any other fossils.”

Stratigraphic paleontologists including Walcott (1884) and Clarke (1908, 1909) exhibited a tendency to apply specific names in accordance with previously described stratigraphic occurrences rather than on detailed morphological study. Such a practice maintains undue taxonomic distinctions, for example, among Lower and Middle and even Lower and Upper Devonian bivalve species. In Europe and North America the resulting succession of stratigraphically applied specific names emulates progressive phyletic change, effectively masking the long-term evolutionary stability seen here in many of these species.

McAlester stated that prior to his study of Upper Devonian (Chemung) bivalves of New York he was skeptical of previous criticisms of the systematics of Devonian bivalves. However, he concluded (1962a, p. 10), “as the revision progressed, my skepticism diminished. I believe that the analysis of morphologic variation in the many large samples available to me has proved conclusively that

the earlier species *were* grossly oversplit and were therefore biologically meaningless." McAlester further described the need for modern critical examination and revision at the specific level as "pressing" and, at the generic level, as "an urgent necessity" stating that "this study [1962a] has convinced me that it is now all but impossible to apply a meaningful generic name to a Devonian pelecypod."

One important reason that the systematics of Devonian bivalves has remained in such turmoil is the general lack of well-preserved material exhibiting the important internal details of hingement and musculature, the past affinities having often been based upon such superficial characters as shell shape and sculpture. Even McAlester's cited study as well as recent paleoecological studies of Paleozoic bivalves, such as that of Stanley (1972), have been in large part similarly based.

A second reason for the continuing confusion is that many American authors have seemed generally unaware of the wealth of European Devonian bivalve literature and vice versa (see for example Babin's remarks, 1973, p. 66). The result has been the proliferation of synonyms and few meaningful transatlantic comparisons.

#### EVALUATION OF PREVIOUS STUDIES

The comprehensive monographs of Frech (1891) and Beushausen (1895) describe extensive new European Devonian bivalve species and summarize similar material described in numerous faunal studies and treatises of earlier authors including d'Archiac and de Verneuil (1842), various works of Kayser, Oehlert, A. Roemer and F. Roemer, and especially Goldfuss (1834–1840), Sandberger and Sandberger (1850–1856), Steininger (1853), Keferstein (1857), Maurer (1886), Holzapfel (1882, 1885), Beushausen (1884, 1889) and Follmann (1885). In North America Hall's twin volumes (1884, 1885) served much the same purpose incorporating all of the bivalve material of Conrad (e.g., 1838, 1841, 1842) as well as the previous studies of Hall (e.g., 1843, 1859, 1883) and

Hall and Whitfield (e.g., 1869, 1872). The significance of Hall's (1884, 1885), Frech's (1891) and Beushausen's (1895) works cannot be overly emphasized, and no works published since have equaled them in regard to their importance in the systematics of Devonian bivalves. The type material on which Hall's studies were based is still mostly extant and is housed in several collections (e.g., the American Museum of Natural History, the New York State Museum, and the National Museum of Natural History, Smithsonian Institution). However, the original materials of Beushausen and Frech have become dispersed and important portions of the collections were lost or destroyed during the Second World War.

In Europe a proliferation of mostly German and French Devonian systematics works which either discuss or mention many taxa described by Beushausen and by Frech appeared during the early part of this century. Many of these authors deserve mention (including Asselberghs, Dahmer, Dienst, Drevemann, Kegel, Maillieux, Maurer, Mauz, Rose, Schmidt, Spriestersbach, and Viëtor) but space here prohibits a complete listing. For an exhaustive bibliography of these early works, see Maillieux's (1937) study of the Lower Devonian bivalves of the Ardennes of Belgium. This comprehensive work is among the most significant since the monographs of Frech, Beushausen, and Hall. However, Maillieux's descriptions are rather superficial, and his plates are occasionally ambiguous and surprisingly few considering the breadth of treatment. His primary contributions are bibliographic compilation and the development of extensive synonymies.

Following Maillieux's studies, interest in European Devonian bivalves has continued. For example, a few fragmentary early Devonian German species were described by Dahmer (1942). Dechaseaux's (1952) well known general treatise on the classification of the Bivalvia mentions a few Devonian taxa. Haffer (1959) examined the hinge structures in numerous European palaeoheterodont species. Babin's studies (1966, 1973) of French and Middle Eastern taxa are among the most significant since Maillieux. Recently, Bailey (1975, 1978a, 1979a, 1979b, 1979c)



compared many European and North American Devonian taxa.

Besides Hall's (1884, 1885) monumental studies, numerous subsequent works have contributed significantly to present knowledge of Devonian bivalves in the Western Hemisphere. Owing to preservation, many of these are rather cursory concentrating largely on external shell morphology. Walcott (1884) described several poorly preserved bivalve taxa from the Devonian of Nevada. Whiteaves (1889, 1891, 1892, 1898) treated a number of species occurring in Canada. Nettleroth (1889) published a few descriptions and drawings of bivalves from the Devonian of Kentucky. Clarke (1899, 1900) discussed Devonian molluscs of Pará, Brazil. Kindle (1901) treated many of the same species considered by Nettleroth from the Sellersburg beds of southern Indiana. Clarke (1904) described a number of species from the Upper Devonian (Portage) beds of western New York. Knod (1908) described a fauna from Bolivia. Clarke (1908, 1909) discussed early Devonian taxa in New York, Maine, and the Maritime Provinces of Canada. Cleland (1911) examined bivalves from the Devonian of Wisconsin (Milwaukee Formation). Kindle (1909, 1912) described bivalves in the Ouray Limestone of Colorado and the Onondaga of the Allegheny region. Ohern and Maynard (1913), Prosser and Kindle (1913) and Clarke and Swartz (1913) treated, respectively, the Lower, Middle, and Upper Devonian bivalve taxa in Maryland and Virginia. Williams and Breger's (1916) revision of Clarke's (1909) bivalves from the Lower Devonian Chapman Sandstone of Maine often resulted in a senseless oversplitting of taxa. Pohl (1929) essentially repeated Cleland's (1911) earlier work. Although photographs used in Pohl's work are generally superior to Cleland's drawings, Pohl's work is rife with new species which appear often unjustified. Cleland's more conservative approach to the systematics of this fauna is, in some respects, more reasonable. Savage (1930, 1931) listed and figured several taxa earlier described by Nettleroth (1889) and Kindle (1901). Willard (1939) made a noteworthy contribution to the knowledge of Middle and Upper Devonian faunas of Penn-

sylvania, but his bivalves are fragmentary, his plates unclear, and misidentifications numerous. Newell (1938, 1942) touched on a few Devonian taxa in his venerable treatments of late Paleozoic Mytilacea and Pectenacea. Stoyanow (1948) described bivalves in a molluscan faunule from the Devonian Island Mesa beds of Arizona. LaRocque (1950) described the pre-Traverse Devonian bivalves of Michigan. McAlester (1962a, 1963a, 1963b, 1965, 1966, 1968) made a number of significant contributions including studies of the Upper Devonian bivalves of New York and Missouri, Devonian bivalves of Antarctica, and Paleozoic nuculoid type species. Ellison (1965) gave an account of numerous taxa from the Mahantango Formation of Pennsylvania. Some discussion of important Devonian ambonychiid genera is presented by Pojeta (1966), and certain Devonian pholadomyaceans are treated by Bambach (1971) and Runnegar (1974). Wilson (1975) described the bivalve fauna of the Devonian Silica Formation of Ohio and summarized occurrences of various taxa in the Midwest. The Treatise volumes (Moore, 1969) represent an invaluable summary of the general knowledge of fossil bivalves, but discussion is largely limited to supraspecific levels.

The Solsville materials presented here were first treated in preliminary form by Bailey (1975); the present work is a revised and expanded version of that earlier study. A discussion of Lower and Middle Devonian bivalve paleobiogeography with specific reference to this bivalve fauna is presented in Bailey (1978a). For an analysis of relict ultrastructure in several of these same taxa, the reader is referred to Carter and Tevesz (1978a, 1978b).

## NOTATION

**CONTRIBUTING INSTITUTIONS:** The following abbreviations are used in the figure explanations and text to denote institutions which have contributed fossil materials, data, or collecting localities:

AMNH, American Museum of Natural History, New York, New York.

NYSM, New York State Museum, Albany, New York.

USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

YPM, Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

Loc., Locality.

Catalogued bivalve types and figured specimens of early authors (e.g., Hall, Hall and Whitfield, Conrad, etc.) in the reference collections of the first three of the above institutions are listed in Whitfield and Hovey (1898–1901), Clarke and Ruedemann (1903), and Merrill (1905).

**SYNONYMIES:** Within the lists North American and European synonyms (or homonyms if preceded by “not”) are grouped separately. If the senior synonym is a North American name, synonymous North American species are listed before European synonyms. If the senior synonym is a European name, European synonyms are given first. Within synonym sets the order is chronological except where variants of a given name are listed together. Synonyms not seen in previously published lists or discussions are noted by a dagger [†]. Names left unmarked include homonyms and common, forgotten, or implied synonyms of either the senior synonym or one of its junior synonyms. Only synonyms and homonyms verified by the writer are included in the lists. All other references are omitted.

## CLASSIFICATION

The scheme adopted here is that of Newell (1965; and Moore, 1969). Pojeta's (1975, 1978) recent modifications have not been used for the following reasons:

(1) Pojeta (1978) proposes subdividing the Bivalvia into seven subclasses on the basis of its primary radiation which he believed occurred in the Ordovician. However, recent evidence (MacKinnon, 1982) suggests that heretofore unrecognized phases in the primary radiation occurred as early as middle Cambrian. Moreover, the odd mixture of morphologies seen in *Tuarangia* MacKinnon does not comfortably fit among the seven subclasses and even suggests possible phyletic relations between palaeotaxodonts and pteriomorphs. Hence, I prefer to retain New-

ell's widely used scheme until the earliest phases of bivalve diversification are more fully explored.

(2) Devonian groups do not always fit subclass diagnoses based on dentition as prescribed by Pojeta (1978). Among the carydiids this would necessitate placement of member species of *Carydium* in two different subclasses.

(3) Pojeta suggests that the Isofilibranchia (the mytilaceans and their ancestors) are at best limited to subumbonal anterior teeth and cites modiomorphids as primary examples. As shown here, however, *Modiomorpha* actually has a heterodont arrangement with weak posterior laterals. Moreover, its morphology seems more similar to certain veneroids (e.g., permophorids and hippopodiids) than it does to the mytilids. Other modiomorphids such as *Tanaodon* have strong posterior elements as part of a continuous actinodont series. For these reasons I prefer tentatively to retain the modiomorphids within Newell's Subclass Palaeoheterodonta.

## SHELL ORIENTATION

**ANISOMYARIAN BIVALVES:** It has been observed that standard orientational terms used for bivalve shells may be partially or wholly inadequate when applied to the soft anatomy (see esp. Stasek, 1963; Stanley, 1970). Among anisomyarian taxa for example, the hinge axis is rarely parallel to either the anteroposterior axis (a straight line touching the lower margins of the two adductors) of Fischer (1886) or the oro-anal axis (a straight line connecting mouth and anus). Following convention as prescribed by Cox (in Moore, 1969, p. N81), the hinge axis was here taken as the anteroposterior direction in genera with long, straight hinge lines such as *Gosseletia*, *Modiomorpha*, *Ptychodesma*, and *Ptychopteria* (fig. 1). For the anisomyarian genus *Paracyclas* (possessing one ventrally elongated adductor) orientation using the hinge axis is problematic as the hinge line is short and poorly understood. Because the anteroposterior axis would unacceptably elevate the mouth and foot dorsally, the modified anteroposterior axis *sensu* Stanley (1970) (i.e., a straight line touching the inferred tops of

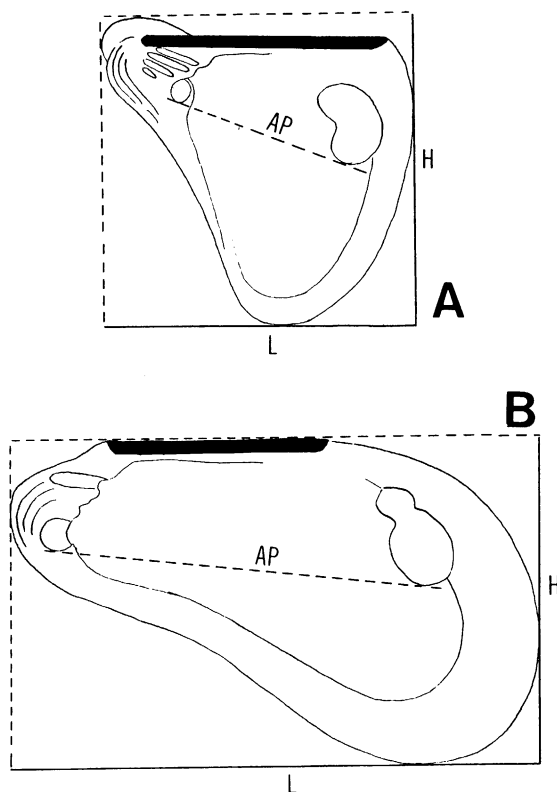


FIG. 1. Dimensions and orientation in anisomyarian bivalves. A. Interior lateral view of right valve of *Gosseletia triquetra* (Conrad) showing length (L) and height (H). Notice that the anteroposterior axis of Fischer (1886) (AP) diverges considerably from direction of length. B. Interior lateral view of left valve of *Modiomorpha concentrica* (Conrad). Anteroposterior axis (AP) here diverges only slightly from length direction.

the adductors) was taken as the anteroposterior direction.

**ISOMYARIAN BIVALVES:** Taxa such as *Palaeoneilo* and *Nuculites oblongatus* have a long, straight external ligament and tooth rows mostly parallel to it. In such cases either the hinge axis or the anteroposterior axis may be used as directional criteria as they are approximately parallel. However, difficulties arise in both *Nuculites triquetra* and *Nuculoidea*. In the former the inferred anteroposterior axis was used because the ligament and dentition are poorly known. In the latter the ligament is a small resilium situated in a tiny internal ligamental pit (resilifer), and the hinge

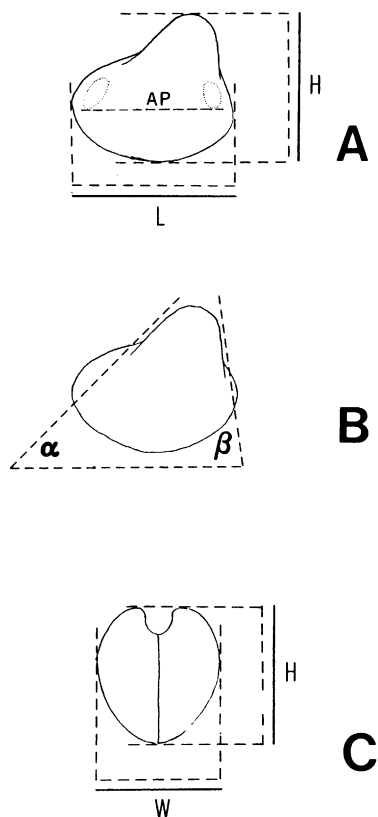


FIG. 2. Dimensions and orientation of isomyarian bivalves. Example: *Nuculoidea* Williams and Breger. A. Left lateral view showing length (L) and height (H). Notice that the anteroposterior axis (AP) is approximately parallel to the length. B. Left lateral view showing anterior umbonal angle ( $\alpha$ ) and posterior umbonal angle ( $\beta$ ). C. End view of articulated specimen showing total width (W) and height (H).

tooth rows meet at a sharp angle. It has been suggested that the hinge axis in taxa such as *Nuculoidea* was roughly subparallel to the steep, posterior tooth row (see Bradshaw and Bradshaw, 1971). Because this would result in an unconventional shell orientation (i.e., a ventrally positioned mouth and foot), the anteroposterior axis was adopted here instead (fig. 2). The resulting orientation is consistent with that of other resiliated nuculoids such as *Phestia* (= *Poldevcia*) and *Yoldia* given by Driscoll (1966). In these genera, however, the anterior and posterior hinge tooth rows do not meet at a sharp angle but are



flatter, and the resulting hinge axis and anteroposterior axis would approach parallelism as in *Palaeoneilo* and *Nuculites oblongatus*.

### MEASUREMENTS

The measurements made for this study were accomplished through four different techniques. For longer dimensions, such as valve length, height, and total depth of free, articulated specimens, a metric dial caliper (Helios, West Germany) was used (no. 60,609, Edmund Scientific Co., Barrington, New Jersey). Finer measurements, such as growth increment counts, were made using either a binocular microscope fitted with an ocular micrometer or a 6× pocket comparator (Edmund Scientific Co., no. 30,325) equipped with a reticle (Edmund no. 30,584) possessing a 20 mm. scale divided into 200 parts. Angular measurements were made with an all-steel contact goniometer (General Hardware Mfg. Co., New York).

Measurements were taken in the manner prescribed by Simpson, Roe, and Lewontin (1960, pp. 23–24). A dimension is considered to be the maximum distance between parallel planes tangential to the designated anatomical element. "For length, the planes are usually considered to be oriented vertically to the axis of the body through the axial anatomical divisions and their parts . . . and vertically to the proximodistal axis for nonaxial elements . . ." Width is the dimension at right angles to the length and most nearly in a horizontal plane, and height is the dimension at right angles to these two and nearly in a vertical plane. This in essence, is the system used in reference to bivalves by Raup and Stanley (1971) and Vokes (1957). Dimensions I used in this study are defined below:

**LENGTH (L)**, Maximum linear dimension in an anteroposterior direction, specimen properly oriented.

**HEIGHT (H)**, Maximum linear dimension in a dorsoventral direction, normal to length, specimen properly oriented.

**WIDTH (W)**, Maximum linear dimension normal to both length and height. Unless otherwise indicated, width refers to the total for both valves

considered together in a free, articulated specimen.

**ANTERIOR UMBONAL ANGLE ( $\alpha$ )**, In *Nuculoidea* (fig. 2), the angular relationship of approximately the upper third of the anterior umbonal slope with respect to the horizontal, specimen properly oriented. This should not be confused with  $\alpha$  of Newell (1942) or of Pojeta (1966).

**POSTERIOR UMBONAL ANGLE ( $\beta$ )**, In *Nuculoidea* (fig. 2), the angular relationship of approximately the upper third of the posterior umbonal slope with respect to the horizontal. This should not be confused with  $\beta$  of Pojeta (1966).

**G-ANGLE ( $\gamma$ )**, In ambonychiid bivalves such as *Gosseletia*, "the angle between the anterior margin and the dorsal margin of the shell . . ." (Pojeta, 1966).

### PREPARATION AND PHOTOGRAPHY

For rough preparation I used a Dremel Moto-Tool and a Chicago Pneumatic air-scribe. The latter is especially recommended and is generally superior to the conventional vibrating stylus used in electric engravers. Fine preparation was performed with a Pennwalt S. S. White Model K Airjet abrasive unit in the manner described by Stucker, Galusha, and McKenna (1965) using #2 dolomite abrasive powder.

Specimens were for the most part photographed 1:1, utilizing a Polaroid MP-3 technical view camera with 127 mm. Rodenstock Ysaron and 150 mm. Rodenstock Apo-Ronar lenses and a 120 roll film back. Most photos were taken on Kodak 120 Verichrome Pan film developed for six minutes at 68°F. in Kodak D-19 developer. Prints are on Agfa Brovira (#3–5) single weight paper, using Simmon Omega and Beseler enlargers fitted with a 105 mm. Rodenstock Rodagon enlarging lens. Before photographing, all specimens were whitened in ammonium chloride sublimate as described by Cooper (1935) and Kier et al. (1965).

### ACKNOWLEDGMENTS

With profound gratitude I extend my thanks to the many friends who have contributed to the completion of this study. I am indebted to Drs. Norman D. Newell, Roger L. Batten,

and Niles Eldredge of the American Museum of Natural History and Columbia University for having initially suggested the work, and who provided a wealth of helpful information, and have been most generous in lending the fossil materials on which I based this study. I am especially grateful for the instructive comments provided by Drs. Newell and Eldredge who critically reviewed the final version of the manuscript. I am also grateful to Dr. Harold B. Rollins, University of Pittsburgh, Dr. Niles Eldredge, and Judith Spiller who collected the bulk of the specimens.

To Dr. Daniel B. Blake I am indebted for supervising a version of this work submitted in May 1975, for the degree of Doctor of Philosophy in the Department of Geology at the University of Illinois (Urbana). I extend additional thanks to other members of the University of Illinois faculty including Drs. Philip A. Sandberg, Ralph L. Langenheim, Daryl C. Sweeney, Donald L. Johnson, and Dennis S. Wood for their helpful criticisms.

For instructive conversations, helpful correspondence, or aid in locating specimens I am grateful to the following: Dr. Ernst Kirsteuer, American Museum of Natural History; Drs. John Pojeta, G. A. Cooper, and Mr. Frederick J. Collier of the National Mu-

seum of Natural History, Smithsonian Institution, Washington, D.C.; Drs. Bruce Bell and Ed Landing, New York State Museum, Albany; Dr. Steven M. Stanley, Johns Hopkins University; Drs. H. K. Erben and H. Remy, Institut für Paläontologie, Bonn, West Germany; Dr. J. Helms, Museum für Naturkunde, Paläontologisches Museum, Berlin, E. Germany; Dr. Richard K. Bambach, Virginia Polytechnic Institute and State University, Blacksburg; Dr. Claude Babin, University of Bretagne Occidentale, Brest, France; and Dr. A. Lee McAlester, Southern Methodist University, Dallas, Texas.

I also thank Dr. Janette Hudson for invaluable assistance and council in the translation of pertinent German texts.

All drawings and photographs are by me except as noted. Thanks to Mr. G. Robert Adlington of the American Museum, Dr. Daniel B. Blake of the University of Illinois, and especially to Dr. Dennis R. Kolata of the Illinois State Geological Survey for introducing me to the subtleties of technical photography.

Partial funding toward publication of this manuscript was provided by the College of Arts and Sciences, Western Illinois University.

## STRATIGRAPHY AND PALEOENVIRONMENT

### GENERAL STRATIGRAPHY

The bulk of the fossil material used in the preparation of this study was derived from mudstones and sandstones of the Solsville Member of the Middle Devonian (Cazenovian; see Cooper et al., 1942; Oliver et al., 1969) Marcellus Formation from the Morrisville Quadrangle, Chenango Valley, Madison County, New York. The collecting localities are among those in table 1 of Rollins, Eldredge, and Spiller (1971) (see fig. 3).

The complex, problematic deltaic facies interrelationships of the Chenango Valley Devonian were first investigated by Cooper (1930, 1933, 1934). Stratigraphically the Marcellus Formation is bounded in the Chenango Valley by the Onondaga Limestone below and by the Mottville Member (Skaneateles Formation) above. As shown in

figure 4, the Solsville Member lies near the top of the Marcellus being bounded by the shales of the Bridgewater Member below and the shales and siltstones of the Pecksport Member above.

Cooper (1930, p. 133) gave the following description of the Solsville:

This member, 45–50 feet thick, of sandy shale, fine sandstone, and calcareous sandstone, is transitional with the soft Bridgewater shales below. It is characterized by typical Hamilton fossils in an unusual assemblage. Common forms are: *Nephriticeras maximum*, *Paracyclas lirata*, *Gosselettia* [sic] *triquetra*, *Pterinea flabellum*, and *Conularia continens*. The member forms ridges on the sides of the hills north of Solsville. The falls in Woods Gully, 2 miles northwest of Solsville (Morrisville Quadrangle), is the type section. The Solsville also occurs in Reilley's Quarry 4 miles northwest of Bridgewater, and forms

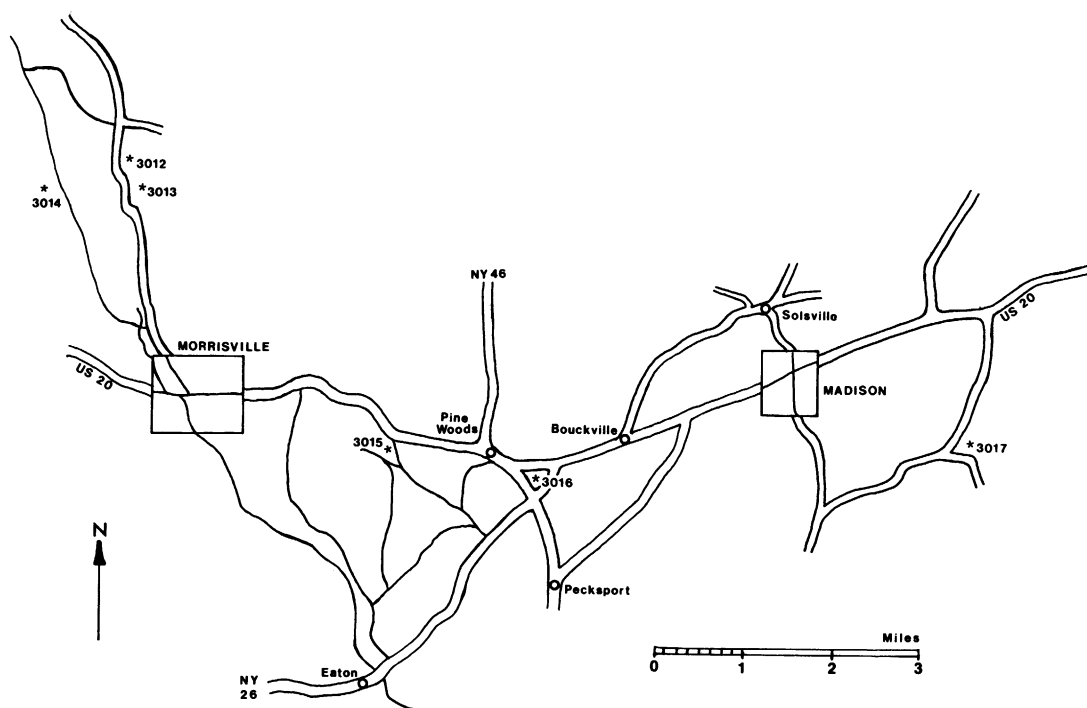


FIG. 3. Collecting localities in the Solsville Member, Chenango Valley, New York. (From Rollins, Eldredge, and Spiller, 1971; see their table 1 for locality descriptions.)

ridges on each side of the Unadilla Valley as far south as Leonardsville. It is not known west of Pine Woods, Morrisville Quadrangle.

At the localities studied the Solsville consists lithologically of dark gray, calcareous silty shales in the lower portions of the outcrops overlain by tan to brownish gray sandy siltstones and fine sandstones. The interdigitating deltaic mudstone and sandstone facies complex of the Chenango Valley is replaced to the west by the Cardiff Shale, homogeneous black argillites probably representing prodelta muds deposited concurrently with the onshore heterogeneous clastic sediments of the Chenango Valley.

As indicated by Rollins, Eldredge, and Spiller (1971), the collecting localities of the present study lie farther westward than Cooper's proposed western limit of the Solsville at Pine Woods. Some of these however, are recent exposures not available at the time of Cooper's original study. Moreover, the presence of the faunal assemblage considered by

Cooper to be uniquely Solsville suggests that these beds are either part of the Solsville *sensu* Cooper or an ecological equivalent.

## PALEOECOLOGY

**DEPOSITIONAL SETTING:** The Solsville beds are a part of the early marine phase of the Catskill fan-delta complex, the subject of extensive past study. Development of the complex began in mid-Devonian with progradation of numerous marine-dominated deltas across a tectonically stable, shallow marine shelf. Growth of the complex culminated in late Devonian with two separate depositional phases: a rapid final stage of deltaic progradation followed by aggradation and subsidence as thick sequences of subaerial red beds and tectonic fanglomerates were emplaced from the east. Late Devonian depositional phases have attracted much study (e.g., Barrell, 1913, 1914; Friedman and Johnson, 1966; Woodrow and Fletcher, 1967; Allen and Friend, 1968; Sutton, Bowen, and



McAlester, 1970; Bowen, Rhoads, and McAlester, 1974; Thayer, 1974). Aside from several notable works (e.g., Cooper, 1930, 1933, 1934, 1957; Chadwick, 1933, 1944; McCave, 1969; Mazzullo, 1973), generally less attention has been given to the initial deltaic growth of the mid-Devonian.

Prior to Hamilton deposition, the region was evidently a widespread, shallow carbonate shelf environment (Onondaga Limestone). Progradation began with deposition of lower Hamilton clays, silts, and sands such as those of the Marcellus. Evidence of shallow water above the shelf is supplied by the considerable effects of wave and tidal action in modifying the geometry and growth of early deltaic deposits and by their analogy to the Holocene Niger River delta (Mazzullo, 1973). Additional evidence is provided by lack of subsidence, relatively limited thickness of marine deltaic strata, widespread and rapid progradation, and lack of bar finger sands which characteristically form when deltas prograde into deep water (Friedman and Sanders, 1978).

That the clastic sediments of the marine Hamilton are bounded and punctuated by shelf carbonates suggests that they represent offshore deposits transitional to open marine environments. This is supported by Friedman and Sanders's figure 10-27 which shows the sediments of the Marcellus through Moscow to be an "inferred foreset" (i.e., delta slope) sequence in the general region of the Solsville study area. In contrast to the Upper Devonian, these authors do not recognize any prodelta (bottomset) or delta platform (topset) facies for the Middle Devonian strata in their figure. Such facies did exist, however, as shown by Mazzullo (1973) who recognized seven subaerial and marine deltaic environments (i.e., alluvial delta plain, beach, channel mouth bar, interdistributary bay, outer delta platform, delta slope, and prodelta) in the Hamilton Group in Orange, Ulster and Sullivan counties of southeastern New York. Mazzullo's study area lies about 140 km. southeast of the Solsville study area. By inference, the central New York shoreline during Hamilton time would be expected to have lain a relatively short distance east of Madison County. This is significant as the bivalve

CHENANGO VALLEY, N. Y.				
DEVONIAN	TAGHANICAN STAGE			Sherburne ss.
				Genesee bl. sh.
				Tully ls.
	TIOGHINOGAN STAGE	MOSCOW FM.		Windom shale
				Portland Point ls.
		LUDLOWVILLE FM.		Ludlowville sandy sh. (undivided)
				Centerfield ls.
	CAZENOVIAN STAGE	SKANEATELES FM.		Chenango ss.
				Butternut sh. & ss.
				Pompey sh. & ss.
				Delphi Station sh. & ss.
		MARCELLUS FM.		Mottville ss. & ls.
				Pecksport sh.
				Solsville ss. & sh.
				Bridgewater sh.
				Chittenango bl. sh.
				Cherry Valley ls.
				Union Springs sh. & ls.
				Onondaga Ls.

FIG. 4. Stratigraphic position of the Solsville Member, Marcellus Formation, in the Middle Devonian section of central New York. (Based upon Cooper et al., 1942; Cooper, 1957.)

assemblages of the Solsville suggest that these beds were deposited closer to the shoreline than delta slope, probably high on the delta platform.

**BIVALVE ASSEMBLAGES:** The taxa studied are part of a diverse molluscan fauna dominated by gastropods and bivalves. Solsville bivalves are largely thick-shelled species of protobranch and mytiliform genera (see table 1). Such assemblages occurring elsewhere (McAlester and Doumani, 1966) were considered as indicative of marine environments colder than those of the Solsville which were evidently tropical (see paleolatitudinal reconstructions of Bambach, Scotese, and Ziegler, 1980).

The majority of the bivalves were collected from two exposures (AMNH loc. 3012, AMNH loc. 3013) roughly separated by a

TABLE 1  
Sample Percentages and Shell Thicknesses of  
Solsville Bivalve Species

Species	Percent	Thickness
PROTOBRANCH BIVALVES		
<i>Nuculoidea deceptiformis</i> , new species	40.2	thick
<i>Nuculites oblongatus</i>	11.3	thin
<i>Nuculites triqueter</i>	0.7	thin
<i>Palaeoneilo filosa</i>	4.8	thick
<i>Palaeoneilo constricta</i>	0.3	thick
MYTILIFORM BIVALVES		
<i>Gosseletia triquetra</i>	20.3	thick
<i>Modiomorpha concentrica</i>	6.1	thick
<i>Modiomorpha mytiloides</i>	1.0	thick
<i>Ptychodesma knappianum</i>	1.7	thick
MISCELLANEOUS BIVALVES		
<i>Ptychopteria fasciculata</i>	7.2	thick
<i>Paracyclas rugosa</i>	3.8	thin
<i>Grammysioidea alveata</i>	1.4	thin
<i>Grammysioidea elliptica</i>	0.3	thin
<i>Nyassa dorsata</i>	0.7	thick

kilometer (see fig. 3). The rich populations at each exposure form an autochthonous thanatocoenosis as shown by the predominance of unabraded, articulated valves, often found in orientations approximating natural life positions. Beyond this, however, the bivalve assemblages from the two localities are strikingly different. At AMNH loc. 3012 a *Nuculoidea* community consists mostly of deposit-feeding infaunal nuculoids such as *Nuculoidea deceptiformis*, new species, *Palaeoneilo filosa*, *Nuculites oblongatus*, *Nuculites triqueter*, and, to a lesser extent, suspension-feeding taxa such as the pholadomyaceans *Grammysioidea alveata*, *G. cf. elliptica*, the lucinacean *Paracyclas rugosa*, the cyrtodontid *Ptychodesma knappianum*, and the pterineid *Ptychopteria fasciculata*. In the *Gosseletia* community at AMNH loc. 3013, the bivalves are more abundant than at AMNH loc. 3012 and consist in addition to several taxa (especially nuculoid species) found at the latter locality of large, byssally attached, epifaunal/semi-infaunal species such as *Gosseletia triquetra*, *Modiomorpha concentrica*, *M. mytiloides*, and *Ptychopteria fasciculata*.

A parallel concomitant taxonomic shift in

TABLE 2  
Probable Life Habits and Facies Distributions of  
Solsville Bivalves

Species	Facies	Life habits
<i>Nuculoidea deceptiformis</i> , new species		
<i>Nuculites triqueter</i>	C1S2	I nSi D
<i>Nuculites oblongatus</i>	CS	I Si D
<i>Palaeoneilo filosa</i>	C1S2	I Si D
<i>Palaeoneilo constricta</i>	C1S2	I Si D
<i>Palaeoneilo constricta</i>	S	I Si D
<i>Grammysioidea alveata</i>	S	I Si D
<i>Grammysioidea elliptica</i>	C1S2	En Su
<i>Ptychodesma knappianum</i>	C	En Su
<i>Modiomorpha concentrica</i>	C1S2	En Su
<i>Modiomorpha mytiloides</i>	S1C2	En Su
<i>Modiomorpha mytiloides</i>	S	En Su
<i>Ptychopteria fasciculata</i>	S1C2	En/Ep Su
<i>Gosseletia triquetra</i>	S	Ep Su
<i>Paracyclas rugosa</i>	S	Ep Su
<i>Nyassa dorsata</i>	C1S2	I pSi Su
	S, ?C	sI Su

FACIES NOTATION: C—clayey facies. S—sandy facies. C1S2—present in both but dominant in clay facies. S1C2—present in both but dominant in sandy facies.

HABITS NOTATION: I—infaunal, vagile. sI—semi-infaunal, vagile. En—endobyssate. Ep—epibyssate. D—deposit (detritus) feeder. Su—suspension feeder. Si—siphonate. nSi—non-siphonate. pSi—partially siphonate.

association with lithologic change was reported by Cooper (1930) among bivalves from the Delphi Station Member of the Skaneateles Formation, New York. Here, again, large byssate bivalves such as *Actinopteria boydi*, *A. decussata*, *Modiomorpha mytiloides*, *Limoptera macroptera*, and *L. obsoleta* were noted in the upper silty beds as opposed to the underlying argillites.

Such changes in bivalve assemblages can be partially attributed to the substrate. Fine-grained sediments settle out in environments where water movements are weak. According to Stanley (1970), when the percentage of mud reaches about 25 percent, the viscosity and density of the sediments are lowered to levels which cause large, thick-shelled epifaunal taxa such as *Gosseletia* to have difficulty in remaining above the sediment/water interface. As a result, suspension-feeding habits cannot be maintained. Accordingly, the relative abundance of deposit-feeders would be much greater in muds than in sands, whereas suspension-feeders would be more common in sands than muds. Davis (1925) and Sanders

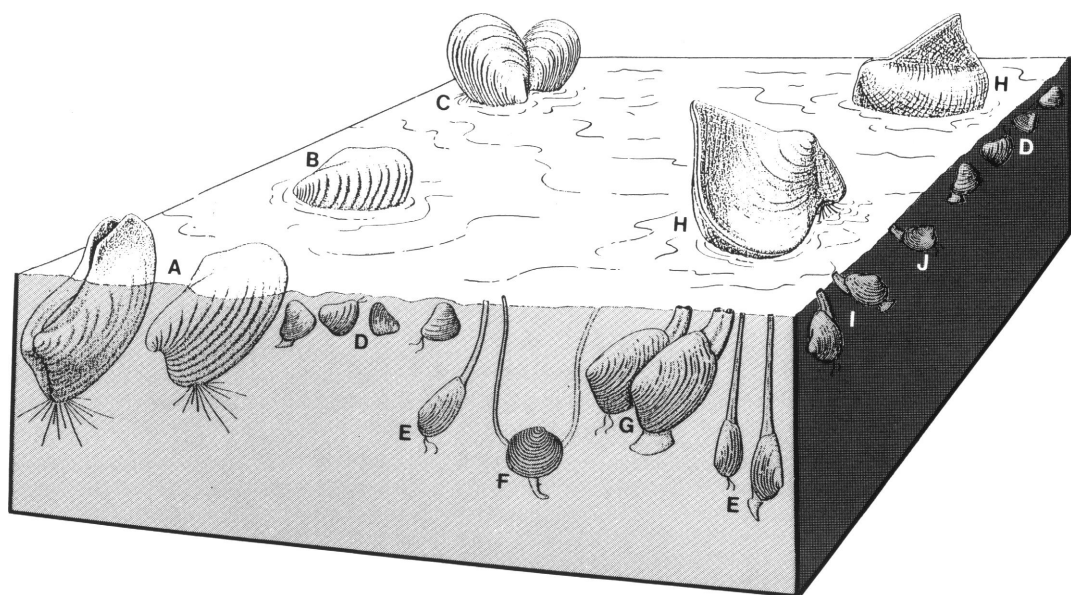


FIG. 5. Life habit reconstructions of Solsville bivalves of the *Nuculoidea* Community (drawn to approximate relative scale). This diagram shows representative bivalve species in their probable life positions within a clayey matrix. Note the preponderance of infaunal taxa. A. *Grammysioidea alveata*. B. *Grammysioidea elliptica*. C. *Ptychodesma knappianum*. D. *Nuculoidea deceptriiformis*, n. sp. E. *Nuculites oblongatus*. F. *Paracyclas rugosa*. G. *Palaeoneilo filosa*. H. *Ptychopteria fasciculata*. I. *Palaeoneilo constricta*. J. *Nuculites triqueter*. Interpretations of life habits are either those of the writer or are interpretations of either the same or related genera by various authors (e.g., Bambach, 1971; Bowen, Rhoads, and McAlester, 1974; Levinton and Bambach, 1975; McAlester and Doumani, 1966; Pojeta, 1966, 1971; Runnegar, 1974; Stanley, 1970, 1972; Thayer, 1974). Also see autecology discussions in the systematics section of the present study.

(1956) have demonstrated this to be the case. The probable life habits of the Solsville bivalves are summarized in table 2 and figures 5 and 6.

Several of the same bivalve taxa (i.e., eight genera and five species) of the Solsville also occur in the Hamilton study area of Mazzullo (1973, table 2) in southeastern New York. Of the 32 bivalve species listed by Mazzullo, 24 occur in the silts and clays of the delta slope environment, whereas the remainder are found in the prodelta. However, because the shells in Mazzullo's study area occur in coquinities ("hashes" of abraded, broken, disarticulated shells associated with penecontemporaneous soft-sediment deformation), it is likely that neither delta slope nor prodelta were the true habitats of the bivalve assemblages listed. More likely the coquinities represent frontal splays or slumps derived from shell lag deposits accumulating at the effective depth of wave erosion (i.e., delta front).

The domination of pterineids, ambonychiids, and modiomorphids of the Solsville *Gosseletia* community is suggestive of the *Cypricardella* community (Sutton, Bowen, and McAlester, 1970; Bowen, Rhoads, and McAlester, 1974) in the Upper Devonian Glen Aubrey Formation (Sonyea Group), New York. Both communities are dominated by epifaunal or semi-infaunal byssate, suspension-feeding bivalves living in relatively stable sediments. The communities have as few as two genera in common (i.e., the infaunal deposit-feeders, *Nuculoidea* and *Palaeoneilo*). The *Cypricardella* community, however, does contain abundant pterineids (e.g., *Leptodesma*) and a few modiomorphids (e.g., *Goniophora*).

The *Gosseletia* community bivalves are also somewhat similar to those of the *Rhipidomella-Leiorhynchus* facies from the Upper Devonian Genesee Group of New York (Thayer, 1974). Although both deposit feed-

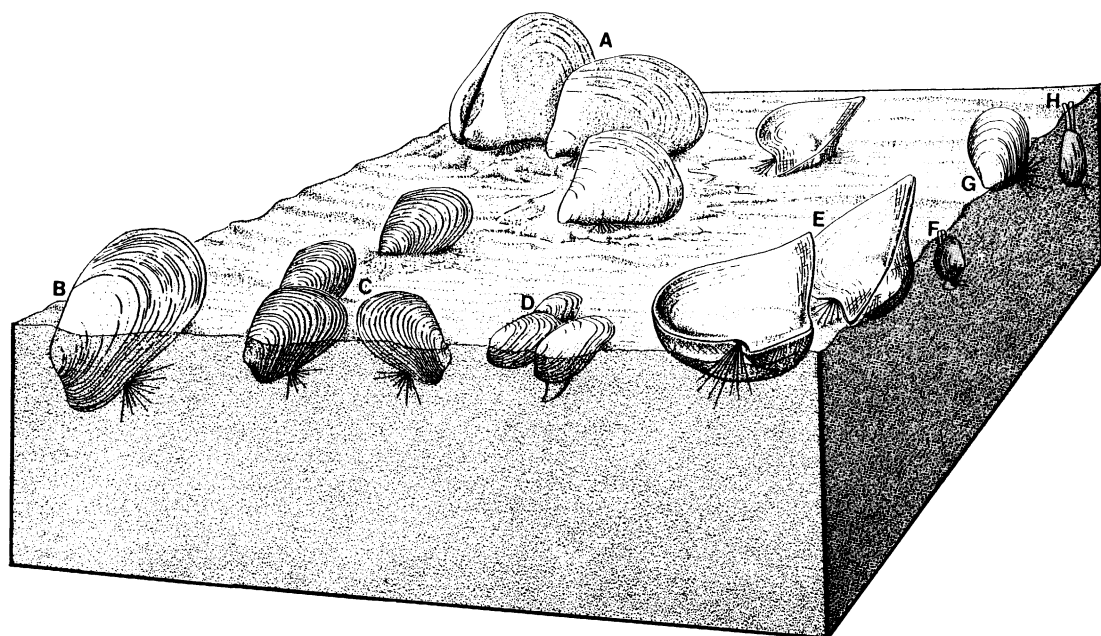


FIG. 6. Life habit reconstructions of Solsville bivalves of the *Gosseletia* Community (drawn to approximate relative scale). This diagram shows representative bivalve species in their probable life positions within a sandy/silty matrix. Note the preponderance of epifaunal–semi-infaunal taxa. A. *Gosseletia triquetra*. B. *Modiomorpha mytiloides*. C. *Modiomorpha concentrica*. D. *Nyassa dorsata*. E. *Ptychopteria fasciculata*. F. *Palaeoneilo constricta*. G. *Ptychodesma knappianum*. H. *Nuculites oblongatus*. Interpretation of life habits of the species shown are either those of the writer or based on interpretations of the same or related genera by past authors listed in figure 5. See autecology discussions in the systematics section.

ers (e.g., *Nuculoidea*) and infaunal suspension-feeders (e.g., *Paracyclas*) are present, the facies is nevertheless dominated by epifaunal and semi-infaunal suspension-feeders including pterineids (e.g., *Actinopteria*) and modiomorphids (e.g., *Modiomorpha*).

The *Nuculoidea* community of the Solsville shows similarities to the *Bellerophon* community from the shaley Triangle Formation (Sonyea Group) of New York (Sutton, Bowen, and McAlester, 1970; Bowen, Rhoads, and McAlester, 1974). In addition to numerous archaeogastropods like those of the Solsville, the *Bellerophon* community contains an abundance of the infaunal deposit-feeders, *Nuculoidea* and *Palaeoneilo*, in association with pholadomyacean suspension-feeders (i.e., “*Sphenotus*”) analogous to the grammysiids of the *Nuculoidea* community.

Even more striking are the parallels be-

tween the *Nuculoidea* community and the *Nuculites-Palaeosolen* facies of the Genesee Group of New York (Thayer, 1974). In addition to archaeogastropods, Thayer reported *Nuculoidea*, *Palaeoneilo*, *Nuculites*, and *Palaeosolen* as well as *Grammysia*, *Paracyclas*, and the pterineids *Actinopteria* and *Leptodesma*.

For several reasons, analogies with the Sonyea and Genesee groups suggest that both the *Nuculoidea* and *Gosseletia* communities represent shallow, nearshore environments:

- (1) In both the Genesee and Sonyea the percentage of benthic molluscs increases onshore, a tendency seen elsewhere by Bretsky (1968, 1969, 1970, 1973). As noted, the Solsville is dominated by benthic molluscs. In addition to the bivalves, a rich assemblage (described by Rollins, El-dredge, and Spiller, 1971) of archaeogas-



tropods, caenogastropods and monoplacophorans is present. Sutton, Bowen, and McAlester (1974) regarded archaeogastropods as largely restricted to nearshore environments.

(2) Taken as a whole, about 57 percent of the Solsville bivalves are nuculoids (see table 1). Although modern nuculoids are distributed among varied cold to warm habitats (see Oldroyd, 1924; Sparck, 1937; J. A. Allen, 1954; Nicol, 1955; Dales, 1957; Ockelmann, 1958; Ellis, 1960) ranging from shallow to abyssal depths (e.g., Bruun, 1957), evidently it was not always so. Sutton, Bowen, and McAlester (1974) and Thayer (1974) have suggested that they were mostly shallow-water dwellers during the Devonian, preferring organic-rich muds of quiet, nearshore lagoons and estuaries.

(3) Synecological parallels discussed above suggest the *Nuculoidea* and *Gosseletia* communities represent habitats no further offshore than middle delta platform. Both the *Cypricardella* community and *Rhipidomella-Leiorhynchus* facies were interpreted as middle delta platform while the *Bellerophon* community and *Nuculites-Palaeosolen* facies were indicated as inner delta platform.

Despite the similarities in the bivalve assemblages of the Solsville, Genesee, and Sonyea, marked differences are evident in the degree of postmortem transport. In the last two, hydraulic mixing is evident; the shelly faunas occur predominantly as coquinites of disarticulated valves. However, the authors of the Genesee and Sonyea studies argued that the degree of transport was not extensive enough to alter their conclusions regarding the composition of the biocoenosis for each of the deltaic habitats. In contrast, the majority of the Solsville bivalves remain articulated in the *Nuculoidea* community and a high percentage remain so in the *Gosseletia* community. Evidently both communities were largely protected from the effects of sedimentary transport that characterize middle and outer delta platform deposits [Sutton, Bowen, and McAlester (1970) noted that Sonyea coquinites, which are abundant in the middle and outer delta platform, volumetrically de-

crease onshore]. Modern environments with these characteristics include the nearshore bar-barrier lagoonal complexes of the Holocene Niger delta (Allen, 1965) which contains both organic rich muds and shelly marginal sands. Sedimentological evidence of such complexes in the upper Hamilton (i.e., Ludlowville and Moscow formations) of the Chenango Valley is given by McCave (1969).

Thayer (1974) has related the composition of Genesee and Sonyea benthic communities to the inferred rate of deltaic progradation. The taxic compositions shown in his table 2 suggest a rapid progradational setting for the Solsville.

### PALEOBIOGEOGRAPHY

Faunal comparisons show broad similarities among middle Devonian Appalachian (Hamilton) bivalve species and those of the early and middle Devonian of the Rhineland of Western Europe. Although a few past authors were aware of occasional taxonomic similarities (e.g., de Verneuil, 1847; Clarke, 1907b, 1909), the breadth of the parallelism was first recognized by Bailey (1975, 1978a) who discussed the geographic distribution of numerous Devonian bivalve taxa (including most Solsville species described here). The Rheinisch-Appalachian faunal similarities were previously obscured by excessive nomenclatural enthusiasm by many early authors (see Introduction), by a widespread but only partially justifiable mistrust of the representational accuracy of Hall's (1884, 1885) figures (see Babin, 1973, p. 43), and by a popular contention that even morphologically similar species must nevertheless be regarded as distinct because of the assumed Atlantic separations of Europe and North America prior to plate tectonic theory.

As Bailey (1978a) indicated the earlier occurrence and greater species diversity of this fauna in Western Europe suggests that this was the point of origin for many of its constituent species. The fauna migrated westward by the middle Devonian (perhaps via northwest Africa; see Sutton's, 1968, paleogeographic reconstruction) in connection with the spread of shallow marine clastic sediments associated with progressively westward episodes of the Caledonian-Acadian

TABLE 3  
North American Distribution of Solsville Bivalves

	Solsv.	Sellersb.	Romney	Pre-Trav.	Milwauk.	Silica	Plum Brook	Arkona	Mahan-tango	Manitoba	Nevada
<i>Nuculoidea deceptiformis</i> , new species	C4	0	0	0	0	00	1?	0 <sup>g</sup>	0	00 <sup>g</sup>	00 <sup>m</sup>
<i>Nuculites triquetra</i>	R	0	1	00	1	00	1	1	1	0	00
<i>Nuculites oblongatus</i>	C3	0	1	00	1	00	1	0	1	0	00
<i>Palaeoneilo filosa</i>	C2	00	1	00?	1	0	00	1 <sup>e</sup>	1	00	00
<i>Palaeoneilo constricta</i>	R	00	1	00?	1	1?	00	0 <sup>h</sup>	1	00	00
<i>Paracyclas rugosa</i>	C2	1	1	0	1	1	1	1	1	1?	0?
<i>Grammysioidea alveata</i>	C1	1	1	00	?	1?	0	0	1	00	0
<i>Grammysioidea elliptica</i>	R	0	1	00	?	00	0	0	0	00	0
<i>Nyassa dorsata</i>	R	00	1	00	00	00	1	1	00	00	00 <sup>o</sup>
<i>Gosseletia triquetra</i>	C3	00	00	0 <sup>b</sup>	00	1	1	00	00	0?	00
<i>Pychopteria fasciculata</i>	C3	1	1	0	0	1	1	1 <sup>e</sup>	1	1?	0 <sup>p</sup>
<i>Modiomorpha concentrica</i>	C2	1	1	0?	1	1?	1	00	1	0?	00
<i>Modiomorpha mytiloides</i>	R	1	1	0?	1	1	1?	00	0	0?	00
<i>Pychodesma knappianum</i>	C1	1	00	00	00	1 <sup>d</sup>	00	00	00	00	00

NOTATION: R—rare. C1—fairly common. C2—common. C3—abundant. C4—very abundant. 0—genus present. 1—species present. 00—genus absent.  
<sup>a</sup> Figured by Wilson (1975, pl. 72, figs. 1–3) as *Grammysia sylvanensis*; holotype similar to *Grammysioidea alveata*. <sup>b</sup> I agree with LaRocque (1950, pl. 6, figs. 12–14) who called this *Gosseletia* sp. Pojeta (1966), however, placed it in *Lophomychia* Pohl [= *Mytilarca* in Newell and LaRocque in Moore, 1969] due to the lack of an auricle. <sup>c</sup> Wilson's (1975, pl. 72, fig. 15) "*Glossites subtenius*" strongly resembles *M. concentrica*. <sup>d</sup> Collected by the author. An internal mold of Wilson's (1975, pl. 72, fig. 9) "*Glossites subtenius*" could be *P. knappianum*. <sup>e</sup> Collected by the author. <sup>f</sup> Stumm's (1942, pl. 81, fig. 28) small, trigonal "*N. corbuliformis*" could be *N. deceptiformis*, new species. <sup>g</sup> An unusual undescribed species of *Nuculoidea* found by the author. <sup>h</sup> Whiteaves (1898) reported *P. plana*, here regarded as a synonym of *P. constricta*. <sup>i</sup> Intermediate between *P. rugosa* and *P. elliptica*. <sup>j</sup> An internal mold called *Gosseletia* sp. by Whiteaves (1892; no fig. given) who regarded its identity as uncertain. <sup>k</sup> One small fragment of Whiteaves's *Pterinea lobata* suggests *Pychopteria fasciculata*; other specimens clearly do not. <sup>l</sup> Internal molds called *Modiomorpha* by Whiteaves (1892); possibly a different genus. <sup>m</sup> Walcott's *N. resciensis* probably not a nuculid. = *Eoschizodus*? <sup>n</sup> Walcott (1884) indicated questionable presence of this genus but gave no figure. <sup>o</sup> Walcott's (1884) *Nyassa* too poorly preserved for generic assignment. <sup>p</sup> Not *Pterinea flabella* [= *Pychopteria fasciculata*] as Walcott (1884) suggested. Lacks an anterior auricle. <sup>q</sup> "*Nucula*" *manitobensis* Whiteaves, 1892 is a possible carydid.

TABLE 4  
North American Devonian Bivalve Species and Closely Related or Conspecific European Counterparts<sup>a</sup>

European Taxa	North American Equivalents
SUBCLASS PTERIOMORPHIA Beurlen	
<i>Ptychopteria fasciculata</i> (Goldfuss) Siegenian-upper Emsian	{ --- <i>Ptychopteria</i> ( <i>Cornellites</i> ) <i>flabella</i> (Conrad), Onondagan-Cazenovian
<i>Ptychopteria subtilicosta</i> (Priestersbach) [in part] upper Emsian or basal Eifelian	
<i>Ptychopteria gracilis</i> (Priest. and Fuchs) [in part] upper Emsian	
<i>Gosseletia alta</i> Follmann upper Emsian	{ --- <i>Gosseletia triquetra</i> (Conrad) Cazenovian
<i>Gosseletia distincta</i> Follmann Eifelian	
<i>Gosseletia securiformis</i> Follmann ?Siegenian-upper Emsian	
<i>Gosseletia schizodon</i> Frech upper Emsian	
<i>Ptychodesma</i> sp. Beushausen ----- upper Emsian	<i>Ptychodesma knappianum</i> Hall & Whitf. Cazenovian
SUBCLASS ANOMALODESMATA Dall	
<i>Grammysia anomala</i> (Goldfuss) ?lower-upper Emsian	{ --- <i>Grammysia bisulcata</i> (Conrad) Cazenovian
<i>Grammysia ovata</i> Sandberger [in part] lower Emsian	
<i>Grammysia johannis</i> Beushausen [in part] lower-upper Emsian	
<i>Grammysia nodocostata</i> Hall var. <i>eifeliensis</i> Beush. ----- lower Emsian	<i>Grammysia nodocostata</i> Hall Cazenovian
<i>Allerisma mosellianum</i> Beushausen ----- upper Emsian	<i>Grammysioidea arcuata</i> (Conrad) Cazenovian
SUBCLASS PALAEOHETERODONTA Newell	
<i>Modiomorpha antiqua</i> (Goldf.) [in part] lower Emsian	{ --- <i>Modiomorpha concentrica</i> (Conrad) Cazenovian
<i>Modiomorpha westfalica</i> (Beush.) [in part] Givetian	
<i>Modiomorpha anulifera</i> Priest. [in part] upper Emsian	
<i>Modiomorpha elevata</i> (Krantz) Siegenian-lower Emsian	{ --- <i>Modiomorpha mytiloides</i> (Conrad) Cazenovian-Chemungian
<i>Modiomorpha siegenensis</i> Beush. Siegenian	
<i>Nyassa dorsata</i> Goldfuss ----- Eifelian-Givetian	<i>Nyassa arguta</i> Hall Cazenovian
<i>Carydium</i> cf. <i>sociale</i> Beush. of Maillieux [not Beush.] ----- Emsian	<i>Carydium varicosum</i> (Hall)– <i>C. bellastriatum</i> (Conrad), Cazenovian
SUBCLASS HETERODONTA Neumayr	
<i>Paracyclas proavia</i> (Goldf.) ----- Eifelian-Givetian	<i>Paracyclas elliptica</i> Hall Onondagan-Chemungian
<i>Paracyclas rugosa</i> (Goldf.) ----- Siegenian-Frasnian	<i>Paracyclas lirata</i> (Conrad) Cazenovian-Fingerlakesian
<i>Paracyclas marginata</i> Maurer ----- Siegenian-lower Eifelian	<i>Paracyclas tenuis</i> Hall Cazenovian
<i>Phenacocyclus antiqua</i> (Goldf.) ----- Eifelian-Givetian	<i>Phenacocyclus ohioensis</i> (Meek) Cazenovian

TABLE 4—(Continued)

European Taxa	North American Equivalents
SUBCLASS PALAEOTAXODONTA Korobkov	
<i>Nuculoidea fornicata</i> (Goldf.) [= <i>Nucula daleidensis</i> Steininger] Emsian? Eifelian? Givetian	} ---- <i>Nuculoidea opima</i> (Hall) Cazenovian
<i>Nuculoidea murchisoni</i> (Goldf.) Eifelian-Givetian	
<i>Nuculoidea</i> cf. <i>lodanensis</i> (Beush.) upper Emsian	
<i>Nuculoidea sandbergeri</i> (Beush.) Givetian (one specimen, doubtlessly, a variant of <i>N. fornicata</i> )	
<i>Nuculoidea pelmensis</i> (Beush.) Givetian	
<i>Nuculoidea aquisgranensis</i> (Beush.) Givetian	} ---- <i>Nuculoidea corbuliformis</i> (Hall) Cazenovian, Chemungian
<i>Nuculoidea trigona</i> (Spriest.) upper Emsian	
<i>Nuculoidea macrorhyncha</i> (Spriest.) upper Emsian	
<i>Nuculites</i> cf. <i>triqueter</i> Conr. (Beush.) lower-upper Emsian	} ---- <i>Nuculites triqueter</i> Conrad Onesquethawan (Gaspé), Cazenovian
<i>Nuculites posthumus</i> (Beush.) Eifelian	
<i>Nuculites truncatus</i> (Steininger) Siegenian, lower-upper Emsian	
<i>Nuculites longiusculus</i> (Beush.) lower Emsian	
<i>Nuculites ellipticus</i> (Maurer) [= <i>Nuculites beushauseni</i> (Fuchs)] Siegenian-upper Emsian	} ---- <i>Nuculites oblongatus</i> Conrad Helderbergian (Maine), Cazenovian
<i>Nuculites longus</i> (Mauz) lower Emsian	
<i>Nuculites vaissieri</i> (Leriche) lower Gedinian	
<i>Palaeoneilo demigrans</i> (Beush.) Gedinian? Lower-upper Emsian	} ---- <i>Palaeoneilo constricta</i> (Conrad) Helderbergian (Maine). Cazenovian-Chemungian. Lower Mississippian?
<i>Palaeoneilo planiformis</i> (Beush.) lower Emsian	
<i>Palaeoneilo daleidensis</i> (Beush.) upper Emsian	
<i>Palaeoneilo krotonis</i> (Roemer) Eifelian-Frasnian	
<i>Palaeoneilo candida</i> (Kegel) Siegenian	
<i>Palaeoneilo maureri</i> (Beush.) [in part] ----- lower Emsian	---- <i>Palaeoneilo emarginata</i> (Conrad) [= <i>P. corrugata</i> Pohl] Cazenovian-Chemungian
<i>Palaeoneilo moehrkei</i> (Dahmer) upper Siegenian	} ---- <i>Palaeoneilo filosa</i> (Conrad) [= <i>P. secunda</i> Hall– <i>P. tenuistriata</i> Hall] Cazenovian-Chemungian
<i>Palaeoneilo beushauseni</i> (Kegel) [= <i>P. oehlerti</i> (Beush.) not Barrois] Siegenian-lower Emsian	
<i>Palaeoneilo bertkaui</i> (Beush.) Siegenian-lower Emsian	

<sup>a</sup> From Bailey (1975a, revised).



orogeny as the suturing of the paleocontinents Baltica and Laurentia was completed (see Bambach, Scotese, and Ziegler, 1980).

As shown in tables 3 and 4, the Solsville bivalve species are typical of the Rheinisch-Appalachian faunal group and show strong similarities to other Hamilton bivalve faunas such as those of the Romney Formation of West Virginia and Maryland (see Prosser and Kindle, 1913) and the Mahantango Formation of Pennsylvania (see Ellison, 1965). Essentially similar bivalve faunas are found in the Sellersburg beds of southern Indiana and northern Kentucky (see Hall and Whitfield, 1872; Nettleroth, 1899; Kindle, 1901; Savage, 1930, 1931), the Silica Formation (Stewart, 1927; Ehlers, Stumm, and Kesling, 1951; Duluk, 1965; Stumm and Chilmann, 1967; Wilson, 1975) and Prout Limestone-Plum Brook Shale (Stauffer, 1916; Stumm, 1942) of Ohio, the Middle Devonian section at Arkona, Ontario (Whiteaves, 1889, 1898; Shimer and Grabau, 1902; Stauffer, 1915, 1916; Stumm and Wright, 1958; Southworth, 1967; Bailey, 1978a), and the Milwaukee Formation of Wisconsin (Cleland, 1911; Pohl, 1929). Differences among these bivalve paleocommunities are largely synecological. For example, the Arkona bivalve community is dominated by infaunal deposit feeders, whereas the Silica and Sellersburg beds contain mostly epibyssate/endobyssate suspension-feeding communities.

As table 3 shows, North American Rheinisch-Appalachian bivalve communities seem almost universally characterized by the occurrence of two ubiquitous species, *Ptychopteria fasciculata* and *Paracyclas rugosa*. The Solsville faunas, however, seem unique in the large numbers of three otherwise relatively rare species, *Gosseletia triquetra*, *Ptychodesma knappianum*, and *Nuculoidea deceptriformis*, new species.

Rheinisch-Appalachian species seem largely absent west of the Transcontinental Arch which was evidently an emergent barrier to migration (Oliver, 1973, 1976). Instead,

North American Devonian taxa west of the arch show certain Asiatic affinities (Stoyanow, 1948; Saul, 1976). Early assertions that species there are closely allied to the Appalachian faunal group are probably exaggerated. Walcott (1884), for example, claimed that 23 genera and eight species of bivalves from the Devonian Nevada Limestone (Eureka District, Nevada) are shared in common with the Devonian rocks of New York and Ohio. However, several of these including *Modiomorpha*, *Nyassa*, and *Nucula* (= *Nuculoidea* of later authors) are either misidentified or too poorly preserved for confirmation; the fauna should be restudied. A second western fragmentary faunule described by Kindle (1909) from the Ouray Limestone of Colorado contains a few bivalves tentatively linked to Appalachian taxa but, again, preservation is too poor for such a conclusion.

Among the few truly endemic North American bivalve taxa are those of the Michigan Basin (see LaRocque, 1950; Yang, 1939) which was probably separated from the Appalachian and Illinois basins during the Silurian and Devonian by the Kankakee and Cincinnati-Findlay-Algonquin Arch systems (Atherton, 1971; Summerson and Swann, 1970; Eardley, 1962).

Gignoux (1950) said the middle Devonian faunas of the Lake Manitoba-Lake Winnipegosis section (Manitoba, south-central Canada, Kindle, 1914) are Asiatic in character. Although most of Whiteaves's (1892) bivalve species from those beds were new, they seem mixed with a few Appalachian-Rheinish species, e.g., a possible *Ptychopteria fasciculata* (Goldfuss) *Phenacocyclus antiqua* (Goldfuss) [= *P. ohioensis* (Meek)], *Nuculoidea lirata* (Conrad), and *Cypricardella belastriata* (Conrad). Further northwest (northern Alberta and Mackenzie District) Whiteaves (1891) described six Appalachian-Rheinish bivalve species (said to be well preserved but mostly unfigured) and noted similar biogeographic links among several other fossil phyla.

## SYSTEMATIC PALEONTOLOGY

CLASS BIVALVIA LINNÉ, 1758

SUBCLASS PTERIOMORPHIA BEURLÉN, 1944

ORDER PTERIOIDA NEWELL, 1965

SUBORDER PTERIINA NEWELL, 1965

SUPERFAMILY PTERIACEA GRAY, 1847

FAMILY PTERINEIDAE MILLER, 1877

GENUS *PTYCHOPTERIA* HALL, 1883

SUBGENUS *CORNELLITES* WILLIAMS, 1908

TYPE SPECIES: *Ptychopteria: Ptychopteria eugenia* Hall, 1883 [= *P. salamanca* Hall, 1884] from the Upper Devonian (Chemung) of New York by subsequent designation of S. A. Miller, 1889. *Cornellites: Pterinaea fasciculata* Goldfuss, 1836 from the Lower Devonian (Emsian) of Germany by original designation of Williams, 1908.

GENERIC USAGE AND SYNONYMY: See Newell and LaRocque in Moore, 1969, p. N302.

*Ptychopteria (Cornellites) fasciculata*  
(Goldfuss), 1836

Figures 5H, 6E, 7–10, 11B

*Pterinaea fasciculata* Goldfuss, 1836, p. 137, pl. 120, fig. 5. De Verneuil, 1847, p. 695. Beushausen, 1884, p. 57, pl. 2, fig. 11. Follmann, 1885, p. 187, pl. 3, fig. 3. Frech, 1891, p. 84, pl. 8, figs. 1, 1a, pl. 9, figs. 1–3. Viëtor, 1919, p. 376. [Other references omitted. See exhaustive list of Maillieux, 1937, p. 32.]

*Pterinea (Cornellites) fasciculata* Goldfuss. Maillieux, 1935, p. 18; 1937, p. 32, pl. 1, figs. 6–8 [esp. fig. 7].

*Ptychopteria fasciculata* (Goldfuss). Newell and LaRocque in Moore, 1969, p. N302.

*Ptychopteria (Cornellites) fasciculata* (Goldfuss). Bailey, 1975, p. 41, pl. 1, figs. 1–6, pl. 2, figs. 1–7, pl. 3, figs. 1–6; 1978a, p. 121. Carter and Tevesz, 1978b, p. 875, fig. 19.

[not] *Pterinea* cf. *fasciculata* Goldfuss. Clarke, 1907a, p. 204; 1909, p. 102, pl. 25, figs. 1–7.

[not] *Pterinea fasciculata* var. *occidentalis* Clarke, 1907a, p. 205; 1909, p. 27, pl. 14, figs. 1–7.

†[?] *Pterinaea gracilis* Priestersbach and Fuchs, 1909. Priestersbach, 1915, p. 30, pl. 8, figs. 4–6; 1925, p. 407, pl. 10, fig. 14 [not Priestersbach and Fuchs, 1909, p. 12, pl. 1, figs. 6–12].

†[?] *Pterinaea subtilicosta* Priestersbach, 1915, p. 31, pl. 8, figs. 7, 8 [?], esp. pl. 23, fig. 1, 1a.

†[cf.] *Pterinaea lorana* Fuchs, 1915, p. 35, pl. 8, fig. 19, pl. 9, fig. 5.

*Avicula flabella* Conrad, 1842, p. 238, pl. 12, fig. 8. Vanuxem, 1842, p. 153, fig. 37, no. 3.

*Pterinea flabella* (Conrad). Hall, 1883, pl. 14, figs. 1–21, pl. 15, figs. 1, 4–6, 8–10; 1884, p. 93, pl. 14, figs. 1–21, pl. 15, figs. 1, 4–6, 8–10, pl. 93, figs. 11, 12. [not] Walcott, 1884, p. 165, pl. 5, fig. 6, pl. 15, fig. 12. Grabau, 1899, p. 244, fig. 159. Whitfield and Hovey, 1900, p. 300. Kindle, 1901, p. 668. Cleland, 1903, p. 65. Merrill, 1905, p. 552.

[?] *Pterinea* near *flabella*. Pohl, 1930, p. 28.

*Cornellites (Pterinea) flabella* (Conrad). Williams, 1908, pp. 89–90.

*Cornellites flabella* (Conrad). Shimer and Shrock, 1944, p. 383, pl. 148, fig. 18. McAlester, 1962a, p. 36. LaRocque and Marple, p. 84, fig. 187. Ellison, 1965, p. 130, pl. 15, figs. 10, 11. Palmer and Brann, 1966, pl. 11, figs. 1–3.

*Pterinea flabellum* (Conrad). Hall and Whitfield, 1872, p. 199. Miller, 1877, p. 201. Lesley, 1889, p. 810, 2 figs. Whitfield, 1890, p. 555, pl. 11, fig. 17. Whiteaves, 1889, p. 116; 1891, p. 238; 1898, p. 416. Shimer and Grabau, 1902, p. 181. Clarke and Ruedemann, 1903, p. 494. Grabau, 1906, pp. 221, 330, fig. 173. Stauffer, 1909, p. 166; 1915, pp. 235, 239; 1916, pp. 477, 483. Prosser and Kindle, 1913, p. 250, pl. 129, figs. 1–4. Cleland, 1916, p. 459, fig. 432a. Branson, 1924, p. 149, pl. 36, fig. 2. Cooper, 1930, pp. 133, 233. Savage, 1930, p. 97. [?] Willard, 1939, p. 478, etc., pl. 23, fig. 16. Butts, 1941, p. 195, pl. 118, figs. 1–3. Stumm, 1942, p. 557, pl. 81, fig. 22, pl. 84, fig. 47.

*Pterinea (Cornellites) flabellum* (Conrad). Grabau and Shimer, 1909, p. 421, fig. 551.

*Cornellites flabellum* (Conrad). Stumm and Wright, 1958, pp. 93, 108, 117, 121. Stumm and Chilton, 1967, p. 130. Rollins, Eldredge, and Spiller, 1971, p. 134.

*Cornellites flabellus* (Conrad). Cooper, 1933, p. 548.

*Ptychopteria flabellum* (Hall) [sic]. Wilson, 1975, p. 134, pl. 68, fig. 7, pl. 72, figs. 13, 18, 19, pl. 101, figs. 28, 29, pl. 114, fig. 2.

†[?] *Pterinea lobata* Whiteaves, 1892 [in part], p. 292, pl. 38, fig. 4 [not pl. 38, figs. 1–3].

DESCRIPTION: Shells medium to large, strongly inequivalve and inequilateral, distinctly alate, prosocline, and prosogyrous. Left valve convexly inflated and strongly so in the central body of the shell. Right valve flattened to concave, commonly resupinate, becoming somewhat convexly inflated only near the umbonal region. Each valve possesses a large posterior wing, broadly embayed posteroventrally, and a lesser, variably

shaped anterior auricle (strongly inflated in the left valve and weakly so in the right valve) with a distinct byssal sinus. Sulci separate the central body of the shell from the wing and auricle. The left valve has a sharply defined posterior sulcus (located between shell body and wing) and a lesser, anteriorly placed auricular sulcus. In the resupinate right valve the posterior sulcus is not well defined, but the auricular sulcus is distinctly defined in the form of a deep byssal notch (fig. 7L) with an associated byssal gape (fig. 7L, M) between the valves where the notch meets the commissure.

The prosopon is distinctive and different in each valve. In both right and left valves the concentric elements (growth lines) in the auricle and central body of the shell have the umbonal region as their center of curvature. The concentric elements of the wing, however, show a center of curvature located posteroventrally. This is a consequence of the aforementioned posteroventral marginal embayment. The right valve possesses only more or less regular, concentric growth increments (which are fine in the umbonal region and progressively coarsen toward the venter) except in a narrow dorsal region of the wing behind the umbo and just beneath the hinge line where a few well-defined, close radial elements are developed in association with a strengthening of concentric elements in the same region, producing a fine dorsomarginal reticulating network (fig. 7B, F, L, N).

The prosopon of the left valve consists of close, regular, well-defined concentric growth lines with a superimposed series of radial elements (i.e., secondary costae; these are coequal in strength with the growth lines) punctuated by varicose radial ribs (primary costae) at regular to irregular intervals. A reticulating pattern is produced by the intersecting network of concentric and radial elements. The ribs take on a segmented, nodose, or rugose appearance where they are intersected by growth lines.

The hinge line, located mostly along the dorsal length of the posterior wing, is situated between 150°–160° with respect to the dorsalmost part of the posterior umbonal slope. A duplivincular, mostly opisthodetic ligament is indicated by a long, straight, narrow, parallel-grooved, ligamental area along the

hinge line in each valve. In form it is geniculate, like a highly asymmetrical chevron whose apex lies directly between the beaks (fig. 7J, N). The anterior limb of the chevron is abruptly truncated in front of the beaks, while the greatly elongated posterior limb accounts for virtually all the ligamental insertion area.

Situated upon a curving hinge plate, the dentition of the left valve, as seen in one specimen (fig. 8A, B, D) and partially in another (fig. 8E), consists of (1) two moderately strong, parallel cardinal teeth with a deep intervening socket and a third, ancillary cardinal tooth lying beneath and diverging from the others and separated from them by a minor socket; and (2) two strong, elongated lateral teeth separated by a strong lateral socket. Lying above these two is a third, ancillary lateral tooth separated from the others below by a minor lateral socket. Based upon the left valve hinge structure, it may be inferred that the right valve dentition consists of (1) one robust cardinal tooth flanked by an ancillary cardinal tooth below and possibly another above<sup>1</sup>; and (2) at least two comparatively strong lateral teeth.

Both cardinals and laterals are roughly subparallel to one another (with the exception of the slightly divergent lower ancillary cardinal tooth) and are oriented obliquely in relation to the hinge line approximately parallel to the trend of the posterior auricular sulcus. As figure 8C shows, there is really no edentulous area between the cardinal and lateral teeth since the posterior cardinal and the lowermost lateral are in mutual continuity forming a cardinolateral tooth which curves broadly along and buttresses the inner edge of the hinge plate. The second and third lateral teeth are arranged in echelon behind the lowermost, first lateral tooth.

The anterior adductor scar (figs. 8D, 9C) is small, circular, and deeply impressed, perforating the hinge plate immediately below the anteriormost cardinal tooth where it is situated on a sloping shell thickening beneath the hinge plate and buttressed there by a small, thick ridge along the dorsoposterior margin of the scar. The posterior adductor scar is

<sup>1</sup> Hall (1884) observed two or three cardinal teeth in the right valve.

TABLE 5  
Measurements (in Millimeters) of *Ptychopteria*  
(*Cornellites*) *fasciculata* (Goldfuss)

Locality	Length	Height	Width <sup>a</sup>
AMNH 3012	60 <sup>b</sup>	49	19
AMNH 3013	44 <sup>b</sup>	46	19.5
	62 <sup>b</sup>	54	—
	47 <sup>b</sup>	42	11.5
AMNH 3014	68 <sup>b</sup>	64	23
	41 <sup>b</sup>	32	13.5
	40 <sup>ab</sup>	30 <sup>ab</sup>	11
Miscellaneous Solsville	63 <sup>b</sup>	45	16.5

<sup>a</sup> Total width, both valves articulated.  
<sup>b</sup> Specimen broken. Dimension approximate and inferred.

large, subcircular (figs. 8C, 9C) or almond-shaped (fig. 9D) and not distinctly lobate (although some minor, irregular lobation is visible in fig. 9C).

The pallial line is simple, somewhat pustulose in internal molds and set well back into the shell interior. In the dorsoposterior portion of its circumference in the left valve, it appears to form a very deep groove (visible in fig. 8B, C) beneath the lateral denticle series and is expressed as a distinct ridge on internal molds (figs. 9C and especially 7G). Within the arc of the pallial line and beneath the forward adductor, numerous small pustules are visible on a left internal mold (fig. 9C) representing small pits (pallial punctae) for muscular attachment of the mantle to the shell. Cox (in Moore, 1969) reported similar punctae in the Lucinidae, and Newell and Boyd (1975, fig. 15) have noted them among trigonaceans.

Neither anterior nor posterior byssal/pedal retractor scars are in evidence.

Recrystallized/replaced shell material on many of the specimens indicate that the original valves were robust and heavy in the region of the anterior auricle and central portions of the shell becoming slightly thinner in the posterior wing which is often broken away. Original shell microstructure is described by Carter and Tevesz (1978b).

*Cornellites*: The term *Cornellites*, first proposed by Williams in 1908, has not received universal acceptance as a generic name. Mailieux (1937) preferred to retain *Cornellites* as

a subgenus of *Pterinea* as did Grabau and Shimer (1909), and Babin (1966). McAlester (1962a), pointing out the “more than usual generic chaos” in regard to Chemung pteriod bivalves, used *Cornellites* tentatively in a generic sense for pteriod species possessing radial ribs or costae. Likewise, he used *Leiopteria* and *Leptodesma* for concentrically sculptured forms and *Actinopteria* for reticulate pteriods. These diagnoses are not entirely adequate since species such as *P. fasciculata* possess both strong radial ribs and reticulate ornament in the left valve but mostly concentric ornament in the right valve. More recently, Newell and LaRocque (in Moore, 1969) have treated *Cornellites* as a synonym of *Ptychopteria* Hall (1883). They recognized two subgenera of *Ptychopteria* on the basis of the form of the anterior auricle: *P. (Ptychopteria)* with an obliquely truncate auricle and *P. (Actinopteria)* with a lobose auricle. However, among certain *Ptychopteria* species of Frech’s (1891) “Gruppe der *Pterinaea costata*” (= *Cornellites* Williams, 1908), e.g., *P. fasciculata*, *P. costata*, *P. costulata*, etc., the auricle is generally unlike that of either *P. (Ptychopteria)* or *P. (Actinopteria)*; it is often larger, more swollen and nasute, with a rugose appearance produced by strong irregular radial ribs. Based upon these distinctions I retain *Cornellites* as a subgenus of *Ptychopteria*.

COMPARISONS: The Solsville specimens are typical examples of *Ptychopteria (Cornellites) flabella* (Conrad), a North American Middle Devonian (Onondaga-Hamilton) species I regard as a synonym of *P. fasciculata* (Goldfuss) from the Lower Devonian of Germany and Belgium. So remarkable is the resemblance of the European species as illustrated by Frech (1891, reproduced here as fig. 10) and by Maillieux (1937, pl. 1, fig. 7) to previously illustrated specimens of *P. flabella* (e.g., in Hall, 1884; Prosser and Kindle, 1913; etc.), that conspecificity would appear difficult to deny. The similarities of the two were noticed by several early authors. Conrad himself (1837, 1838) listed *P. fasciculata* as one of the fossils of New York State (see remarks of Whiteaves, 1891, p. 238). The synonymy of the two was affirmed by de Verneuil (1847, p. 695): “*Pterinea fasciculata* Goldf. (*Avicula flabella* Conrad).—Après avoir

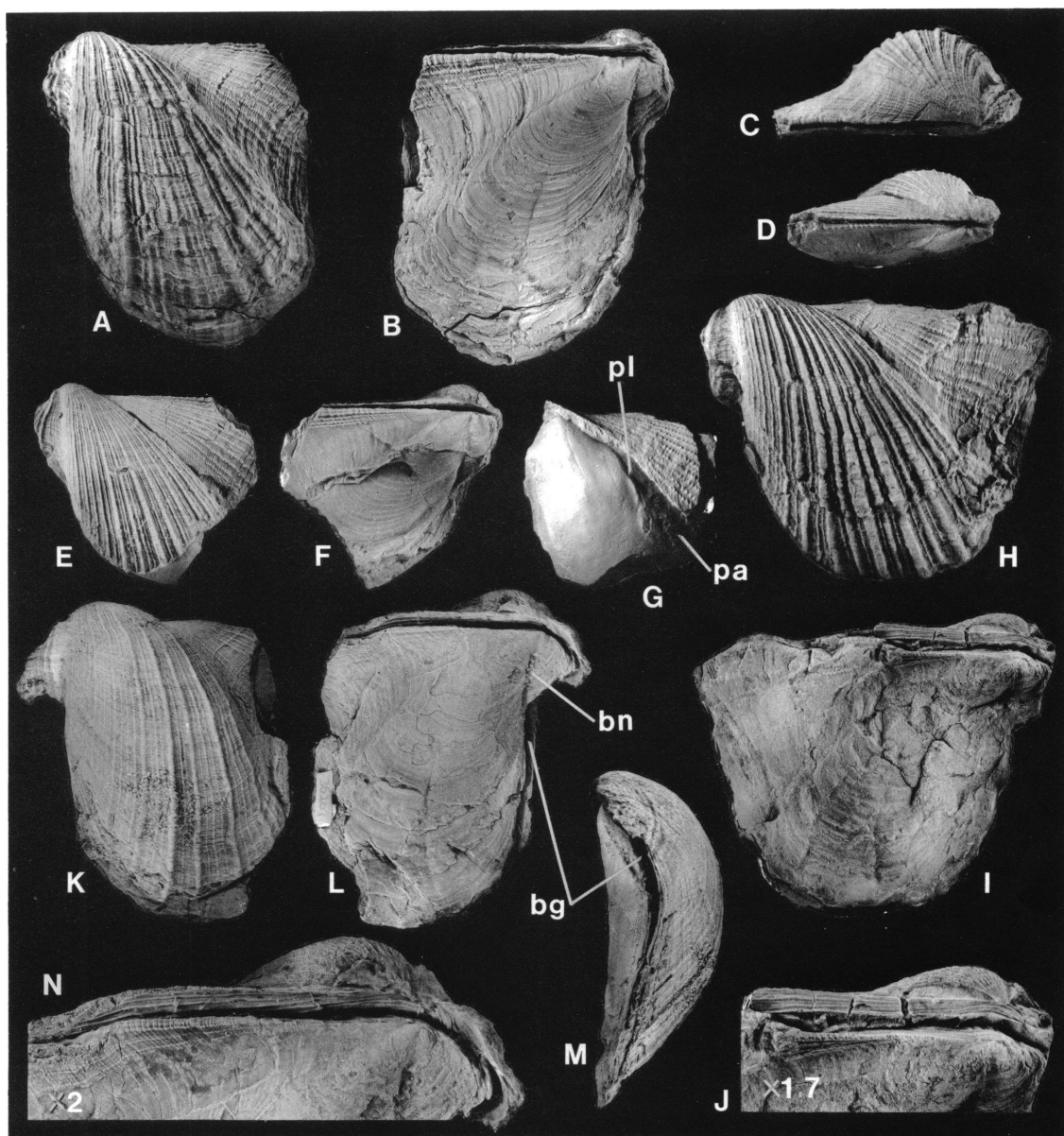


FIG. 7. *Ptychopteria* (*Cornellites*) *fasciculata* Goldfuss. A–C. Articulated specimen (AMNH 36170) from AMNH loc. 3012. A. Left valve. B. Right valve. C. Hinge line. D–F. Articulated specimen (AMNH 36171) from AMNH loc. 3014. D. Hinge line. E. Left valve. F. Right valve. G. Broken left internal mold and shell (AMNH 36178) from AMNH loc. 3014. H–J. Articulated specimen (AMNH 36172) from AMNH loc. 3013. H. Left valve. I. Right valve. J. Enlarged hinge line. K–N. Articulated specimen (AMNH 36167) from AMNH loc. 3013. K. Left valve. L. Right valve. M. Anterior. N. Enlarged hinge line.

Abbreviations: bg—byssal gape, bn—byssal notch, dla—duplivincular ligamental area, pa—posterior adductor scar, pl—pallial line. All figures  $\times 1$  except as noted.

comparé avec soin l'*A. flabella* à la description que Goldfuss a donnée de la *P. fasciculata*, nous avons cru pouvoir les ré-

nir; l'une provient *Hamilton Group* (New York), et l'autre des *grauwackes* des environs d'Ems (Nassau). On sait que ces *grauwackes*,

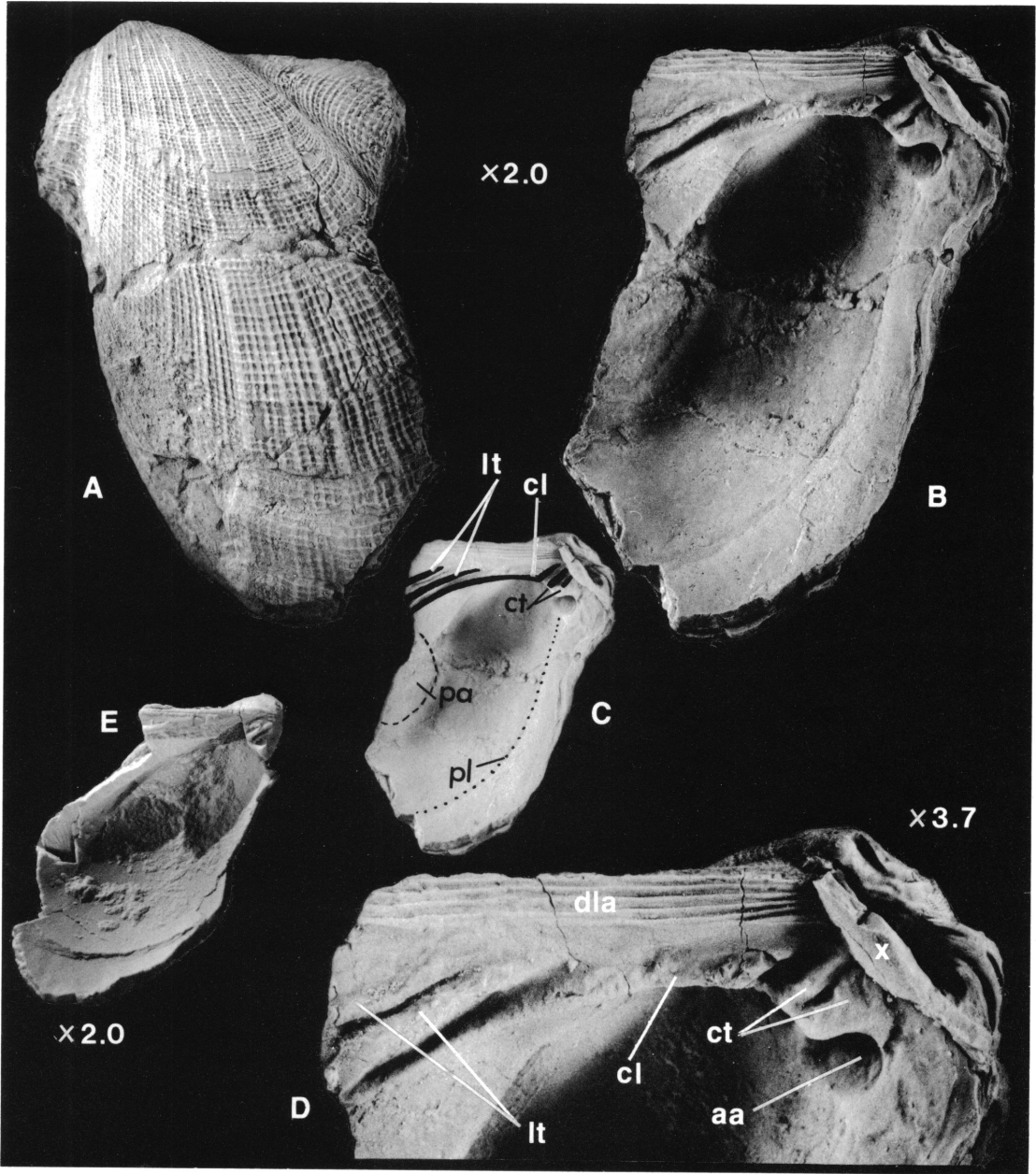


FIG. 8. *Ptychopteria* (*Cornellites*) *fasciculata* (Goldfuss). A–D. Left valve (AMNH 36173) from AMNH loc. 3017. A. Valve exterior. B. Valve interior. C. Functional morphology of valve interior. (X1). D. Enlargement of hinge region. E. Partial left valve (AMNH 36174) from AMNH loc. 3013.

Abbreviations: aa—anterior adductor scar, cl—cardinolateral tooth, ct—cardinal tooth, dla—duplivincular ligamental area, lt—lateral tooth, pa—posterior adductor scar, pl—pallial line, x—foreign shell fragment fortuitously inserted into crack in shell; this could not be removed without jeopardizing the integrity of the specimen.



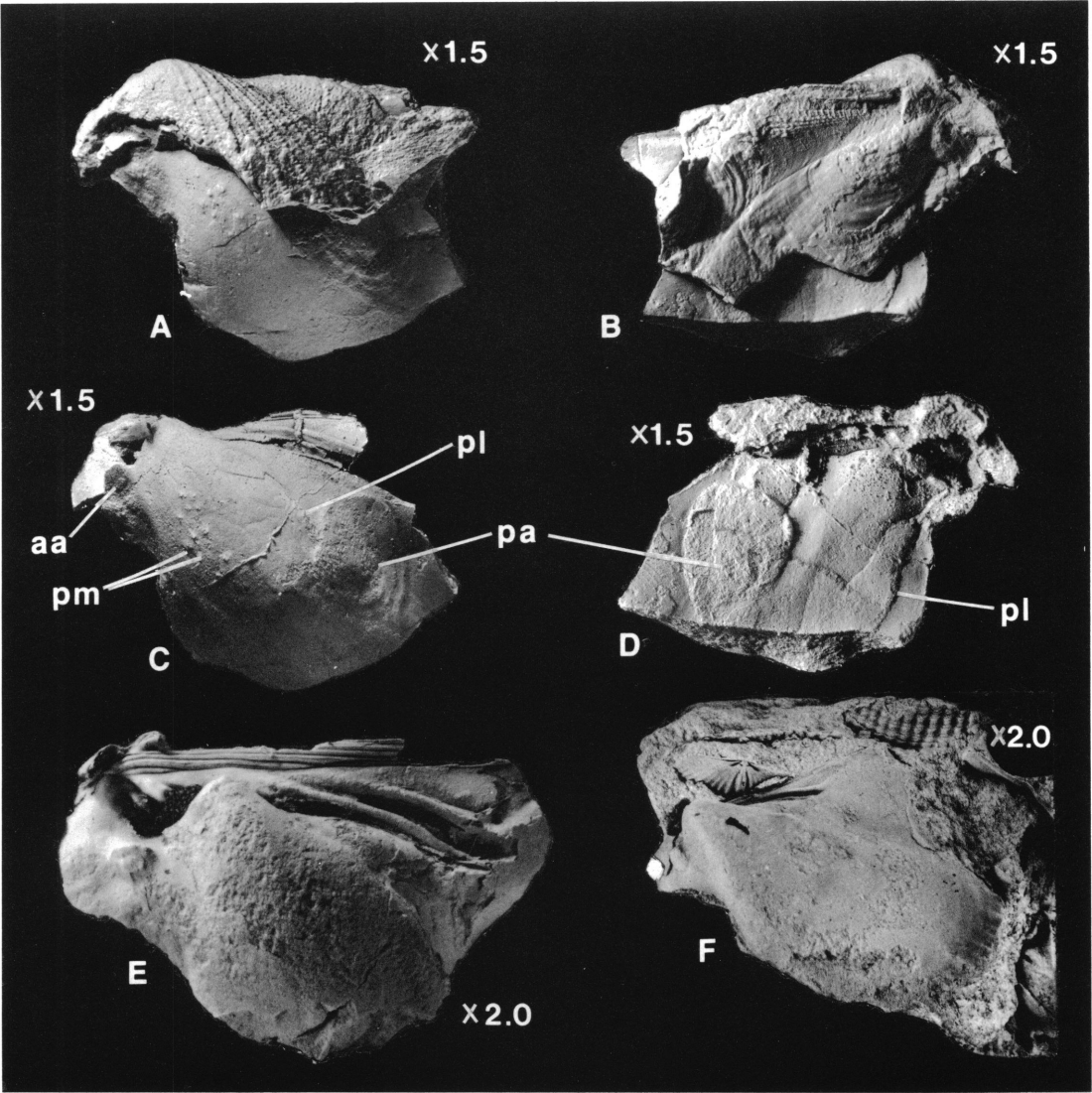


FIG. 9. *Ptychopteria* (*Cornellites*) *fasciculata* (Goldfuss). A–D. Near complete internal mold with partial shell (AMNH 36177) from AMNH loc. 3017. A. Left valve. B. Right valve. C. Internal mold with left shell material removed. D. Internal mold with right shell removed. E. Left view of near complete internal mold (AMNH 36176) from miscellaneous Solsville; shell removed with muriatic acid. F. Internal mold of left valve (AMNH 36175A) from AMNH loc. 3013. Abbreviations: aa—anterior adductor scar, pa—posterior adductor scar, pl—pallial line, pm—pallial muscle punctations.

placées au-dessous du calcaire de l’Eifel, contiennent encore quelques espèces dévonniennes.” Sandberger and Sandberger (1856), after

receiving a type specimen (i.e., “Original-Exemplar”) of *P. flabella* from Conrad for direct comparison with *P. fasciculata*, concluded that the two are one in the same. Williams

(1908) remarked at the morphologic ties between the two, and Hall (1884) suspected their conspecificity as did Kayser (1878) and Viëtor (1919). Follmann (1885, p. 188) believed the two to be identical: "*Pt. fasciculata* ist auch in Amerika in den Schieferen der Hamiltongroup verbreitet und wird von den amerikanischen Geologen *Pt. flabella*, Conr. benannt. Nach den sehr ausführlichen Beschreibung und Abbildungen Hall's (l. c.) kann es nicht Zweifelhaft sein, dass die genannte amerikanische mit unserer rheinischen Art identisch ist."

Frech (1891), however, disagreed on the following basis: (1) the primary ribs appeared weaker to Frech and the secondary radial elements coarser in the left valve of *P. flabella* (the contrasting ornamentation of the right valve Frech assumed to be similar in both *P. flabella* and *P. fasciculata*); (2) the anterior auricle in *P. flabella* seemed covered with only weakly developed radial lineations and lacked the strong radial ribs seen in *P. fasciculata*; (3) only two lateral teeth were observed in the left valve of *P. flabella* in contrast to the three lateral teeth in *P. fasciculata*; (4) *P. flabella* is middle Devonian and *P. fasciculata* is early Devonian; and (5) the two species, Frech maintained, are too widely separated geographically to be considered as conspecific, although he did admit that they must be closely linked.

For the following reasons I reject Frech's objections: (1) the Solsville specimens reveal a high degree of intraspecific variability with respect to relative placement, strength and number of the primary and secondary costae (compare figs. 7A, E, H, K, 8A). Similar proportional variability was recognized in *P. flabella* also by Hall (1884, pl. 10, figs. 8, 9, 10 and explanations). The observed variability broadly overlaps that of the European form. (2) Contrary to Frech's opinion, strong radial ribbing is, indeed, well developed on the anterior auricles as shown in both the Solsville specimens and the *P. flabella* individuals figured by Hall. (3) Three lateral teeth have been observed in one Solsville specimen (fig. 8B, C, D), and Hall (1884) stated that he had observed two to three lateral teeth in various left valves of *P. flabella*. (4) The age difference between *P. flabella* and *P. fasciculata* is no barrier to conspecificity. As indicated pre-

viously, many other Appalachian middle Devonian bivalve species are also found in European early Devonian deposits. Moreover, common middle Devonian Hamilton bivalve taxa have been reported from the late Devonian. Hall (1884, pl. 15, fig. 6, pl. 83, fig. 11), for example, recovered *P. flabella* from the Chemung beds. Although McAlester (1962a) doubted the age of one of these specimens, he (1963a) has shown that there are many other bivalve species (including *Palaeoneilo constricta*, *Nuculoidea corbuliformis*, *Phestia rostellata*, *Actinopteria boydi*, *Modiomorpha mytiloides*, *Pseudaviculopecten fasciculatus*, *Cypricardella bellastriata*, etc.) which range widely throughout Middle and Upper Devonian rocks. Evidently many bivalve species were evolutionarily stable (see also Bailey, 1978b). (5) Geographic separation, in view of recent reconstructions of Devonian paleogeography cited previously, must be considered an obsolete argument.

Frech indicated four cardinal teeth in *P. fasciculata* and observed a similar number in *P. flabella* (see Hall, 1884, pl. 15, fig. 5). However, as determined previously, only three were observed in the one really good Solsville valve interior (fig. 8B, C, D). Hall (1884, pl. 14, figs. 15-20) indicated from as few as two to as many as four or five cardinal teeth in *P. flabella* (his fig. 30 shows three).

Hall (1884) and Beushausen (1884) indicated conspecificity for *P. fasciculata* with *P. costulata* (Roemer) from the Siegenian of Europe. Roemer's (1854, pl. 1, fig. 3) single figure depicts a small (juvenile?) rounded specimen with an angular auricle and the general outline, radial ribbing, and reticulating growth lines of *P. fasciculata*. Frech (1891), Dahmer (1943), and Babin (1966), however, considered *P. costulata* a separate species because of its small size, reduced wing, expanded auricle and two emphasized radial ribs along the anterior margin. According to Beushausen (1884) the ribs were not costae but plicae (i.e., they are also visible on the shell interior), but this is not the case in Frech's figure (1891, pl. 9, fig. 9). The form of *P. costulata* is reminiscent of the European *P. costata* (Goldfuss) (see Babin, 1966), a strongly angular species with robust, widely spaced radial plicae (as shown by Frech, 1891, pl. 9,

figs. 4–8) whose specific identity seems certain (Maillieux, 1937). In some respects the earlier (ancestral?) *P. costulata* seems morphologically intermediate between the two later species, *P. costata* (early Emsian) and *P. fasciculata* (late Emsian–?Frasnian). The specimens attributed to *P. costulata* by Frech, for example, seem more rounded and in greater agreement with *P. fasciculata*. The few published examples of *P. costulata* are so fragmentary that proper evaluation is difficult.

*Pterinea subtilicosta* from the German (Lower?) Devonian is, at least in part, a junior synonym of *P. fasciculata*. One set of Spriestersbach's (1915, pl. 8, figs. 7–9) original figures are indeterminate, consisting of drawings of a partial hinge, an internal mold and a (distorted?) left valve. However, his plate 23, figure 1 and 1a, are photographs showing another specimen which, although partially hidden in matrix, so profoundly resembles Holsville *P. fasciculata* as to leave little doubt.

Aside from suggestive prosopon shown on a small shell fragment figured by Spriestersbach and Fuchs (1909), there are insufficient data in their remaining illustrations to link their species, "*Pterinea*" *gracilis* from the German Remscheider Schichten (Emsian), with *P. fasciculata*: one figure is too stylized; three figures show small, specifically indeterminate internal molds; and two figures show hinges which, if accurate, easily exclude this species as a possible synonym. However, three of the four later figures of "*Pterinea*" *gracilis* shown by Spriestersbach (1915, 1925) strongly favor *P. fasciculata*.

"*Pterinea*" *lorana* from the German Hunsrückschiefer (Siegenian–Emsian) as originally figured by Fuchs (1915) is like *P. fasciculata* but too distorted and fragmentary to be sure.

Walcott (1884) described "*Pterinea*" *flabella* from the Devonian lower Nevada Limestone, Lone Mountain, Nevada. Although superficially similar to *P. fasciculata* the western specimens probably belong to a separate species for the following reasons: (1) the specimen in Walcott's plate 5, figure 6 completely lacks the characteristic anterior auricle; (2) the auricle seems too small in his other figure and the radial ribbing too discontinuous anteriorly.

One incomplete specimen of Whiteaves' "*Pterinea*" *lobata* (1892, pl. 38, fig. 4) from the Devonian of Manitoba suggests *P. fasciculata* but is too fragmentary for verification. However, his remaining *Tridacna*-like specimens of *P. lobata* are probably not pterineids and belong to a species not seen elsewhere in North America but strikingly like Holzapfel's (1895) "*Aviculopecten*" *lobatus* from Germany.

Ohern and Maynard (1913) described specimens from the Ridgeley Sandstone (=Oriskany; see Oliver et al., 1969), Cumberland, Maryland, which they placed in "*Pterinea*" *halli* Clarke [and Ruedemann], 1903 [= "*Avicula*" *securiformis* Hall, 1859; renamed by Clarke because Hall had unwittingly coined *Avicula securiformis* as a new species on two occasions (1852, 1859) in reference to two different taxa]. The two illustrated specimens (Ohern and Maynard, 1913, pl. 78, figs. 11, 12) show strong prosopon similarities in the left valve to *P. fasciculata*, but the radial ribs appear to be much narrower than is typical in the latter. More importantly, however, the auricle does not appear to have the strongly inflated, rugose character of subgenus *Cornellites*, but, instead, seems more obliquely truncate as in subgenus *Ptychopteria* as diagnosed by Newell and LaRocque (in Moore, 1969).

Clarke and Swartz (1913) described "*Pterinea*" *nodocostata* based on three left valves from the Jennings Formation (Chemungian) near Oakland, Maryland. Two specimens (their pl. 61, figs. 19, 20) are like *P. fasciculata* except for a less prosocline attitude and flattened, bladelike obliquely truncated auricles. In certain specimens of *P. fasciculata* figured as *Pterinea flabella* by Hall (1883, 1884), the auricles occasionally approach a similar form (preservation?). McAlester (1962a) suggested possible conspecificity for "*Pterinea*" *nodocostata* with "*Cornellites*" *chemungensis* (Conrad) [probably not *Cornellites* as understood here but assignable to subgenus *Ptychopteria* using Newell and LaRocque's criteria; emended name here designated *Ptychopteria* (*Ptychopteria*) *chemungensis*]. Figure 20 of Clarke and Swartz is, indeed, similar to *P. chemungensis* in its manifold narrow radial ribs and almost acline form. Their other two figures, however, seem in-

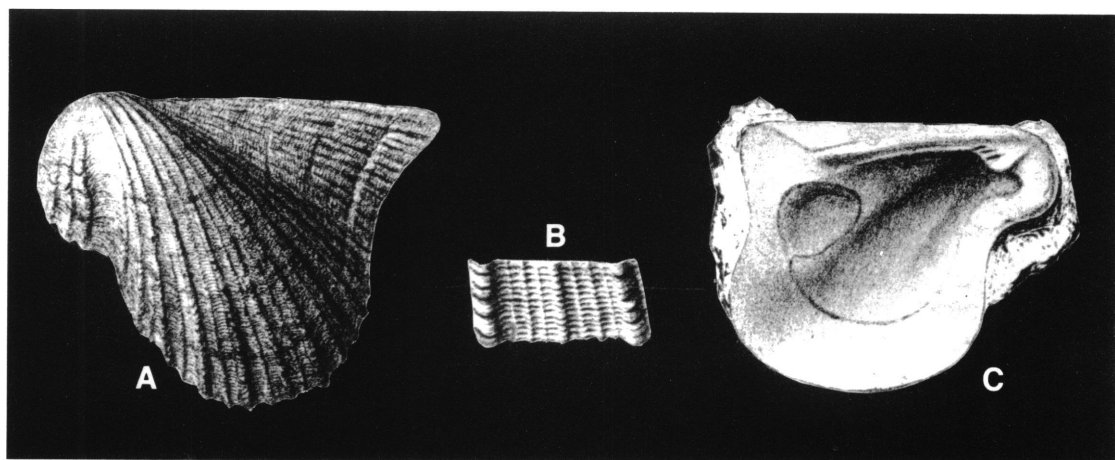


FIG. 10. *Ptychopteria* (*Cornellites*) *fasciculata* (Goldfuss). A–C. Figures of Frech (1891, pl. 9, figs. 1, 1a, 2) from the early Devonian Emsian (upper Coblenzschichten) of Germany (Miellen bei Ems). A. Left valve ( $\times 1$ ). B. Elements of prosopon (enlarged). C. Interior of a left valve showing cardinal teeth, cardinolateral and lateral teeth, anterior and posterior adductor muscle scars, and simple pallial line.

intermediate between either *Ptychopteria halli* (Clarke and Ruedemann) or *P. fasciculata*, on the one hand, and *P. chemungensis* on the other.

Clarke (1907, 1909, pl. 4, figs. 1–7) reported “*Pterinea*” *fasciculata* Goldfuss var. *occidentalis* from “horizon 11” in the Lower Devonian Dalhousie Shale (Helderbergian) of New Brunswick. This species has been misidentified and is, in fact, quite different from *P. fasciculata*. Numerous distinctions are evident: Clarke stated that in the Helderbergian form *both* valves are convex although the left member is strongly favored; the reticulating growth lines and ribs of the right valve are similar to those of the left [his pl. 4, fig. 12 shows two strong ribs on the anterior margin (cf. *P. costulata*?)] though they are markedly less prominent in the umbonal region of the lesser valve; the convex anterior lobe is proportionately larger, more obliquely truncate and less nasute than in *P. fasciculata*, and the byssal sinus is much less pronounced; and, finally, the main body of the shell is rather extreme in its prosoclinal attitude. Morphologically, var. *occidentalis* seems more nearly akin to “*Pterinea*” (= *Actinopterella* Williams, 1908, a synonym of *Ptychopteria* according to Newell and LaRocque in Moore, 1969) *radialis* Clarke, 1907 from the Lower Devonian Chapman Sandstone of Maine.

Clarke (1907, 1909, pl. 25, figs. 1–7) also reported “*Pterinea*” cf. *fasciculata* Goldfuss from the Chapman Sandstone of Maine. This species is even more remarkably distinct from *P. fasciculata* than is var. *occidentalis*. Although a reticulating ornament is present, the character, in its simplicity, is clearly not that of *P. fasciculata*. Moreover, this species exhibits a strongly prominent, rather pectenoid, obliquely truncate, bladelike anterior auricle and is exceedingly similar to the specimen Clarke attributed to “*Pterinea*” *radialis* shown in the upper right hand figure on page 207 in Clarke (1907) from the same beds.

AUTECOLOGY: *Ptychopteria fasciculata* from the Solsville seem most numerous in the sandy/silty facies (*Gosseletia* community) and are rarer in the darker silty argillites (*Nuculoidea* community) although, when found in the latter, individuals are normally better preserved. This appears consistent with McAlester’s (1962a, p. 37) observations of “*Cornellites*” *chemungensis* shells which, he stated, “are abundant in the sandier horizons of the middle Chemung . . . but rare elsewhere.” However, the mode of life of this late Devonian species, as portrayed by Stanley (1972), was, based upon morphological distinctions, probably different from *P. fasciculata*.

McAlester (1962a) proposed that “*Cornellites*” *chemungensis* represents the end mem-

ber in a pterineid lineage preceded respectively by *Actinopteria taberi* and *A. boydi*. Stanley (1972, p. 184) indicated that the proposed ancestral species, *A. boydi*, is "moderately inflated and nearly equivalve with a lobate anterior and a shallow byssal sinus." A shell of this shape, he concluded, would not be positionally stable in significant water currents if the life position were either epibyssate reclining or epibyssate erect. He therefore proposed that this species grew in an erect endobysate, semi-infaunal position. This conclusion has apparently been supported by Thayer (1974). According to Stanley (1972), the proposed transition of *A. boydi* through *A. taberi* to "*Cornellites*" *chemungensis* involved the following morphological changes: (1) flattening of the right valve; (2) transformation of the inflated auricle and shallow byssal sinus into a bladelike auricle and deep byssal sinus; and (3) a prosocline to acline change of umbonal posture. These changes, he indicated, were stabilizing adaptations for epifaunal attachment with the sagittal plane at a low angle with respect to the substrate as in the case of many modern pectinids and pteriids (see figs. 16 and 17f of Stanley, 1972).

Kauffman (in Moore, 1969) included "*Cornellites*" along with *Pteria* and *Pinctada* in his group of epibyssate, free-swinging bivalves adapted to attachment on exposed, elevated surfaces (e.g., marine plants), the rudder-like streamlining enabling the shells to swing freely with fluctuating currents much as a weather-vane. Water flow orients such bivalves into the currents with the hinge line parallel to the direction of flow, the wing pointing downcurrent. Positioned thusly, the water is first channeled along the anteroventrally located inhalant region of the commissure and thence over the convexity of the body chamber resulting in a temporary increase in the hydrostatic pressure exerted on the shell (see Kauffman, p. N146; Cox, fig. 35, p. N34, in Moore, 1969). The pressure is then immediately relieved just behind the central convexity where water is channeled along the sulcus (where the wing attaches) and discharged along the embayment of the wing, effectively removing waste from the exhalant opening. Most free-swinging pterioids are equivalved for streamlining and, as Kauffman noted, thin-shelled due to the limita-

tions imposed by weight in an elevated, attached position, their ability to swing to and fro with current changes being their primary protective device to prevent shell damage. In *P. fasciculata*, however, the shells are strongly inequivalved and very thick. In view of these observations as well as Stanley's interpretation of the mode of life of "*C.*" *chemungensis* above, Kauffman's conclusions on the mode of life of "*Cornellites*" seem improbable.

Although the wing and auricle of *P. fasciculata* seem indicative of an ancestry among the elevated, free-swinging pterioids, its unique morphologic modifications suggest a more benthic life style. These modifications include: (1) pronounced inequity in valve development with swollen left and resupinate right shells; (2) deeply etched radial ribbing and nodose reticulations confined mostly to the left valve; (3) a strongly inflated left auricle with accentuated byssal sinus, permanent byssal gape, and a deep byssal groove or notch on the right valve; and (4) no internal evidence for strongly attached byssal musculature. Reduction of convexity and ornament of one valve and weakly attached byssal musculature are, according to Stanley (1972), indications of a low angle shell posture. The extreme flattening of the right valve might be evidence of a completely reclining attitude with the right valve in contact with the substrate and the left valve upward, the ribbing serving to reduce hydraulic friction by breaking up currents flowing over the shell surface (see Kauffman's comments regarding the adaptive significance of shell ribbing, in Moore, 1969, p. N145). The resupinate shape of the lowermost valve might indicate a mode of byssal attachment to firm, rounded surfaces of low convexity (rocks, shell debris, etc.). However, since some specimens are found in the dark Solsville argillites, it is also conceivable that a near vertical, partial burial of the umbonal and hinge region (an endobysate mode<sup>2</sup> of life as proposed by Stanley, 1972, for *A. boydi*) was adopted.

A more satisfying alternative view of the life position of *P. fasciculata* is proposed here (see figs. 5, 6, and 11) in analogy to that of

<sup>2</sup> Stanley (1972) apparently considered the inflated auricle in *A. boydi* to be a possible indication of endobysate attachment.

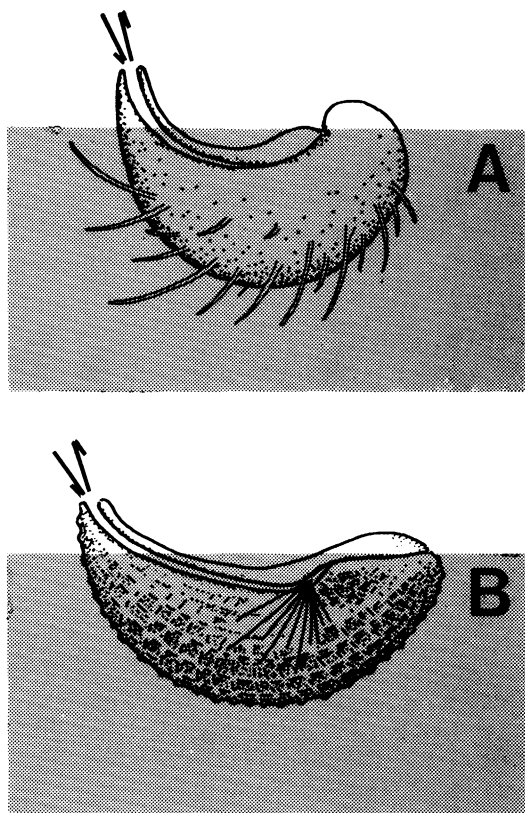


FIG. 11. Life habit reconstruction of *Ptychopteria* (*Cornellites*) *fasciculata* (Goldfuss) compared with that of a productid brachiopod. A. Lateral view of a partially buried productid in growth position (based upon Grant, 1966, 1968). B. Anterior marginal view of reclining, partially buried *P. fasciculata* showing radiating byssal filaments. Arrows show inhalant and exhalant water flow.

productid brachiopods (see Grant, 1966, 1968; also Raup and Stanley, 1978; and Valentine, 1973). Among productids a boatlike, deeply convex, nodose or spiny-ornamented ventral valve lies underneath to maintain positional stability in soft, thixotropic muds in which it is largely buried. The dorsal valve, with its smoother ornament, is flattened or develops a concave/resupinate shape during growth forming a snorkel-like commissural lip projecting above the sediment/water interface for suspension feeding. By analogy, *P. fasciculata* had a byssally attached reclining posture, the strongly inflated valve positioned below and partially or mostly buried in the mud. Aided by the broad wing and

swollen auricle, the strong radial ribs and nodose reticulations would serve the same purpose as the productid spines. Likewise, the flattened right valve would have lain above, its resupinate shape forming a similar commissural lip above the mud. Such a lifestyle would enable *P. fasciculata* to live on a broad range of substrates, even in muds too soft for other suspension feeders. This would appear to explain the ubiquitous distribution of this species among a variety of lithologic types and among both infaunal deposit-feeding and endobyssate/epibyssate suspension-feeding bivalve paleocommunities (see table 3).

SUPERFAMILY AMBONYCHIACEA MILLER, 1877

FAMILY AMBONYCHIIDAE MILLER, 1877

GENUS *GOSSELETIA* BARROIS, 1882

TYPE SPECIES: *Gosseletia devonica* Barrois, 1882, from the Lower Devonian of Spain (Asturias) by subsequent designation of Follmann (1885) and Maillieux (1937).

GENERIC USAGE: Pojeta (1966) has summarized the status of *Gosseletia* with respect to other members of the Ambonychiidae and has presented an exhaustive generic synonymy. An earlier diagnosis of Maillieux (1937) was adopted by LaRocque (1950; see LaRocque's English translation of Maillieux's text); and a more recent diagnosis is given by Newell and LaRocque (in Moore, 1969).

*Gosseletia* was first proposed by Barrois (1882) on the basis of ambonychiid material from the early Devonian of Spain. DeKoninck (1883) subsequently applied *Gosseletia* to a gastropod genus which later (see Fischer, 1885) was properly replaced by *Gosseletina*. As Pojeta (1966) indicated, beginning with Hall (1883), many later American authors have consistently misspelled *Gosseletia* as "*Gosselettia*" although Grabau (1906), LaRocque (1950), Pojeta (1966), Bailey (1975, 1978a), and Carter and Tevesz (1978b) have used Barrois's original spelling. Clarke and Swartz (1913) spelled it "*Gosselletia*," and Stauffer (1916) even used "*Glosseletina*."

*Lophonychia* Pohl was considered by LaRocque (1950) as synonymous with *Gosseletia*. Pojeta (1966), however, regarded them as distinct because of the lack of an auricle and the possession of costellate prosopon in the type species of *Lophonychia*. I reject this



distinction since the type species of *Gosseletia* also lacks an auricle. Moreover, study of the Solsville material shows the auricle to be variably developed. Its presence or absence should not therefore be used here as a generic character. More recently, Newell and LaRocque (in Moore, 1969) have accepted *Lophonychia* as a synonym of *Mytilarca* Hall and Whitfield, 1869.

*Cyrtodontopsis* was proposed by Frech (1891) as a subgenus of *Gosseletia* comprising four species. Maillieux (1937) dissolved this distinction, as Pojeta (1966) noted, on the following basis:

- (A) *Cyrtodontopsis kayseri* Frech and *C. quarzitica* Frech should be placed in *Cyrtodonta* Billings.
- (B) *Cyrtodontopsis praecursor* Frech should be placed in *Modiomorpha* Hall and Whitfield.
- (C) *Cyrtodontopsis halfari* is a species of *Gosseletia*.

Frech (1891) gave three categories of *Gosseletia*: smooth species without radial ribbing, the prosopon consisting dominantly of concentric growth lineations (Gruppe der *Gosseletia devonica* Barrois); species with pronounced radial ribbing (Gruppe der *Gosseletia truncata* Roemer); and species with very small hinge teeth showing both emphasized radial ribbing and concentric growth lines (Gruppe der *Gosseletia microdon* Frech). Drevermann (1907) used one species of the last group, *G. pseudaelectryonia* as the type species for *Follmannia*, later considered a subgenus of *Nathorstella* Kayser, 1901 by Newell and LaRocque (in Moore, 1969). The remaining species of this group are poorly documented. *Gosseletia cancellata* Frech (1891, pl. 15, fig. 8) was based upon a prosopon fragment with abraded coarsely reticulating ornament of doubtful affinities, an internal mold probably belonging to *Follmannia* or *Mytilarca* (Frech's pl. 14, fig. 8a), and another internal mold with a prominent auricle and byssal sinus distinctly pterineid in form (Frech's pl. 14, fig. 8b). Ironically, *G. microdon* Frech, the namesake of the group, was based upon a single internal mold with no preserved prosopon whatsoever. The specimen (Frech's pl. 13, fig. 5) has an outline resembling *Gosseletia*, but it lacks

an auricle, has obsolescent hinge teeth, and logically belongs elsewhere.

Maillieux (1920, 1937) did not recognize Frech's Gruppe der *Gosseletia microdon* but did maintain a bipartite subdivision of *Gosseletia*, erecting *G. (Gosseletia)* to contain Frech's Gruppe der *Gosseletia devonica* Barrois and *G. (Stappersella)* for *Gosseletia* species with radial ribbing (costae near the umbones becoming plicae ventrally), i.e., Frech's Gruppe der *Gosseletia truncata* Roemer. Pojeta (1966) eliminated the subgeneric division of *Gosseletia* by raising *Stappersella* to generic rank, a decision supported by Newell and LaRocque (in Moore, 1969).

*Gosseletia* as diagnosed by Newell and LaRocque (in Moore, 1969) is restricted to species lacking radial prosopon elements. However, even the smooth forms (i.e., *Gosseletia, sensu stricto*) also have a few radial lineations in the prosopon as noted by Follmann (1885) and by Frech (1891, p. 117) who made the following observation: "Die Oberfläche ist mit deutlichen concentrischen Anwachsstreifen und ganz feinen, nur mit Lupe einigermaßen erkennbaren radialen Linien bedeckt." The same radial elements can occasionally be observed among some Solsville specimens of *G. triquetra*. However, these lineations in both German and American species are faint (fig. 13A) and variably developed over the shell; they cannot be confused with the costae/plicae of *Stappersella*. With this emendation, I accept the diagnosis of *Gosseletia* given by Newell and LaRocque.

RANGE: In North America *Gosseletia* has been reported from the Middle Devonian (Hamilton) where it is relatively rare (see table 3). It is noticeably absent from the Lower Devonian (e.g., Clarke, 1900, 1908, 1909; Ohern and Maynard, 1913; Williams and Breger, 1916) as well as the Upper Devonian (Clarke, 1904; McAlester, 1962a, 1962b, 1963a, 1963b). Clarke and Swartz (1913, pl. 63, fig. 20) reported "*Gosseletia* sp.?" from the Upper Devonian Jennings Formation of Maryland; however, this specimen shows strong plicae on the internal mold and is clearly not *Gosseletia* but, perhaps, *Stappersella*.

In the Devonian of the Rhineland *Gosseletia* has a greater stratigraphic range, appearing in the Lower Devonian (Siegenian?)

and lingering into the Upper Devonian (Frasnian) (Follmann, 1885; Frech, 1891).

*Gosseletia triquetra* (Conrad), 1838

Figures 1A, 6A, 12-16, 18B

*Pterinea triqueter* Conrad, 1838, p. 116.

*Mytilarca triqueter* (Conrad). Hall and Whitfield, 1869, p. 22.

*Mytilarca triquetra* (Conrad). Miller, 1877, p. 197.

*Gosseletia* [sic] *triquetra* (Conrad). Hall, 1883, pl. 31, figs. 9-17; 1884, p. 265, pl. 31, figs. 9-17, pl. 87, fig. 12. Whitfield and Hovey, 1900, p. 278. Clarke and Ruedemann, 1903, p. 394. Cooper, 1930, p. 133. Cooper et al., 1942, p. 1779. Stumm, 1942, p. 557. Shimer and Shrock, 1944, p. 387, pl. 150, fig. 6. Ehlers, Stumm, and Kesling, 1951, p. 20, pl. 5, fig. 15. Stumm and Chilman, 1967, p. 130. Rollins, Eldredge, and Spiller, 1971, p. 134. Wilson, 1975, p. 126.

*Gosseletia triquetra* Hall [sic]. Follmann, 1885, pp. 211, 214. Frech, 1891, p. 115.

*Glosseletina* [sic] *triquetra*. Stauffer, 1916, p. 477.

*Gosseletia triquetra* (Conrad). Grabau, 1906, p. 330. Pojeta, 1966, p. 183, pl. 35, figs. 2-4, 8-18. Bailey, 1975, p. 60, pl. 3, figs. 7-9, pl. 4, figs. 1-8, pl. 5, figs. 1-3, text-figs. 7-9; 1978a, p. 121. Carter and Tevesz, 1978b, p. 867, fig. 16.

†[?] *Lophonychia cordata* Stewart, 1933, p. 179, pl. 24, figs. 15-17. Ehlers, Stumm, and Kesling, 1951, pl. 5, figs. 13, 14.

†[?] *Gosseletia securiformis* Follmann, 1885, p. 209, pl. 4, fig. 3[?] [not fig. 3a, b]. Frech, 1891, p. 114, pl. 16, figs. 2-5.

†[?] *Gosseletia distincta* Follmann, 1885, p. 214, pl. 5, fig. 5, 5a. Frech, 1891, p. 117, pl. 16, fig. 17.

†[?] *Gosseletia alta* Follmann, 1885, p. 211, pl. 4, fig. 1, 1a, 1b. Frech, 1891, p. 115, pl. 16, figs. 6-7a. Maillieux, 1933, p. 61; 1937, p. 86.

†[?] *Gosseletia schizodon* Frech, 1891, p. 115, pl. 13, fig. 6, 6a. [Compare with Solsville specimen fig. 14E.]

†[?] *Gosseletia minor* Frech, 1891, p. 116, pl. 16, fig. 18.

**DESCRIPTION:** Shells alate, subtrigonal in outline, equivalve, prosogyrous/prosocline, medium to large in size; height often greater than length; very inequilateral, the prominent umbones anteriorly terminal and extending moderately to well above the straight, posteriorly positioned hinge line. Behind the umbones the valves are expanded into a broad, moderately inflated wing smoothly curving posteroventrally. The anterior um-

bonal slope forms an oblique, ventricose carina with a truncate, flattened to faintly concave anterior face with a cordate outline in articulated specimens (see fig. 12G). The carina shows its greatest inflation in the mid-dorsal region, rapidly decreasing dorsally (and abruptly anteriorly) and gently decreasing ventrally and posteriorly. In the dorsal region of the flattened, anterior face immediately below the umbones is a weakly developed to obsolescent swelling, a dorsoanterior lobe (auricle) (=anterodorsal salient of Newell, 1942) (see fig. 12) with a very shallow byssal sinus beneath. Byssal gape is lacking. The mean value of the G-angle ( $\gamma$ , the angle between the hinge line and anterior face) for 16 specimens is 65°.

The prosopon consists almost solely of moderately fine, concentric growth lines with a number of weak growth varices, variably spaced. Some extremely subtle, fine, radiating elements, however, may be occasionally seen in low angle light especially along the anterior face of well preserved specimens (see fig. 13A).

An external, opisthodontic ligamental area is present as a deep furrow (fig. 12J, L) along the straight hinge line between the valves. The inner surfaces of the furrow have a series of fine, parallel grooves (figs. 14A-D, G, 15) indicative of a duplivincular ligament.

Behind the umbones the hinge plate beneath the ligamental area is narrow (fig. 14A) to (?)obsolescent (fig. 14G) expanding beneath the umbones into a trigonal platform supporting a variable series of cardinal teeth. Two right valves contain four subparallel, only slightly radiating cardinal teeth oriented obliquely with respect to the hinge line. The upper and lower pair may be separate (e.g., fig. 14A) or lightly joined anteriorly to form  $\Lambda$ -shaped, i.e., bifid members (fig. 14B and especially C) diverging posteroventrally. The upper three cardinal teeth are strong and elongate, becoming shorter ventrally. The lowermost cardinal tooth may be little more than a short, linear pustule.

The cardinal dentition of three comparably sized left valves (fig. 14D, G, and fig. 15 which is a reconstruction based upon a plastilina cast of a natural mold, fig. 14E, of the hinge of a left valve) show three (or four) cardinal teeth. Two strong, elongate, oblique cardinal

teeth are positioned on the hinge plate above a shorter, variably shaped, often schizoid lower cardinal tooth (somewhat  $\Lambda$ -shaped). In one case (fig. 15) a faint, minor denticle bisects the diverging limbs of the lower cardinal tooth.

The presence of lateral teeth in *G. triquetra* has been noted by Pojeta (1966, pl. 35, fig. 13) and Hall (1884) who indicated that they are elongate and extend nearly to the shell margin. However, none were here observed since the wing is so often broken away on single valves. Pojeta's figure indicates at least two lateral teeth in the left valve. Frech (1891) noted two lateral teeth in the right valve of *G. securiformis* and three in the left valve.

The anterior adductor scar (figs. 14A–G, 15, 16A, B) is small and circular and placed beneath the anteriormost lower cardinal tooth on a round, sloping (i.e., not coplanar with the hinge plate but dipping posteroventrally away from it) myophoric shelf lying beneath the hinge plate where it is supported underneath by an elongate, ridgelike buttress or pedestal extending a short distance ventrally from the hinge plate.

Mailieux (1937) described the posterior adductor scar of *Gosseletia* as large and faint. It normally is not well preserved on internal molds. In one exception (figs. 12A, B, 13D, E), however, it is evident in the dorsoposterior region of both valves. In each case it is a distinctly bilobate structure, reniform in outline. The dorsoanterior lobe possibly marks the position of attachment of the posterior byssal/pedal retractor musculature (e.g., compare with the bilobate posterior adductor scar of *Modiomorpha concentrica*, fig. 46H, and *Ambonychia*, fig. C257b of Newell and LaRocque in Moore, 1969), whereas the ventroposterior lobe appears to denote the position of attachment of the posterior adductor muscle proper. Extending immediately forward of the dorsoanterior lobe of the scar is a deep groove in the shell beneath and parallel to the hinge line. In analogy to Recent *Mytilus* this may alternatively represent a line of attachment of byssal/pedal retractor muscle fibers.

The possible point of attachment of the anterior byssal/pedal retractor musculature is shown in figure 16B immediately behind the anterior adductor myophoric shelf where a

TABLE 6  
Measurements (in Millimeters) of *Gosseletia triquetra* (Conrad)

Locality	Length	Height	Width <sup>a</sup>	G-Angle ( $\gamma$ ) <sup>b</sup>
AMNH 3012	21.7	26.3	17.5	70°
AMNH 3013	33.4	30.4	21.1	62°
	37 <sup>c</sup>	42.1	29.9	74°
	47.4	37 <sup>c</sup>	41.2	65°
	28 <sup>c</sup>	29 <sup>c</sup>	20 <sup>d</sup>	60°
	47.9	57.8	45.9	84°
	40 <sup>c</sup>	42 <sup>c</sup>	—	58°
	36.7	33 <sup>c</sup>	—	64°
	34 <sup>c</sup>	36 <sup>c</sup>	—	67°
	—	36.3	28.3	—
	33 <sup>c</sup>	38.9	22.5 <sup>d</sup>	63°
	26 <sup>c</sup>	29 <sup>c</sup>	35.3	68°
	37 <sup>c</sup>	35 <sup>c</sup>	20.7 <sup>d</sup>	67°
AMNH 3014	50 <sup>c</sup>	48 <sup>c</sup>	24.9 <sup>d</sup>	65°
Miscellaneous Solsville	78 <sup>c</sup>	51 <sup>c,e</sup>	54.4	43° <sup>ee</sup>
	67 <sup>c</sup>	54.5 <sup>e</sup>	49.2	40° <sup>ee</sup>
	47.5	50.0	36.4	60°
	42 <sup>c</sup>	47 <sup>c</sup>	23 <sup>d</sup>	53°
	—	—	—	54°

<sup>a</sup> Total width, both valves articulated.

<sup>b</sup> See Pojeta (1966, p. 139);  $\gamma$  = angle between carina and hinge line.

<sup>c</sup> Specimen broken. Dimension approximate and inferred.

<sup>d</sup> Width of a single valve. Articulated width would have been roughly double. Width in the remainder of specimens represents maximum inflation of carina of articulated valves.

<sup>e</sup> Specimen distorted. Measurement does not reflect original valve.

small, shallow, irregular depression or scar in the buttressed border of the shelf is visible. In a second specimen (fig. 16A) this pit appears to be shifted a bit dorsally, and its margins are more clearly defined. In some well-preserved specimens the anterior byssal/pedal retractors were evidently so weakly attached that no anterior pit is apparent.

The pallial line is simple and weakly impressed, running along and close to the shell margins. Within the arc of the pallial line are numerous pallial punctae (fig. 13B, C) randomly distributed in the anterior dorsolateral and umbonal regions. These, as earlier noted, represent points of muscular attachment of the mantle to the shell.

Recrystallized/replaced shell material in-

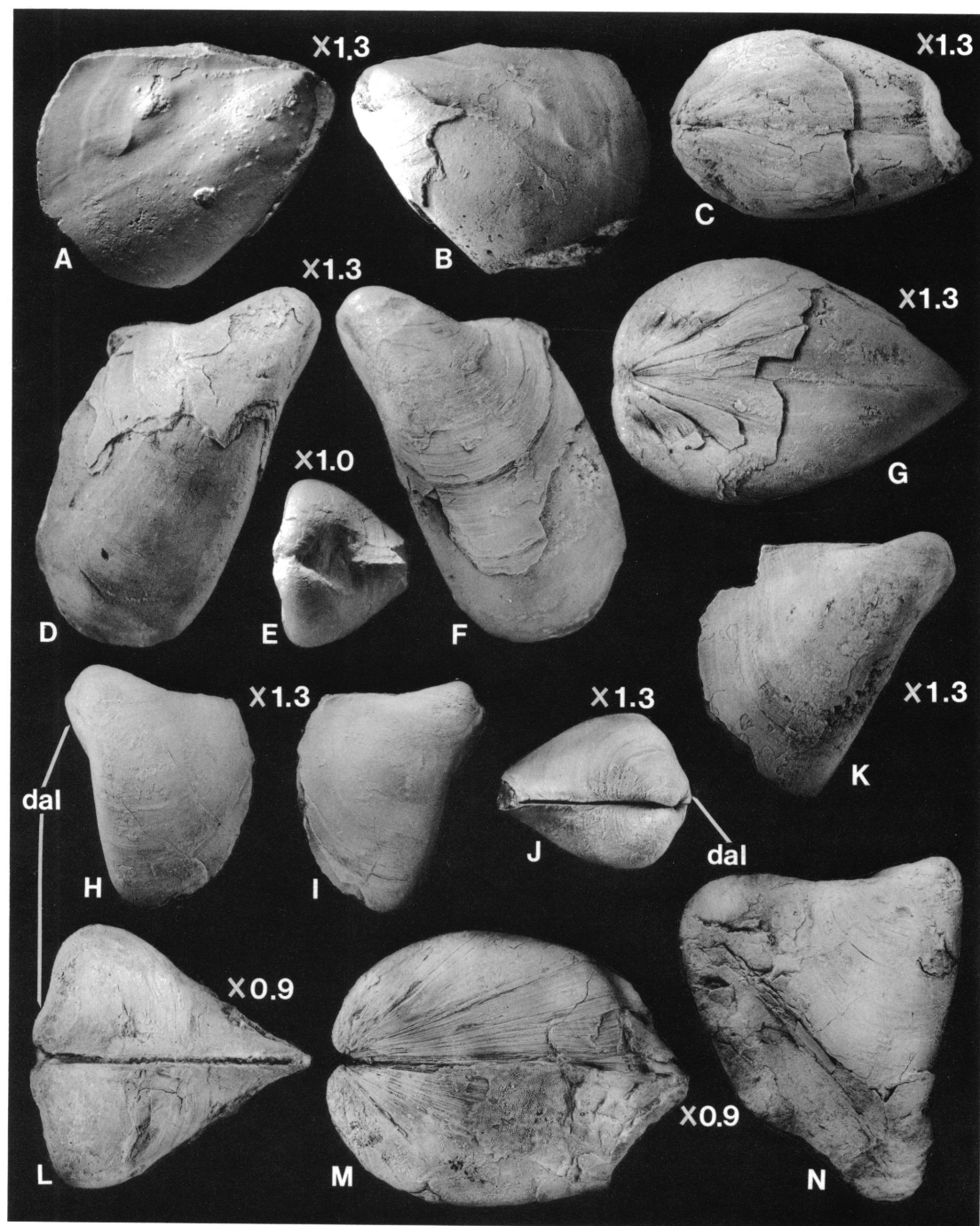


FIG. 12. *Gossioleteria triquetra* (Conrad). A–C. Internal mold with shell fragments (AMNH 36179) from AMNH loc. 3013. A. Right valve. B. Left valve. C. Anterior with partial shell. D–G. Internal mold with partial shell (AMNH 36181) from AMNH loc. 3013. D. Right valve. E. Dorsal view. F. Left valve. G. Anterior view. H–J. Articulated specimen (AMNH 36184) from AMNH loc. 3012. H. Left valve. I. Right valve. J. Dorsal (hinge) view. K. A right valve (AMNH 36162) from AMNH loc 3013. L–N. Articulated specimen (AMNH 36242) from AMNH loc. 3013. L. Dorsal (hinge) view. M. Anterior view with encrusting bryozoan. N. Right shell (crushed).

Abbreviation: dal—dorsoanterior lobe (auricle).

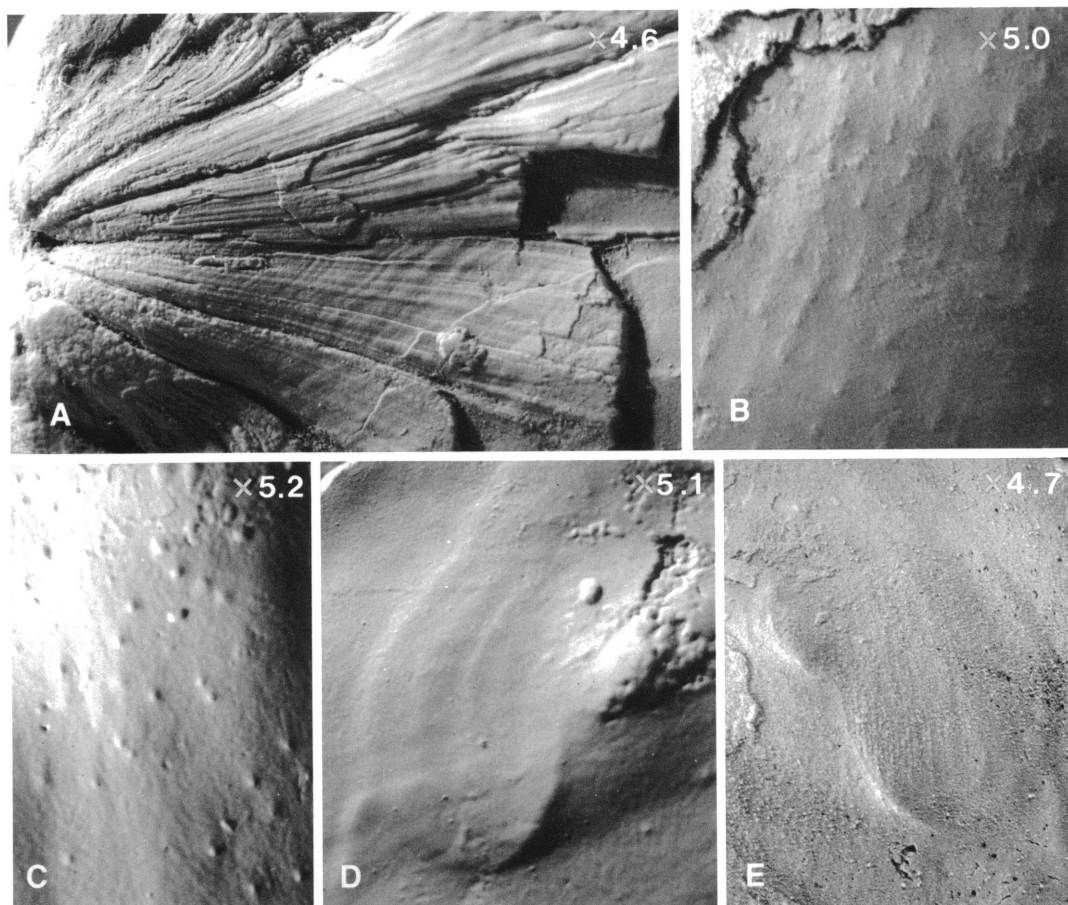


FIG. 13. *Gosseletia triquetra* (Conrad). A–C. AMNH 36181 from AMNH loc. 3013. A. Anterior shell detail showing growth lines marked by fine to obsolescent radial ornament. B, C. Pallial punctae on internal mold. D, E. Internal mold, AMNH 36179 from AMNH loc. 3013. D. Right posterior adductor scar. E. Left posterior adductor scar.

indicates that the valves were of only moderate thickness in the wing region becoming extremely thick in the umbones and along the carina and thinning slightly along the anterior face. Original shell microstructure has been described by Carter and Tevesz (1978b).

REMARKS: As noted above, the height of *G. triquetra* is usually greater than the length. This is confirmed by Pojeta (1966) who measured a length of 43 mm. and a height of 51 mm. in the probable holotype. However, in Hall's (1884) dimensions the reverse seems true. He listed two specimens having lengths of 58 mm. and 80 mm. and heights of 43 mm. and 55 mm., respectively. Since Hall

inaccurately referred to the carina as being situated "ventrally," it seems likely that Hall's procedure for orienting the shells of this species was different from the accepted method employed here.

COMPARISONS: Pojeta (1966, pl. 35, figs. 8–10) showed Conrad's probable holotype (AMNH 5274/1) of *G. triquetra*. Only one other North American species has been described, *G. retusa* Hall (1883) which Hall based upon a single specimen from "the Hamilton Group, Eighteen Mile Creek, Erie Co., N.Y." Hall indicated that this species "differs from *G. triquetra* in its proportionally longer form which is less expanded pos-

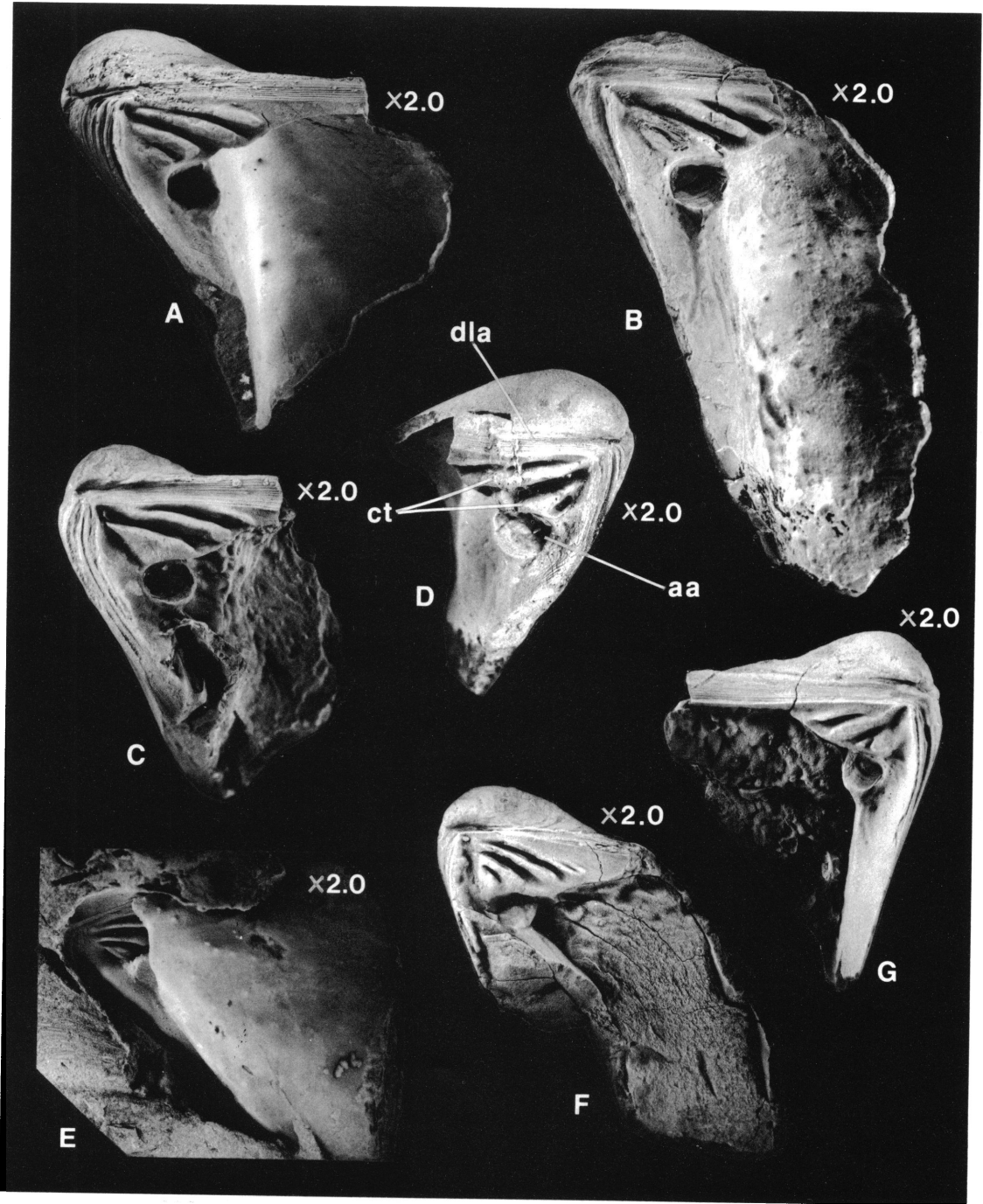


FIG. 14. *Gosseletia triquetra* (Conrad). Hinge views. A. Right valve (AMNH 36162) from AMNH loc. 3013. B. Right valve (AMNH 36160) from AMNH loc. 3013. C. Right valve (AMNH 36161) from AMNH 3013. D. Left valve (AMNH 36216) from AMNH 3013. E. Mold of left hinge (AMNH 36180) from AMNH loc. 3014 (see also fig. 15). F. Right valve (AMNH 36182) from AMNH loc. 3013. G. Left valve (AMNH 36183) from AMNH loc. 3013.

Abbreviations: aa—anterior adductor scar, ct—cardinal teeth, dla—duplivincular ligamental area.



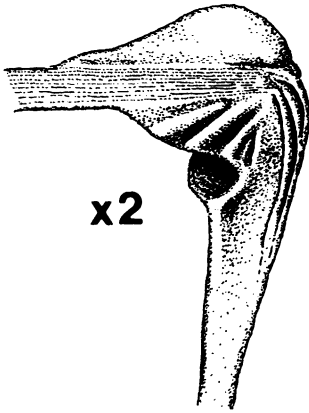


FIG. 15. *Gosseletia triquetra* (Conrad). Partial hinge reconstruction based upon a plastilina cast of a hinge mold (AMNH 36180) from AMNH 3014 (see fig. 14E). Note the bifid anteriormost cardinal tooth and the ancillary denticle bisecting it.

teriorly; hinge line shorter and less oblique to the body of the shell; and the ventral umbonal slope less angular along its length.” Of *G. retusa* Pojeta (1966, p. 184) stated: “I have

not been able to locate Hall’s types of *G. retusa*. The specimen illustrated by Hall has a shell shape which differs from that of *G. triquetra*, however, nothing is known of the dental structures of *G. retusa*.” Although this species is admittedly poorly documented, it likely represents a distinct taxon since none of the numerous Solsville specimens of *G. triquetra* approach the shell shape of *G. retusa* which is distinctive in several respects: (1) the umbones are more erect; (2) the anterior umbonal slope seems less carinate and too rounded to obtain an objective determination of the G-angle; and (3) the shell seems to have a slight anterodorsal alation or wing.

Föllmann (1885) and Frech (1891) described several smooth gosseletias (Gruppe der *Gosseletia devonica* Barrois) comparable to *G. triquetra* from the Devonian of the Rhineland [the writer’s English translation of Frech’s descriptions is given in Bailey (1975)]. Three of these, summarized below, do not seem significantly different from *G. triquetra* and are, perhaps, conspecific with it:

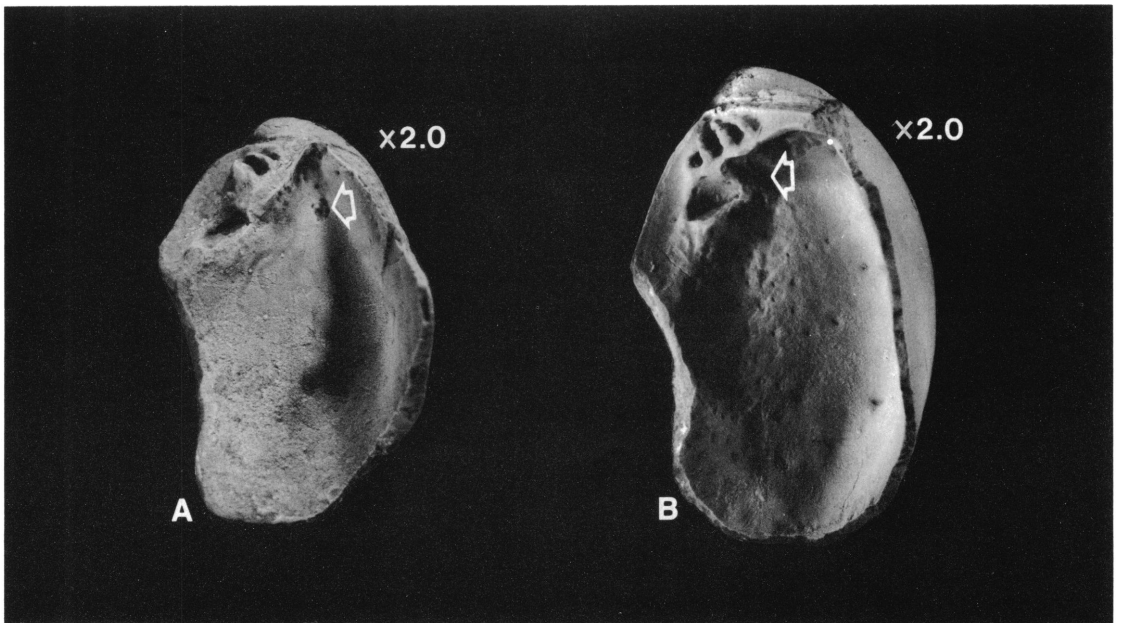


FIG. 16. *Gosseletia triquetra* (Conrad). Tilted right valve interiors from AMNH loc. 3013. A. AMNH 36163. Arrow shows probable site of anterior byssal/pedal retractor scar. Note the numerous pallial punctations beneath the hinge plate. B. AMNH 36162. Arrow shows irregular depression—site of byssal/pedal retractor scar?



1. *G. securiformis* Follmann. Lower Devonian (Emsian) of Germany. Follmann (1885) compared this species to *G. triquetra* as figured by Hall (1884) indicating the dentition and lack of fine radial prosopon lineations as important distinctions. However, it is evident here (fig. 13A) that radial lineations, though undescribed by Hall, are nevertheless present in the American species. Furthermore, the original dental descriptions of *G. securiformis* were based on an internal mold (Follmann's pl. 4, fig. 3a, b) which, owing to its exaggerated, pterineid-like development of the anterior auricle, is definitely not *Gosseletia*. However, the specimens of *G. securiformis* as later understood by Frech (1891) are markedly similar to *G. triquetra* as he himself (p. 115) attested: "In der äusseren Form ist *Gosseletia triquetra* Hall aus der Hamilton Group des Staates New York sehr ähnlich; auch die Zähne sind nicht wesentlich verschieden."
2. *G. distincta* Follmann. Middle Devonian (Eifelian), Germany. Originally based on a single specimen formerly called *Avicula saturni* by Goldfuss. Although the original figures show only an unrevealing anterior view and an enlargement of the prosopon detail, Follmann made the following remarks (p. 214), again emphasizing the radial elements in the prosopon as a trait distinguishing it from the American species: "Diese Art hat einige Aehnlichkeit mit *Gosseletia triquetra*, Hall, von der sie sich aber schon durch die radialen Linien unterscheidet. Unter den schon beschriebenen Arten steht ihr *Goss. securiformis* am nächsten." Frech (1891) later noted that the differences between *G. distincta* and *G. securiformis* are few.
3. *G. alta* Follmann. Originally based on six specimens from the Lower Devonian (Emsian) of Germany. Of the *gosseletias* figured by Follmann, this species is best documented and seems closest to *G. triquetra*. His figures show both the shell exterior and internal morphology including ligamental area, anterior adductor scar and dentition. Frech remarked that the differences between *G. alta* and *G. securiformis* are slight and not always perceptible.

The best examples of these three species were figured by Frech whose drawings are reproduced in figure 17. As shown shell outline and prosopon of *G. securiformis*, *G. alta*, and *G. distincta* are like those of *G. triquetra* and are generally similar to each other. Moreover, G-angles ( $65^\circ$ ,  $60^\circ$ , and  $63^\circ$ , respectively) are well within one standard deviation of the mean G-angle of *G. triquetra* (see table 6), and shell shape and musculature descriptions are largely in agreement. Except for the following anomalies there appears no material basis for drawing a specific distinction among them: (1) the shell shape of one specimen of *G. securiformis* (fig. 17F, H) has a more equilaterally trigonal outline with less protracted umbones, but appears incomplete and, perhaps, distorted; and (2) the shape of the posterior adductor scar shown in Frech's (1891, pl. 16, fig. 5) drawing is circular in outline instead of reniform as in *G. triquetra*.

Described dentitions of these Rheinisch species are also more or less similar to the variable hinge of Solsville *G. triquetra*: (1) four progressively elongated parallel cardinal teeth were described by Frech in both valves of *G. securiformis* with three lateral teeth in the right valve and two in the left; (2) a right hinge of *G. alta* observed by Frech had four subparallel cardinal teeth, the middle two joined above [an apparent anomaly; in *G. triquetra* joining of the first with the second and third with the fourth cardinals is occasionally observed here, e.g., fig. 14C, E, (?)G]; (3) a left hinge of *G. distincta* described by Frech had three or four parallel cardinal teeth; and (4) a right internal mold of *G. alta* figured by Follmann (1885, pl. 4, fig. 1b) suggests three subparallel cardinal teeth (with the uppermost two cardinal socket infillings joined above) and two or (?)three lateral teeth behind.

Although ligamental areas are mentioned by Frech in some of the smooth Rheinisch *gosseletias*, the precise nature is not given. Judging from Frech's figures, the parallel-grooved, duplivincular ligamental areas are all similar to that of *G. triquetra* except in *G. distincta*, *G. minor*, and *G. ibergensis* in which the ligamental area was not preserved.

*Gosseletia ibergensis* Roemer (Frech, 1891, pl. 17, fig. 5a, b, c) was based on several smooth specimens from the basal Upper De-

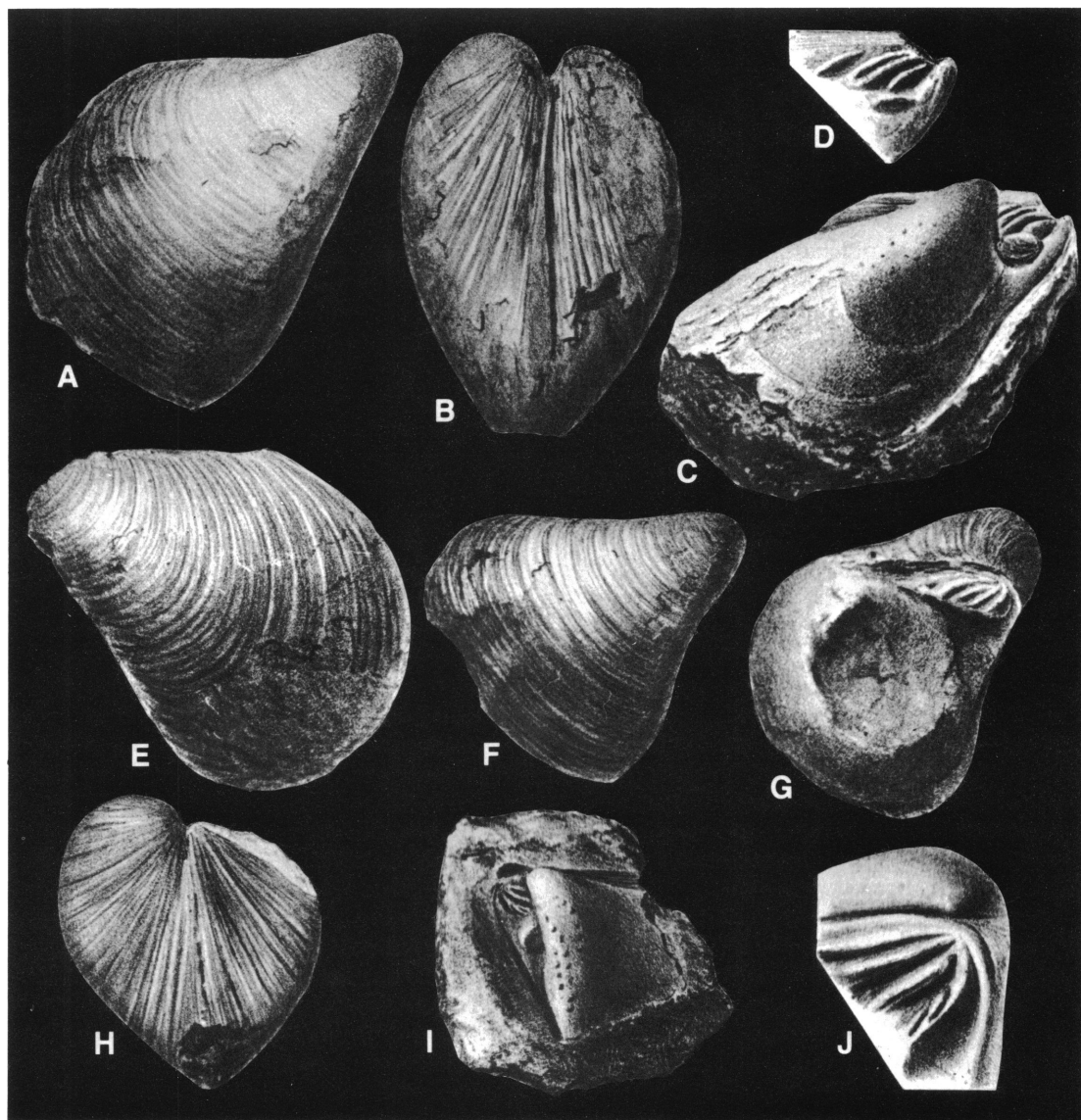


FIG. 17. Rhineland *Gosseletia* species. A-D. *G. alta* Follmann. Frech, 1891, pl. 16, figs. 7, 7a, 6, 6a; Lower Devonian (upper Coblenzschichten), Lieserthal bei Wittlich. A. Right valve of articulated specimen. B. Anterior view of same. C. Internal mold with cardinal teeth, anterior adductor scar and pallial punctations. D. Dental detail of same (enlarged). E. *G. distincta* Follmann. Frech, 1891, pl. 16, fig. 17; Middle Devonian, Eifel. Left valve. F-H. *G. securiformis* Follmann. Frech, 1891, pl. 16, figs. 3, 3a, 4; Lower Devonian (upper Coblenzschichten), Lieserthal bei Wittlich. F. Right valve of articulated specimen. G. Left valve with cardinal teeth partially inferred. H. Anterior view of F. I, J. *G. schizodon* Frech, 1891, pl. 13, figs. 6, 6a; Lower Devonian (Coblenzquarzit), Ems. I. Internal mold with hinge. J. Hinge detail (enlarged) of same (artificial cast?). All figs.  $\times 1$  except as noted.

vonian (Frasnian) of Germany. Little is known of the dentition. A single specimen showing the cardinal teeth was distorted in preparation; hence the anomalous dental

structure in Frech's plate 17, figure 5b. The ligament is duplivincular. In outline the shells resemble those of *G. triquetra* but clearly represent a distinct species: the umbones are

lower and smaller, and the G-angle is much higher, approaching 90°.

"*Gosseletia* (?) *minor*" Frech (1891, pl. 16, fig. 18) is based on a single specimen from the Frasnian of Germany. It has a shell shape similar to *G. triquetra* with a G-angle of approximately 65°. However, it is very small and may represent nothing more than a juvenile stage. The internal morphology is unknown. Frech was uncertain as to the membership of *G. minor* in *Gosseletia*, noting some similarities to *Myalina bodana* Roemer.

*Gosseletia schizodon* Frech (1891) is based upon a partial left internal mold of the umbonal and hinge region from the Lower Devonian (Emsian) of Germany. The specimen (fig. 17I) shows a duplivincular ligament, deeply impressed, small, circular adductor scar and pallial punctae almost identical with a Solsville *G. triquetra* internal mold (compare with fig. 14E). The hinge shows four subparallel cardinal teeth; the first two and the last two seem lightly joined to each other above as in some *G. triquetra*. The uppermost tooth is a simple ridge diverging from the rest. The remaining cardinal teeth are schizoid, showing an ancillary denticle splitting off the ventral margin of each; the lowermost seems (?) split in twain. Among the Solsville specimens limited schizoid modifications of the cardinal dentition has also been observed (see fig. 15).

Four additional species from the Lower Devonian of Germany are given comment below:

1. "*Gosseletia*" *radiata* Follmann (1885) is based upon two unfigured specimens. Evidently they are not *Gosseletia*, but the radial ribbing in Follmann's description suggest *Stappersella*.

2. "*Gosseletia*" *eifeliensis* Follmann (1885) is based upon a single unfigured internal mold of uncertain affinities.

3. "*Gosseletia*" *flabellcosta* Fuchs (1915, pl. 9, fig. 1) is not *Gosseletia*. The strong plumose radial ribs suggest *Follmannia* Drevemann, 1907.

4. "*Gosseletia*" *intermedia* Viëtor (1919, pl. 16, fig. 6) shows strong radial plicae and is here placed in *Stappersella*.

AUTECOLOGY: Evidence suggests that *G. triquetra* was an epibyssate suspension feeder adapted to relatively firm substrates in mod-

erately energetic to energetic shallow marine waters. As indicated in table 2, this species is abundant in the silty/sandy facies of the Solsville (*Gosseletia* community) but absent in the argillites (*Nuculoidea* community) which were probably too soft to support such heavy-shelled taxa.

Studies of the relationships of shell forms of Recent bivalves to their life habits have permitted reasonable reconstructions of the life positions among many extinct taxa. Stanley (1970) has noted that among infaunal and semi-infaunal species maximum shell width occurs midlaterally, the shells tapering ventrally to form a wedgelike cross-sectional outline. Among epibyssate species, such as *Mytilus edulis*, however, maximum shell width is more ventrally placed, and the lower shell margins in contact with the substrate are flattened rather than tapered. This modification of shell shape, Stanley indicated, results in increased positional stability (i.e., the "snowshoe effect" *sensu* Bambach, 1971) by lowering the center of gravity of the shells and providing a broadened base of contact with the substrate.

By analogy, the flat face of the carina or keel (the heaviest portion of the shell) of *G. triquetra* was placed downward, the posterior wing extending upward into the currents with the plane of commissure normal to the substrate (see fig. 6). The internal morphology suggests a byssus which probably emerged between the shells along the same flat face at the faint byssal sinus beneath the auricle. No byssal gape is visible, but Pojeta (1966) has shown that a byssal gape occurs in few byssate ambonychiids.

Stanley (1972) has suggested that the extinct ambonychiids occupied epibyssate habitat niches presently held by mytilids. Stanley concluded, however, that, in general, ambonychiids were adapted to quieter, less exposed habitats than the mytilids due to weaker byssal musculature and normally more compressed shells which are likely to be positionally less stable than more broadly based mytilid shells. However, *Mytilarca*, *Stappersella*, and *Gosseletia* are exceptional ambonychiids in the relative development of flattened carinate basal platforms. In *Gosseletia* the base seems particularly broad compared with other ambonychiids and considerably

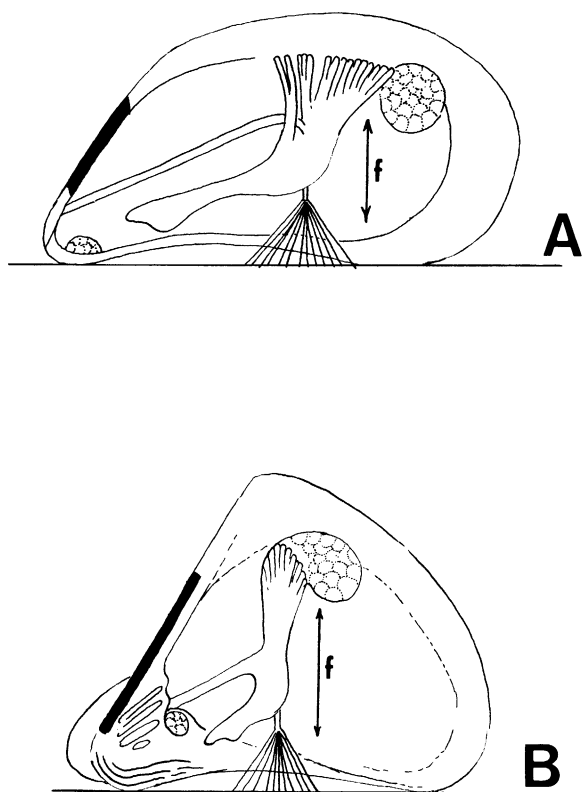


FIG. 18. Comparative adaptations for epibyssate life habits in *Mytilus edulis* (Linné) and *Gosseletia triquetra* (Conrad). A. *M. edulis*. Contraction of byssal/pedal musculature shown produces a net force (f) normal to the lowermost shell margin. (Based on Stanley, 1972.) B. *G. triquetra*. Contraction of the reconstructed byssal/pedal musculature would produce a net force (f) similar to that shown in *M. edulis*.

broader and thicker than in Recent *Mytilus edulis*. On the basis of design alone, the shells of *G. triquetra* suggest superior positional stability to those of *M. edulis*. Even if the byssal musculature were weaker in *G. triquetra* than in *M. edulis* (internal evidence does not seem to support such a conclusion), byssal weakness would be, to some extent, offset by the lower center of gravity and wider shell base in *G. triquetra*. Hence, it seems evident that *G. triquetra* was better adapted to more exposed habitat niches, such as those of *M. edulis*, than most other ambonychiids.

Further evidence for the ecological similarities of *G. triquetra* and *M. edulis* is supplied by the relative positions of attachment of the byssal retractor musculature within the valves. Unlike the condition of *Modiolus demissus* (and probably *Modiomorpha concentrica* as well) where the posterior byssal re-

tractor is located well behind the byssus resulting in a net force nearly parallel to the long axis of the shell (fig. 49) thus acting to pull this semi-infaunal byssate species more deeply into the substratum when disturbed (Stanley, 1972), the position of the byssal retractor musculature in *G. triquetra* is more nearly analogous to that of *M. edulis*, the posterior byssal retractor having been shifted anteriorly to lie almost directly above the byssus. The relatively strong development of the posterior byssal retractor [as evidenced by the large size of the dorsal lobe of the posterior muscular scar and/or the long (?) byssal muscular insertional groove in front of it] and corresponding weakness of the anterior retractor would appear to have produced a fairly strong downward force for maintenance of position in energetic current conditions (see fig. 18).

ORDER ARCOIDA STOLICZKA, 1871

SUPERFAMILY CYRTODONTACEA

ULRICH, 1894

FAMILY CYRTODONTIDAE ULRICH, 1894

GENUS *PTYCHODESMA*

HALL AND WHITFIELD, 1872

TYPE SPECIES: *Ptychodesma knappianum* Hall and Whitfield (1872) from the "Hydraulic beds" at Louisville, Kentucky, by original designation and monotypy.

TYPE SECTION: Savage (1930) reported the type species from the Silver Creek Limestone near the Louisville, Kentucky waterworks. The term "Hydraulic Limestone," according to Sutton and Sutton (1937), was formerly applied to the Silver Creek Member *sensu* Siebenthal (1900), an argillaceous limestone unit beneath the crinoidal Beechwood Limestone Member (Butts, 1915). Together these constitute the Sellersburg Limestone (*sensu* Kindle, 1899) which lies stratigraphically above the Jeffersonville Limestone and below the New Albany Shale. Cooper et al. (1942) and Collinson (1967) correlated the Sellersburg with the Hamilton of New York. Oliver et al. (1969) indicated the Silver Creek to be stratigraphically equivalent to the lower Silica Shale and Plum Brook Shale of Ohio and the Delphi Station Member of the Skaneateles Formation of central New York State.

GENERIC USAGE: *Ptychodesma* is here restricted to anisomyarian, integripalliate, submodioloid cyrtodontids with small, anteriorly placed umbones, straight hinge line and a broad, mostly opisthodontic, geniculate, duplivincular ligamental area underlain by a thick hinge plate with well-developed anterior and posterior hinge teeth. Separated by an edentulous area are two or more short, oblique or arcuate cardinal teeth (at least one may be varyingly bifurcated) and about two lateral teeth. A broad anterior lobe defined by a broad, shallow sulcus (a feature variably developed in the type species) may have generic value as well (Newell in Moore, 1969).

Although many modioloid bivalve species have been assigned to *Ptychodesma* by past authors, all, save the type species, are here excluded for the following reasons:

1. *Macrodesma* Isberg, 1934 (Upper Ordovician-Silurian, Sweden) was tentatively placed in synonymy with *Ptychodesma* by Newell (in Moore, 1969). It has a modioloid shell, a nongeniculate, anteriorly tapering duplivincular ligamental area and, according to Isberg is edentulous.
2. "*Ptychodesma*" *neglectum* Hall, 1883 (= "*P.*" *minor* Hall, 1885 according to McAlester, 1962a) from the Upper Devonian (Chemung) of New York has a shell form suggestive of *Ptychodesma*. McAlester (1962a), however, speculated that the flattened area along the posterodorsal margin represents an edentulous hinge plate. Provisionally, this species is here assigned to *Macrodesma*.
3. "*Ptychodesma*" *nanum* Hall (1885, pl. 93, figs. 17, 18) from the Upper Devonian (lower Chemung) of New York. Hall's figures show two distinct genera. His figure 17 shows a small, suborbicular, ventrally embayed shell with a small umbo and a relatively long hinge line. His figure 18 shows an eccentrically elliptical shell with a prominent umbo, short hinge line and no ventral embayment; a narrowly elongate anterior auricle is defined by a sharp, radial cincture or groove. Neither figure shows demonstrable affinities to *Ptychodesma*.
4. "*Ptychodesma*" *nilsoni* (Hisinger) from the Silurian of Sweden and England is here excluded on the basis of its edentulous hinge and internal ligamental pit (Angelin and Lindström, 1880; Williams and Breger, 1916; Carter and Tevesz, 1978a).

Saul, Boucot, and Finks (1963) described *Ptychodesma* sp. from the Devonian of Ghana. Although the shape of their figured shells is suggestive of the genus, their identity cannot be verified without hinge and ligamental data.

### *Ptychodesma knappianum*

Hall and Whitfield, 1872

Figures 5C, 6G, 19–22, 23?, 24, 25

*Ptychodesma Knappiana* Hall and Whitfield, 1872, p. 192.

*Ptychodesma knappanum* Hall [and Whitfield]. Miller, 1877, p. 202.

*Ptychodesma Knappianum* Hall and Whitfield. Hall, 1883, pl. 51, figs. 22–27; 1885, p. 352, pl. 51, figs. 22–27.

*Ptychodesma knappianum*. Nettleroth, 1889, pl. 2, figs. 13, 15–18.

*Ptychodesma knappiana* Hall and Whitfield. Nettleroth, 1889, p. 201.

*Ptychodesma knappiana* Hall [and Whitfield]. Nettleroth, 1889, p. 201. Savage, 1930, p. 97; 1931, p. 232.

*Ptychodesma knappianum* Hall and Whitfield. Kindle, 1901, p. 671, pl. 15, fig. 2, 2a–c. Grabau

and Shimer, 1909, p. 456, fig. 606a-c. Williams and Breger, 1916, p. 153. McAlester, 1962a, p. 41. Bailey, 1975, p. 109, pl. 5, figs. 4-8, pl. 6, figs. 1-6, text-figs. 13-17; 1978a, p. 121. Carter and Tevesz, 1978a, p. 368, pl. 1; 1978b, p. 859. *Ptychodesma knappanum* Hall and Whitfield. Newell, in Moore, 1969, p. N250, fig. C1, 11a, b. †[?] *Modiomorpha tioga* Hall. Willard, 1939, pl. 25, fig. 23. [not] Hall, 1885, p. 291. †[?] *Ptychodesma* ? sp. Beushausen, 1895, p. 32, pl. 3, fig. 10a, b.

**DESCRIPTION:** Equivalved, strongly inequilateral, prosocline, moderately inflated, thick-shelled bivalves of medium size. Shape is somewhat mytiloid or modiomorphoid though more nearly ovoid or subcircular in outline, lacking the greater elongation and ventrally embayed curvature. Umbones are anteriorly terminal, appressed, in no instance rising noticeably above the straight hinge line. The extreme anterior margin is more or less vertically truncate.

The prosopon consists of irregular, fine to coarse, concentric growth lines lacking in radial elements. In addition, a number of varices of growth consisting of irregularly placed concentric furrows and broad, concentric rugae mark the shell exterior. The rugae may also be apparent on inner valve surfaces.

A mostly opisthodontic, duplivincular ligament is manifested by a deeply excavated ligamental area (fig. 19C, D) marked by a series of closely spaced, parallel ridges and intervening grooves. These form, between the beaks, an inequilateral geniculation or chevron with a strongly obtuse apex angle (about 170°), the grooves and ridges inclining slightly toward the hinge line on both sides of the apex. One specimen (fig. 19D) shows an anomalous sinuosity or inflection of the ridges and grooves behind the apex about midway along the ligamental area.

A broad, thick hinge plate lying beneath the ligamental area shows a series of short, oblique, parallel to slightly diverging cardinal teeth separated from a set of lateral teeth by an edentulous space. The cardinal teeth lie in a roughly circular area near the anterior extremity of the hinge plate beneath the beaks and just above the anterior adductor scar. Placement, form and articulation of the left and right cardinal teeth are shown in figures 21 and 22.

In the left valve a strong, primary cardinal tooth ( $P_L$ ) is flanked by a deep, bifid ( $\Delta$ -shaped) anterior socket and a deep, undivided, posterior socket. A shorter, secondary cardinal tooth ( $S_L$ ) lies between the limbs of the anterior socket. Marked by a ventrally widening medial groove, the secondary cardinal tooth is very narrowly  $\Delta$ -shaped. Two ancillary cardinal teeth ( $A_L$ ) are each expressed as thin, raised borders or lips along socket margins; a straight one ( $A_{L2}$ ) lies along the rear margin of the posterior socket, and an arcuate one ( $A_{L1}$ ) is placed along the anterior margin of the forwardmost limb of the bifid anterior socket.

In the right valve a strong,  $\Delta$ -shaped, primary cardinal tooth ( $P_R$ ) is flanked by deep, anterior and posterior sockets. A third socket is placed medially between the limbs of the primary tooth. An undivided secondary cardinal tooth ( $S_R$ ) is placed along the rear margin of the posterior socket.

Along the posterior length of the hinge plate, a pair of straight or faintly arcuate lateral teeth lie parallel to the dorsal hinge margin in each valve. In the right valve both lateral teeth are prominent, subequal, and separated by a deep, elongate socket. In the left valve a strong, primary lateral tooth is bounded above and below by similar sockets. Below the ventral socket in the same valve is a second lateral tooth of lesser prominence. As shown in figure 21C, the lateral teeth of the left valve underlie those of the right valve.

An internal mold (fig. 19G, H) removed from a left valve (the corresponding right valve was destroyed in preparation) reveals a simple, deeply recessed pallial line and a strongly anisomyarian condition with a small, circular, deeply impressed anterior adductor scar, and a large, rounded, faint, posterior adductor scar. Both scars are dorsally placed just beneath the anterior and posterior extremities of the hinge plate. Neither byssal/pedal muscle scars, byssal gape, nor byssal sinus were observed.

Original shell microstructure has been described by Carter and Tevesz (1978a).

**COMMENTS:** Carter and Tevesz (1978a) have noted that past dental descriptions of *P. knappianum* have often been vague and contradictory. Although their two figured hinges are among the best in the literature, neither

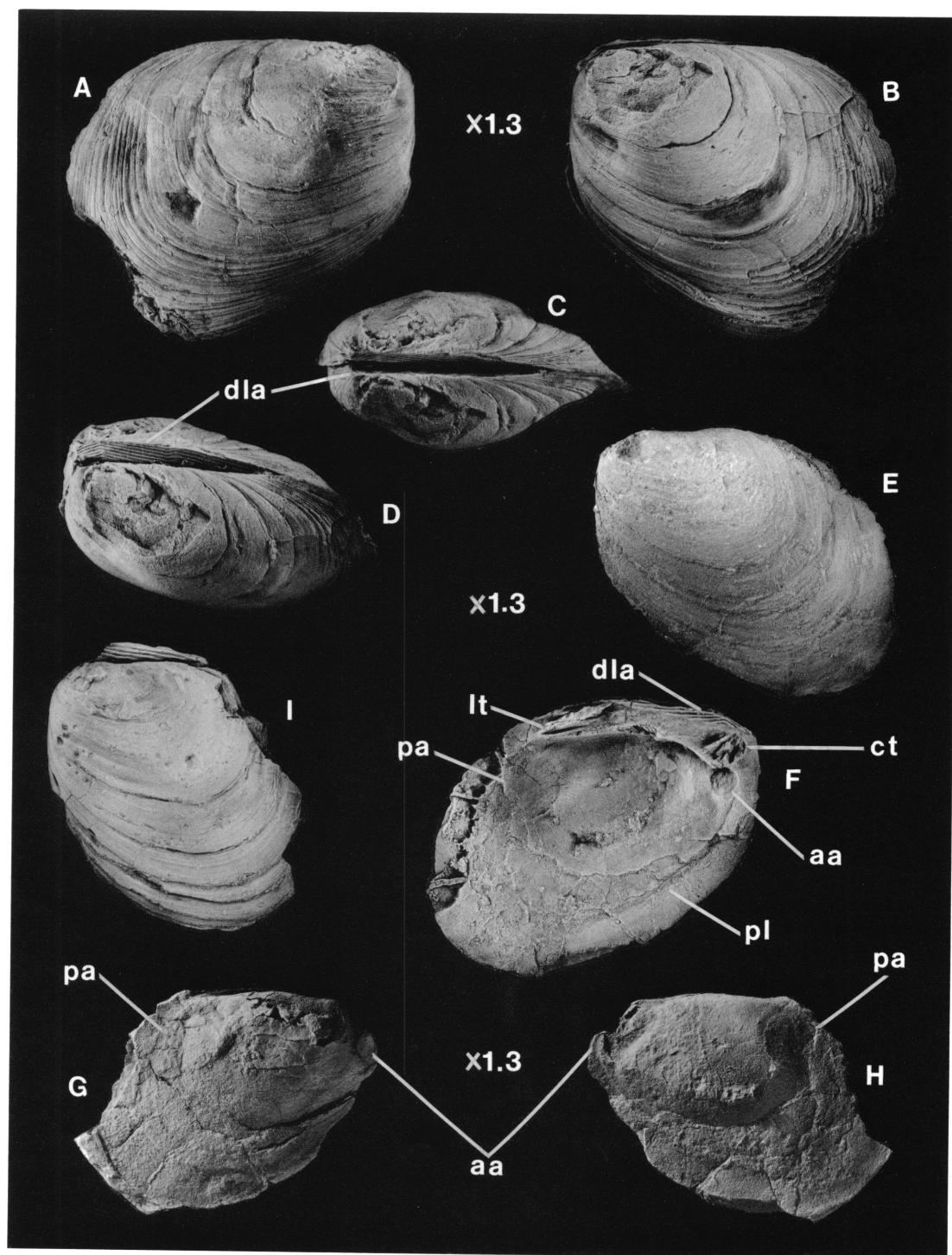


FIG. 19. *Ptychodesma knappianum* Hall and Whitfield. A–D. Articulated specimen (AMNH 36185) from AMNH loc. 3014. A. Right valve. B. Left valve. C. Dorsal view showing ligament area. D. Tilted dorsal view showing chevron-shaped insertional grooves for duplivincular ligament. Note anomalous posterior inflection of the grooves. E–H. Left valve with its internal mold (AMNH 36187A, B) from AMNH loc. 3013. E. Left valve exterior (AMNH 36187A). F. Pallial view of same valve. G. Right view of internal mold (AMNH 36187B). H. Left view of same internal mold. All figures  $\times 1.3$ .

Abbreviations: aa—anterior adductor scar, ct—cardinal teeth, dla—duplivincular ligamental area, lt—lateral tooth, pa—posterior adductor scar, pl—pallial line.



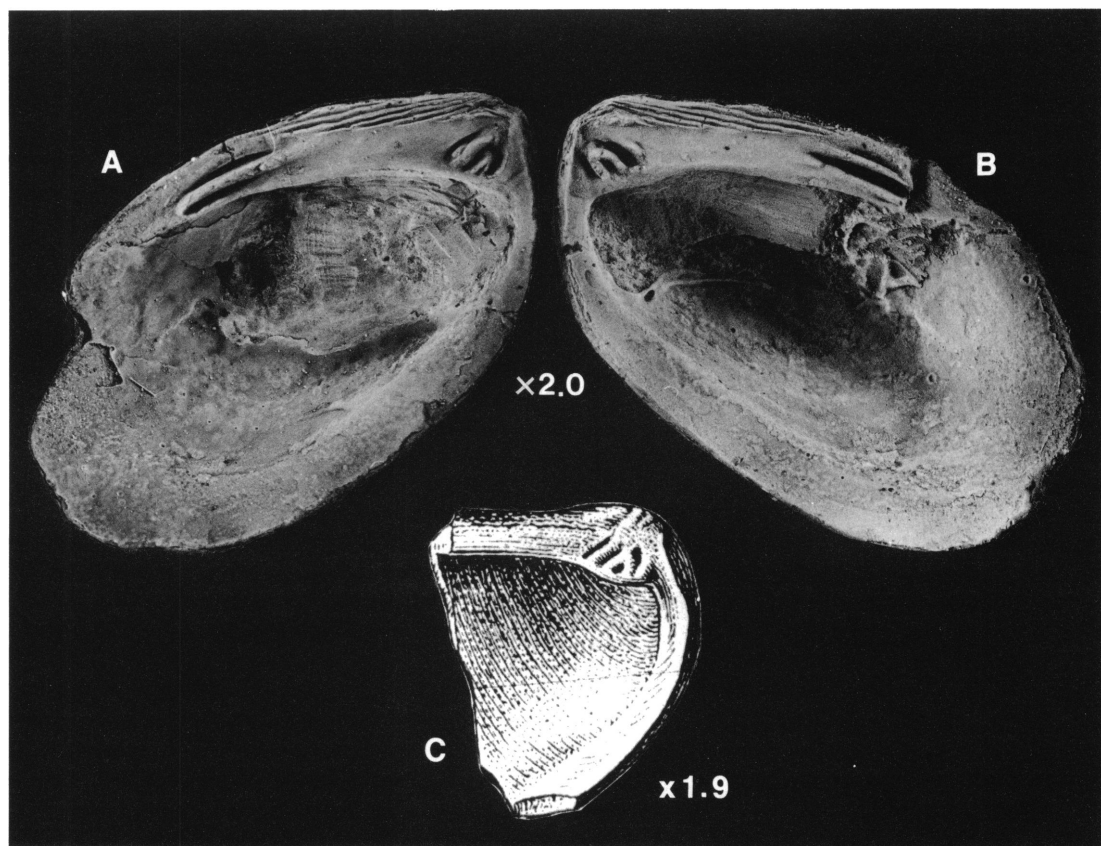


FIG. 20. *Ptychodesma knappianum* Hall and Whitfield. A, B. Left and right valves from an articulated specimen (AMNH 36188A, B) from AMNH loc. 3013. Prepared by Mr. Frank Lombardy. A. Left valve (AMNH 36188A). B. Right valve (AMNH 36188B). C. View of cardinal teeth and hinge plate in a partial left valve as figured by Kindle (1901, pl. 15, fig. 2c from the Sellersburg near Charlestown, Indiana).

is adequately preserved to settle the question. The hinge descriptions here are based on unusually well-preserved left and right hinges (AMNH 36188A, B). Since the tooth and socket arrangements of each valve neatly complement each other (fig. 22), there seems little basis for further doubt. The cardinal teeth of another specimen, however (fig. 19F), are seemingly at odds with those of the others. But the anomalous appearance resulted from damage in preparation. In separating the destroyed right valve from the figured left valve, small-cardinal tooth remnants from the right valve remain cemented by calcite to the sockets of the left valve.

**REMARKS ON MORPHOLOGY:** Although the duplivincular ligamental area has long been recognized in *Ptychodesma* (e.g., Hall and Whitfield, 1872; Hall, 1885; Nettleroth, 1889;

Beushausen, 1895; Kindle, 1901; Williams and Breger, 1916; Newell, 1937; McAlester, 1962a; Newell in Moore, 1969; Bailey, 1975; Carter and Tevesz, 1978a), its form and importance have been disputed. Among figured specimens in the literature, the asymmetrically geniculate, grooved pattern seems consistent, the number of grooves increasing with shell growth (Hall and Whitfield, 1872). Williams and Breger (1916), however, remarked that the figures of Kindle (1901) demonstrated that the morphology of the ligamental area was of less taxonomic importance and constancy than Hall and Whitfield had supposed. Ironically, Kindle's (1901, pl. 15, fig. 2a) single figure of the ligamental area only confirms the description of Hall and Whitfield as do the Solsville specimens illustrated here.

Less well known than the ligamental area

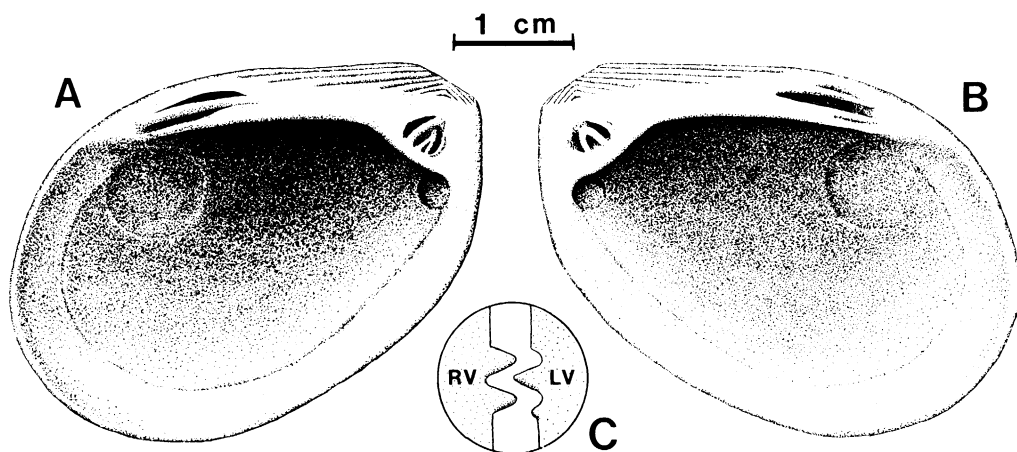


FIG. 21. *Ptychodesma knappianum* Hall and Whitfield. A, B. Reconstruction of interior morphology based upon prepared specimens. A. Left valve. B. Right valve. C. Relative development and articulation of lateral hinge teeth and sockets viewed in cross section, i.e., normal to plane of commissure (drawing not to scale).

Abbreviations: LV—left valve, RV—right valve.

is the dentition of *Ptychodesma*. Dental data are lacking in Hall and Whitfield's original description of *P. knappianum*, but Hall (1885) later reported "two or three cardinal teeth" although these were not illustrated. Nettle-roth (1889) essentially repeated Hall's description, adding nothing new. Beushausen (1895) reported and figured two or more cardinal teeth in "*P. ? sp.*" (see fig. 23) from the Lower Devonian of Germany.

Kindle (1901, p. 672) first accurately portrayed the dental morphology of *P. knappianum*: "The hinge has about three short, oblique teeth just below the beaks and two long teeth near the posterior end of the hinge and having a direction parallel with it." Whereas the "long teeth" (laterals) are not evident in Kindle's figures, his drawing of a left hinge (see fig. 20) shows a pronounced, bifid cardinal tooth (cf.  $S_L$ ) flanked posteriorly by an undivided, oblique cardinal tooth (cf.  $P_L$ ) and anteriorly by an arcuate cardinal tooth (cf.  $A_{L1}$ ). Except for the greater degree of bifurcation in cf.  $S_L$ , the pattern is similar to that of Solsville *P. knappianum*. Williams and Breger (1916), however, interpreted Kindle's figure somewhat differently; they counted four cardinal teeth in the left valve (with nos. 2 and 3 uniting above to form a  $\Delta$ -shape) and five intervening sockets implying five cardinal teeth in the right valve.

The present analysis of the left and right cardinal and lateral teeth of *P. knappianum*, which first appeared in Bailey (1975), has since been partly confirmed by Carter and Tevesz (1978a) who described a right valve with a bifid anterior cardinal tooth (cf.  $P_R$ ) with an oblique cardinal tooth (cf.  $S_R$ ) immediately behind as in figure 22. However, they described one additional oblique cardinal tooth behind cf.  $S_R$ , a feature neither clearly visible in their figures nor indicated in any of the hinges figured here. Two of their right valves confirm the structure of the right lateral teeth as described in Bailey (1975). The dental morphology of their left valve, however, is poorly preserved and the dental elements unclear.

Other internal features described here have been noted by few past authors. Hall (1885) observed a strong anterior adductor scar. Beushausen's (1895) figures of "*P. ? sp.*" show a small, but distinct adductor scar, and the anterior arc of the pallial line. The figures of Bailey (1975) show anterior and posterior adductor scars of the left and right valves as well as the pallial line; these features are confirmed in the figures of Carter and Tevesz (1978a).

COMPARISONS: From the upper Emsian of Germany, Beushausen (1895) described a fragmentary internal mold (see fig. 23) which

he tentatively placed in *Ptychodesma*. The outline of the mold and geniculate duplivincular ligamental area (described by Beushausen but incompletely visible in his figures) as well as the cardinal dentition and muscular features noted above are consistent with *P. knappianum*. However, the umbonal region of the internal mold shows numerous pallial punctae, features seen in other genera treated here (i.e., *Ptychopteria*, *Gosseletia*, and *Modiomorpha*). Among *P. knappianum* from the Solsville these features were observed neither on inner shell surfaces nor on the single internal mold, although, in view of the preparatory techniques applied here only to this species and the surface condition of the internal mold, the absence of such delicate structures is hardly surprising. Moreover, they are not apparent on the internal mold of *P. knappianum* shown by Carter and Tevesz (1978a, pl. 1, fig. 1d, e).

"*Modiomorpha*" *schucherti* Cleland (1911, pl. 24, figs. 1–3; Pohl, 1929, pl. 13, figs. 6–12, pl. 14, figs. 1–4, 9) from the Devonian Milwaukee Formation has a shell shape and external features suggestive of *Ptychodesma* but is too poorly preserved to permit generic determination. One dorsal view of a partly gaping specimen (Pohl's pl. 13, fig. 9) shows no evidence of the characteristic ligamental area of *Ptychodesma*, but this feature is easily obscured by diagenetic flattening.

Wilson's (1975, pl. 72, figs. 9, 10) internal mold of "*Glossites*" *subtenuis* Hall from the Silica Formation of Ohio has shape and pallial features similar to those of *Ptychodesma*, but data are insufficient to be certain.

A less modioloid species combining the morphologic features of *Cyrtodonta* Billings and *Ptychodesma* is *Cyrtodonta declivis* Roemer from the German Lower Devonian Hauptspiriferensandstein. As illustrated by Frech (1891, pl. 4, fig. 2–2b), *C. declivis* has the more circular outline of *Cyrtodonta* but is very similar to *Ptychodesma* in other respects: it is anisomyarian (many cyrtodontids are isomyarian), integripalliate; it has a long, duplivincular ligamental area (this feature seems to lack the chevronal geniculation of *Ptychodesma*; rather, it appears to taper anteriorly as in *Cyrtodonta*, but Frech's figure is unclear); and it has a prominent hinge plate with long lateral teeth separated by a thin

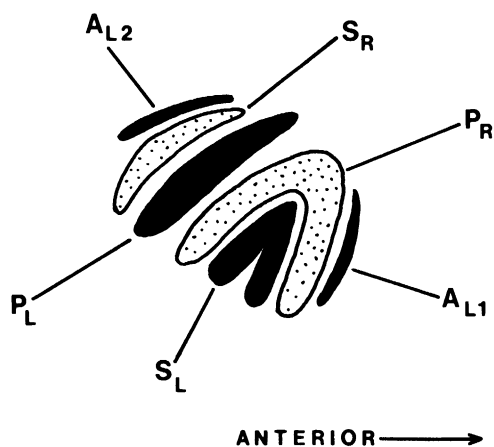


FIG. 22. *Ptychodesma knappianum* Hall and Whitfield. Articulation of left (solid black) and right (stippled) cardinal teeth.

Abbreviations: P<sub>L</sub>—left primary cardinal tooth, S<sub>L</sub>—left secondary cardinal tooth, A<sub>L</sub>—left ancillary cardinal tooth, P<sub>R</sub>—right primary cardinal tooth, S<sub>R</sub>—right secondary cardinal tooth.

edentulous area from a short series of radiating, oblique to arcuate cardinal teeth (one of these is similarly bifurcate). Like *Ptychodesma*, *C. declivis* also seems to lack the typical, elevated, auricular shelf for a deeply impressed anterior adductor as in many cyrtodontids (e.g., *Vanuxemia*). Since the cardinal teeth of *Cyrtodonta*, *sensu* LaRocque (in Moore, 1969), are recumbent and posteriorly directed, *C. declivis* would be excluded from *Cyrtodonta* using his diagnosis. However, *Cyrtodonta*, *sensu* Pojeta (1971), shows more diverse hinge morphology including many of the hinge features seen both in *C. declivis* and *P. knappianum*. *Cyrtodonta declivis* is provisionally excluded from *Ptychodesma* on the basis of its cyrtodontiform outline and (?)nongeniculate ligamental area. Nevertheless, it does seem to represent a morphologic grade intermediate between *Ptychodesma* and earlier (Ordovician-Silurian) cyrtodontids (see fig. 25).

*Matheria* Billings is an Ordovician bivalve whose taxonomic position has been regarded as uncertain (Pojeta, 1971). Chavan (1966; and in Moore, 1969) and Vokes (1967) placed it in the Astartidae while LaRocque (in Moore, 1969) considered it a possible cyrtodontid. The morphologic similarities of

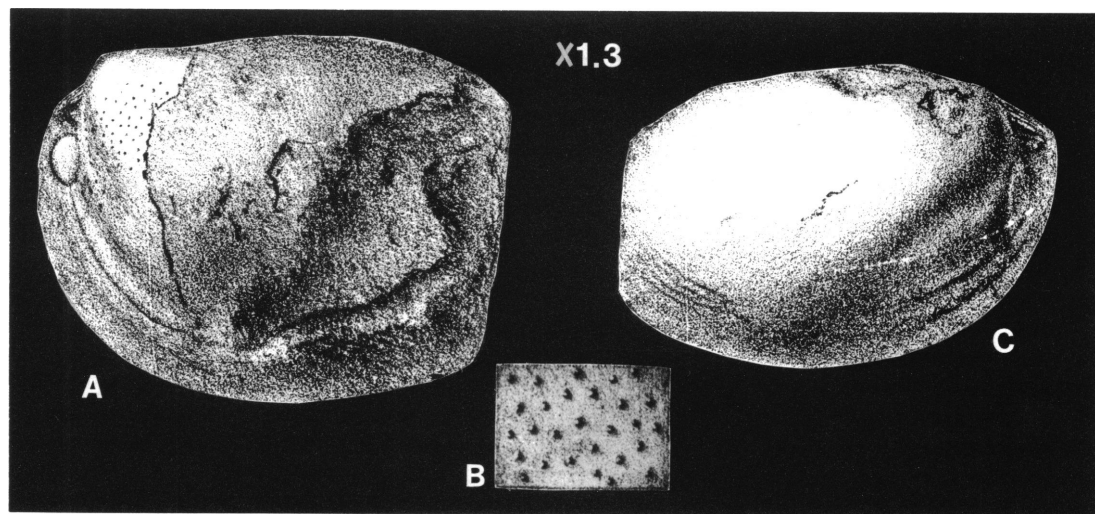


FIG. 23. *Ptychodesma? knappianum* Hall and Whitfield. A–C. Partial internal mold of “*Ptychodesma? sp.*” figured by Beushausen (1895, pl. 3, fig. 10a, A, b) from the upper Coblenz beds (Emsian), Failzer Hof bei Wittlich, Germany. A. Left view. B. Enlargement of pallial punctae. C. Right view.

*Matheria rugosa* to *Ptychodesma* and *Macrodesma* support the latter view (see Ulrich, 1894, 1897, pl. 36, figs. 29, 30; and Pojeta, 1971, pl. 16, fig. 6). Except for the absence of lateral teeth and the duplivincular ligamental area which tapers forward as in *Cyrtodonta* and *Macrodesma* (the chevronal geniculation of *Ptychodesma* is lacking), the remaining aspects of *Matheria rugosa* are highly suggestive of *Ptychodesma*. Significant similarities are: (1) the moderately thick, anteriorly subtruncate, modioloid shell with small, anteriorly placed umbones; (2) concentric rugae and finer lines of growth; (3) a strong, flat hinge plate with small radiating cardinal teeth (Ulrich, 1894, 1897, indicated one in the left valve flanked on either side by a deep socket inferring two cardinal teeth with a medial socket in the right valve; Pojeta’s figure suggests two right cardinal teeth). The lack of lateral teeth suggests a condition intermediate between the more heterodont-like cyrtodontids and the edentulous *Macrodesma* (fig. 25).

**CLASSIFICATION:** Recent studies of *Ptychodesma* confirm the placement of this problematic genus among the Cyrtodontidae (Newell and LaRocque in Moore, 1969; Bailey, 1975; Carter and Tevesz, 1978a). Those morphologic features of *Ptychodesma* which

seem especially cyrtodontid in character include:

- (1) The strong duplivincular ligament.
- (2) A hinge plate with oblique to arcuate cardinal teeth separated from lateral teeth by an edentulous area.
- (3) One distinctly bifurcated cardinal tooth per valve (a condition seen in some species of *Cyrtodonta*—e.g., *C. beckneri* Conkin [see Pojeta, 1971, pl. 7, fig. 7] and *Vanuxemia* Billings, 1858 [see pls. 7–9 of Pojeta, 1971]).
- (4) The strongly impressed anterior adductor scar.
- (5) The anteriorly reduced, equivalve, integripalliate shells (anterior reduction is not universal among cyrtodontids but is common among many species).

There are, however, three major areas in which *Ptychodesma* seems morphologically atypical of other cyrtodontids:

- (1) Although the anterior adductor scars are reminiscent of those of other cyrtodontids, they are not placed in the hinge plate nor upon an elevated shell thickening or auricular shelf just below it as in some *Cyrtodonta* and *Vanuxemia* (see Pojeta, 1971).
- (2) The prominent duplivincular ligamental area possesses the chevronal form seen in arcids (e.g., *Arca*) and pterineids [e.g., *Leptodesma* (*Leiopteria*) and *Ptychopteria* (*Cornellites*)]. In other cyrtodontids (e.g., *Cyrtodonta*, *Vanux-*

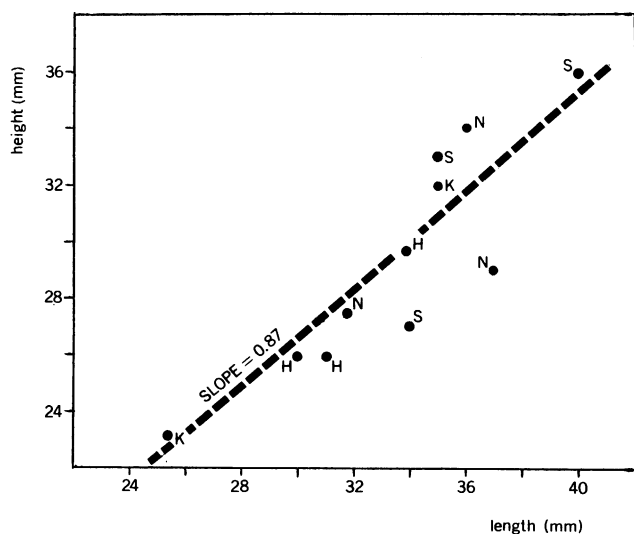


FIG. 24. Compiled dimensions of *Ptychodesma knappianum* Hall and Whitfield.

Abbreviations: S—Solsville specimens, H—dimensions given by Hall (1885), N—dimensions given by Nettleroth (1889), K—dimensions given by Kindle (1901).

*emia* and *Macrodesma*) the ligamental area tapers forward, and the geniculation seems lacking.

- (3) As members of the Arcoida (see Newell in Moore, 1969), the cyrtodontids have been included in an order consisting of generally isomyarian taxa. However, *Ptychodesma* exhibits a strongly anisomyarian condition superficially akin to the pteroids and mytiloids. In certain instances an isomyarian condition has, indeed, been verified among certain cyrtodontids (e.g., *Cyrtodontula* in Moore, 1969, fig. C1 (6b); *Cyrtodonta suecica* Isberg, 1934, pl. 20, fig. 4; Newell, 1954, fig. 1; Cox, 1960, fig. 2); but in other cyrtodontids (e.g., *Cyrtodonta declivis*) an anisomyarian condition has been identified. Moreover, among certain cyrtodontid species whose internal morphologies are poorly known, anteriorly reduced or modioloid shell shapes directly imply anisomyarian adductor musculature.

In addition to the cyrtodontids, *Ptychodesma* also shows morphological features seen among the Arcacea Lamarck, 1809, the Ambonychiacea Miller, 1877, and the Pteriacea Gray, 1847, providing some measure of support for phyletic relationships among these superfamilies as inferred by Newell (1937, 1954, and in Moore, 1969) and Cox (1959, 1960). The possible relationships of *Ptychodesma* or other cyrtodontids to the Arcacea

have been especially discussed by Newell (1937), Cox (1959) and Stanley (1972) and need not be repeated here. Morphological features of *Ptychodesma* seen among the Ambonychiacea and Pteriacea include:

- (1) Equivalve shells (Ambonychiacea only).
- (2) Reduction of the shell anterior.
- (3) Presence of both cardinal and lateral teeth separated by an edentulous area of the hinge plate, e.g., *Mytilarca chemungensis* (Conrad) in Pojeta (1966, pl. 38, fig. 10), *Ambonychia alta* Meek in Pojeta (1966, pl. 29, fig. 12, pl. 30, figs. 1, 16, pl. 31, figs. 1, 2), *Opisthopteria griffini* (Hussey) in Pojeta (1966, pl. 42, figs. 20, 21), *Mytilarca (Cyrtodontopsis) kayseri* Frech (1891, pl. 13, fig. 2), *Gosseletia schizodon* Frech (1891, pl. 13, fig. 6, 6a), *Gosseletia triquetra* (Conrad) in Pojeta (1966, pl. 35, figs. 15, 18) and figures 14 and 15 of the present paper among the ambonychiaceans; and *Pterinea laevis* Goldfuss in Frech (1891, pl. 2, figs. 10–13), *Pterinea expansa* Maurer in Frech (1891, pl. 9, fig. 11) and *Ptychopteria fasciculata* in Frech (1891, pl. 9, fig. 2) and figures 8B–E and 9C, E, F of the present paper among the pteriaceans.
- (4) Some development of bifurcated cardinal teeth largely in the Ambonychiacea, e.g., *Mytilarca chemungensis* (Conrad) in McAlester (1962a, pl. 15, figs. 6, 7 (=Hall, 1884, pl. 32, fig. 9, pl. 33, fig. 8, AMNH 6109/2:2), *Mytilarca (Cyrtodontopsis) kayseri* Frech (1891, pl. 3, figs. 1–

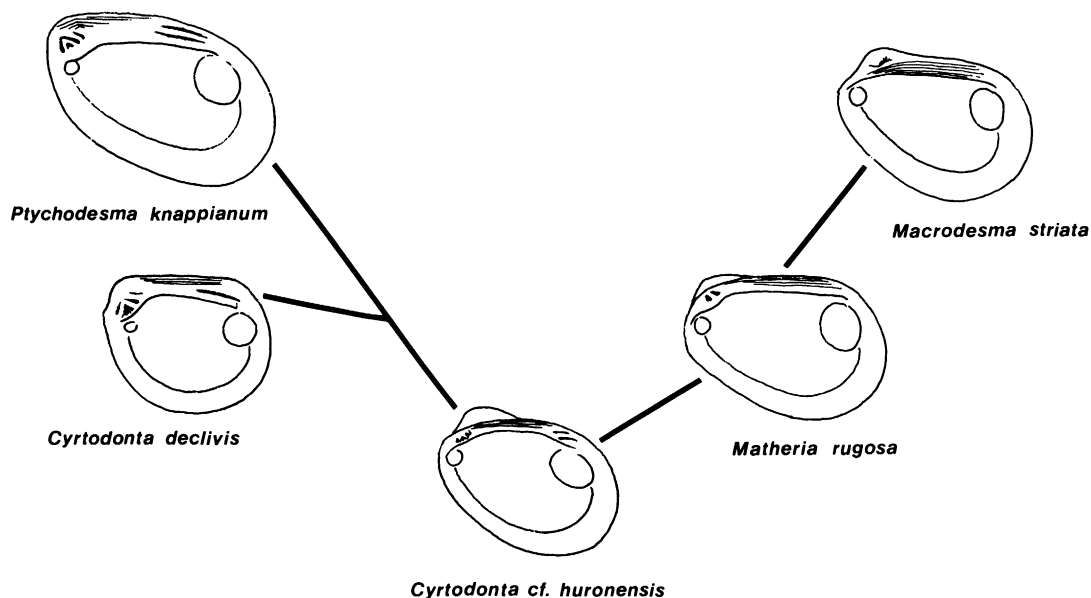


FIG. 25. Phyletic models among early-middle Paleozoic anisomyarian cyrtodontids. Two possible trends are shown: (1) development of an enlarged, "heterodont" dentition with bifid cardinal teeth (*Cyrtodonta-Ptychodesma*) and (2) development of an edentulous hinge (*Cyrtodonta-Matheria-Macrodesma*). *Cyrtodonta cf. huronensis* (Ordovician, Canada) shows small, radiating, unspecialized cardinals and weak laterals which might be anticipated in the ancestor (drawings of *Matheria* and *C. cf. huronensis* based, in part, on figures of Pojeta (1971)).

- 3), *Gosseletia schizodon* Frech (1891, pl. 8, fig. 6, 6a), and *Gosseletia triquetra* (see figs. 14C-E, G, and 15 of the present paper). Cardinal teeth within many of the pteriaceans (especially the Pterineidae) appear to normally be elongate and subparallel, or sometimes radiating. However, bifurcated cardinal teeth are developed in *Pterinea ventricosa* Goldfuss (Frech, 1891, pl. 10, fig. 1a) and in the Upper Silurian *Pteronitella* Billings, 1874 (in Moore, 1969, fig. C35, 7b).
- (5) Prominent duplivincular ligamental area. Retention of the chevronal geniculation is apparent among many pteriaceans, e.g., *Pterinea laevis* (in Frech, 1891, pl. 2, fig. 10a) and *Ptychopteria fasciculata* (fig. 7B, F, I, J, L, N of the present paper). However, if one assumes that the geniculation represents an ancestral condition as Newell (1937, 1954) has suggested, it appears that the forward limb of the chevron has been largely lost in the ambonychiaceans due to the extreme reduction of the shell anterior (e.g., see ligamental area of *Gosseletia triquetra* in fig. 14); although the vestiges of the forward limb are apparent in two Ordovician species, *Ambonychia gigantea*

Miller and *A. alata* Meek (Pojeta, 1971, pl. 10, figs. 6, 8).

Further evidence of phyletic linkage between cyrtodontids and pteriaceans is suggested by the problematic *Eurymya* Ulrich (placed provisionally within the Pterineidae by Newell and LaRocque, in Moore, 1969). Ulrich (1894, 1897) compared the shell similarities of two cyrtodontids, *Matheria rugosa* and *Cyrtodonta affinis*, with *Eurymya plana* (= *Modiolopsis plana* Hall, 1861) whose modioloid outline and small umbones are reminiscent of *Ptychodesma*. Like *Matheria*, *E. plana* lacks lateral teeth; in addition, cardinal dentition is virtually obsolescent, there being a single cardinal tooth in the left valve and a corresponding socket in the right valve. Furthermore, *E. plana* possesses a flat, narrow hinge plate with a long, anteriorly tapering duplivincular ligamental area like that seen in cyrtodontids and pteriaceans. A cyrtodontid-pteriacan connection is also suggested in *E. plana* by the anterior adductor

scar which shows superficial similarities to the distinctive anterior scar of the cyrtodontid, *Vanuxemia*. It is a circular, (?)elevated, very deeply impressed structure filling an anterior auricle and separated from the valve interior by a wall or septum along its posterior margin. Connecting with this septum is a transverse bar which posteriorly divides off the upper third of the scar. This bar is suggestive of the infoldings of the posterior wall marginal to the anterior adductor scar as seen in *Vanuxemia gibbosa* Ulrich (see Pojeta's 1971, pl. 7, figs. 9, 10). In *V. gibbosa* there are two such infoldings separated by a gap forming a myophoric notch which Pojeta interpreted as a passageway for an accessory muscle. The single bar of *E. plana* suggests fused infoldings, i.e., a collapsed myophoric notch.

**AUTECOLOGY:** Although no evidence either for a byssal retractor apparatus or a byssal gape has been observed in *P. knappianum*, Yonge (1953), Pojeta (1971), and Stanley (1972) have indicated that reduction of the shell anterior, reduction of the forward adductor, and extreme anterior displacement of the umbones strongly suggests byssal attachment. In addition, the small, flattened, anterior face just below the umbones may have served as a resting platform to balance the shells with the stabilizing aid of a byssus thereby maintaining a life pose similar to that shown in figures 5, 6.

Although the collected sample of *P. knappianum* is small, since more Solsville individuals were encountered in the gray-black argillaceous facies (*Nuculoidea* community), a preference for quiet, sheltered, muddy bottoms is suggested. This supports the conclusion that *P. knappianum*, like its cyrtodontid relatives *Vanuxemia* and *Cyrtodonta*, did not possess an exposed, epibyssate mode of life like *Mytilus* as one might infer from the somewhat mytiloid shell shape, but, instead, may have been endobyssate or partially buried in the soft sediments after the fashion of some pinnids, *Modiolus* (see Stanley, 1970; Pojeta, 1971) and burrowing arcs (Lim, 1966; Pojeta, 1971). At least partial burial seems further supported by the fairly narrow shell cross section and the tapering ventral margin.

The external shell morphology of *P. knappianum*

strongly resembles *Cyrtodonta subovata* Ulrich (1894, 1897, pl. 39, figs. 28–33) from the Upper Ordovician of Kentucky (although the dentition of the latter species seems to confirm its generic independence from *Ptychodesma*). Stanley (1972, text-fig. 15) indicated the shell form of *C. subovata* (and, hence, *P. knappianum*) as being best adapted for an endobyssate mode of life.

#### SUBCLASS PALAEOTAXODONTA

KOROBKOV, 1954

ORDER NUCULOIDA DALL, 1889

SUPERFAMILY NUCULACEA GRAY, 1824

FAMILY NUCULIDAE GRAY, 1824

GENUS *NUCULOIDEA*

WILLIAMS AND BREGER, 1916

**TYPE SPECIES:** *Nuculoidea opima* (Hall), 1843 (= *Nucula randalli* Hall and Whitfield, 1869) from the Hamilton Group of New York by original designation of Williams and Breger (1916).

**GENERIC USAGE:** Nuculid bivalves seem to have been particularly plagued by nomenclatural chaos. Past generic or subgeneric diagnoses are often contradictory or extensively overlap each other. In many cases the only apparent distinction among genera is stratigraphic occurrence. Despite several noteworthy attempts at clarification (e.g., DeFrance, 1825; d'Orbigny, 1844; Adams and Adams, 1858; Quenstedt, 1930; Schenck, 1934, 1939; McAlester, 1964, 1968; Keen in Moore, 1969) many nomenclatural difficulties remain. Except for a single occurrence of *Nuculopsis* Girty in the Michigan Basin (Bailey, 1979b), all other North American Devonian bona fide nuculids I have examined belong to a single genus, *Nuculoidea*.

*Nuculoidea* was originally proposed as a subgenus of *Nucula* Lamarck, 1799, by Williams and Breger (1916, p. 173) for nucas with "a distinct cartilage pit as in *Ctenodonta albertina* Ulrich from the Upper Ordovician, and a nonpectenated ventral margin, which differentiates them from the true nucas of the Cenozoic." Unfortunately, both criteria in the original diagnosis of *Nuculoidea* have significant problems. The cartilage pit (i.e., resilifer) of "*C.*" *albertina* [= *Deceptrix albertina* (Ulrich) of Pojeta, 1971] was figured



by Ulrich (1894, 1897, pl. 42, fig. 80). However, a syntype of *D. albertina* I personally examined (also figured by Pojeta, 1971, pl. 5, fig. 14) shows no evidence of a resilifer. Indeed, Pojeta (personal commun.) has indicated that no Ordovician nuculoids are resiliated.

Quenstedt (1930) considered *Nuculoidea* to be a subdivision of his subgenus, *Nucula* (*Palaeonucula*). He applied *Palaeonucula* to moderately to not at all opisthogyrate nuculids with (1) smooth inner shell margins; (2) a not at all to slightly spoon-shaped resilifer projecting into the valve interior; and (3) lacking either the resilifer tooth ("Bandgrubenzahn") or plain connecting piece ("Verbindungsstück") seen in *Nucula*. Quenstedt, however, later admitted that some forms of his *Palaeonucula* did, in fact, possess a resilifer tooth (see Schenck, 1934, p. 36).

Schenck (1934) stated that the hinge morphology of *Nuculoidea* was too poorly known to settle its systematic rank but tentatively included it in his nuculid group "B" (nuculid taxa with smooth inner margins).

Maillieux (1937) promoted *Nuculoidea* to full generic status but pointed out that its distinction from *Palaeonucula* is problematic, suggesting that the two may be synonymous. He tentatively restricted *Palaeonucula* to opisthogyrous species and *Nuculoidea* to prosogyrous species while conceding inadequacy of this distinction since *Nuculoidea* is sometimes opisthogyrous. This usage was followed by LaRocque (1950) who noted that if *Palaeonucula* and *Nuculoidea* are synonymous, the latter deserves priority.

Vokes (1949) first described the hinge of *Nuculoidea opima* (Hall), the type species, from the Hamilton of Pratt's Falls, New York. His figure 1(1) shows a taxodont hinge whose anterior tooth row is only slightly longer than the posterior row; they meet above a small, triangular resilifer which does not protrude into the valve interior as in many later nuculids. Vokes stressed the generic identity of *Nuculoidea* largely on a single feature, a set of fine, marginal denticulations (micropectenations) shown in Vokes's figure 1(2). On this basis he removed *Nuculoidea* from Schenck's group "B" but did not relocate it in Schenck's group "A" (nuculids with denticulate inner margins) as might be antici-

pated. Since the thin, striate character of the micropectenations are like that seen in no other nuculids, he proposed a separate group for the reception of *Nuculoidea*.

McAlester (1962a) cited the micropectenations of Vokes's specimen as evidence that the presence or absence of marginal denticulations lacks generic value. He thus only tentatively accepted the generic status of *Nuculoidea* concluding that no clear distinction had been made between it and other nuculids. McAlester (1968) later designated a lectotype and paratypes of the type species, *N. opima*, none of which show any internal morphology.

Soviet authors have applied *Nuculoidea* to Devonian nuculid taxa on the basis of stratigraphic occurrence without distinguishing it morphologically from other nuculids (see Eberzin, 1960, and Babin, 1966).

Babin (1966) recognized two major nuculid genera, *Nucula* Lamarck with ventral denticulations and a shell structure consisting mostly of "éléments individualisés" and *Nuculoma* Cossmann, 1907, with smooth or weakly denticulate inner margins and a shell consisting mostly of a homogeneous layer. Babin provisionally regarded *Nuculopsis* Girty, 1911, as well as *Nuculoidea* and *Palaeonucula* as junior synonyms of *Nuculoma*. However, recent microstructure studies of both *Nuculopsis* and *Nuculoidea* show that both lack the homogeneous shell structure attributed to them by Babin; instead, they both show prismatic and nacreous layers more like that of Recent *Nucula* (see Carter and Tevesz, 1978b; Bailey and Sandberg, 1979, and ms). Moreover, the weakly dentate inner shell margins Babin attributed to *Nuculoma* seem based upon the assumption that *Nuculoidea* and *Nuculoma* are congeneric. *Nuculoma*, *sensu stricto*, however, is a Jurassic genus with only smooth inner margins. Babin (1973) later accepted *Nuculoidea* as a Devonian genus with a triangular resilifer and micropectenate inner ventral margins.

Keen (in Moore, 1969) recognized the generic status of *Nuculoidea* and gave a diagnosis emphasizing the triangularity of the resilifer and the micropectenate inner shell margins; however, her geologic range (Ordovician-Devonian) is evidently based upon Ulrich's and Williams's and Breger's incor-

rect assumption that the Ordovician *Deceptrix albertina* was resiliated. *Nuculoidea* as understood here seems confined to the Devonian.

Study of the Solsville material as well as many hundreds of specimens of other species (collections of AMNH, NYSM, and USNM) have led to the following revised diagnosis of *Nuculoidea*: Nuculids with erect (subvertical) to only slightly opisthogyrous or only slightly prosogyrous umbones. Fasciculate growth lines with faint, discontinuous to continuous prosoponal radii and inner marginal micropectenations (both of the latter are often best defined posteriorly). Resilifer small, usually erect (nonreclining), triangular and nonprotruding or only faintly protruding into the valve interior and lying beneath the inner ends of the taxodont anterior and posterior hinge tooth rows. The resilifer shows little or no excavation into the hinge plate.

***Nuculoidea deceptriformis*, new species**

Figures 5D, 26–34

†[cf.] *Nucula corbuliformis* Hall and Whitfield. Stumm, 1942, pl. 81, fig. 28. See also note f, table 3 of present paper. [Not *Nucula corbuliformis* Hall and Whitfield, 1869, p. 2.]

†*Nuculoidea* cf. *N. opima* Carter and Tevesz, 1978b, p. 865, text-fig. 12. [Not *N. opima* (Hall), 1843.]

**DIAGNOSIS:** A nuculid with all the diagnostic characters of *Nuculoidea* as understood here, i.e., fine, radial prosoponal elements, inner marginal micropectenations, erect umbones and a nonprotruding, erect, triangular resilifer. *Nuculoidea deceptriformis* differs from other species of *Nuculoidea* in its (1) more pronounced umbones which are straighter and more angular, (2) steeper anterior and posterior umbonal angles, (3) more inequilateral outline with umbonal placement at posterior extremity, (4) less anterior elongation and reduced anterodorsal marginal flange, (5) generally less prominent and less fasciculate concentric growth lines, (6) generally more continuous radial prosoponal elements, (7) less smoothly curving ventral margin, and (8) lack of an outer prismatic layer (Carter and Tevesz, 1978b, p. 865).

**ETYMOLOGY:** Named after the praenuculid, *Deceptrix* Fuchs, 1919, whose shell shape it

superficially resembles as suggested by John Pojeta (personal commun.).

**TYPES:** Holotype: AMNH 36202 from AMNH loc. 3013. Paratypes: AMNH 36237A, B and 36241A–E from AMNH loc. 3012; AMNH 36164A, B, AMNH 36219 and 36165A–E from AMNH loc. 3013; and AMNH 36207 and 36204 from AMNH loc. 3017.

**DESCRIPTION:** Valves small, strongly inflated, nuculiform, inequilaterally trigonal, anteriorly elongate and posteriorly abruptly truncate. Valves subequal, the right valve being sometimes very slightly favored (see figs. 33, 34). Umbones very prominent, gibbous and erect (subvertical; sometimes slightly opisthogyrous to faintly prosogyrous), rising well above the hinge line. Height only slightly less than length. Umbonal slopes are straight, steep and rather angular. Ventral margin smoothly curving anteriorly, becoming rather straight posteriorly.

Escutcheon and lunule obsolescent but occasionally weakly defined (figs. 27C, H, J, 28D). Lunular region variable, ranging from slightly concave to subplanar to slightly convex.

Prosopon highly variable, there being two extremes, here designated variety “A” (*N. deceptriformis*, *sensu stricto*) and variety “B” (*N. deceptriformis*, *sensu lato*). Not only do both varieties morphologically intergrade continuously with var. “A” the dominant form, but articulated specimens often show a var. “A” aspect on one valve and a “B” appearance on the other. In var. “A” (fig. 27) the sculpture consists of poorly defined, fasciculate growth lines with a characteristic “fused” appearance and weak, continuous, radial lineations especially well defined posteriorly and ventrally. In var. “B” (fig. 28) the concentric growth lines show better definition; they are often lirate, punctuated by poorly to moderately well marked varices of growth producing a fascicular appearance with as few as two to as many as seven growth lines per mm. (values about four lines per mm. being most common) within each fascicle, and the spacing between growth lines increasing ventrally. Fine radial elements are best seen between growth lines and varices and, again, are emphasized posteriorly and ventrally; however, the radii seem less ob-

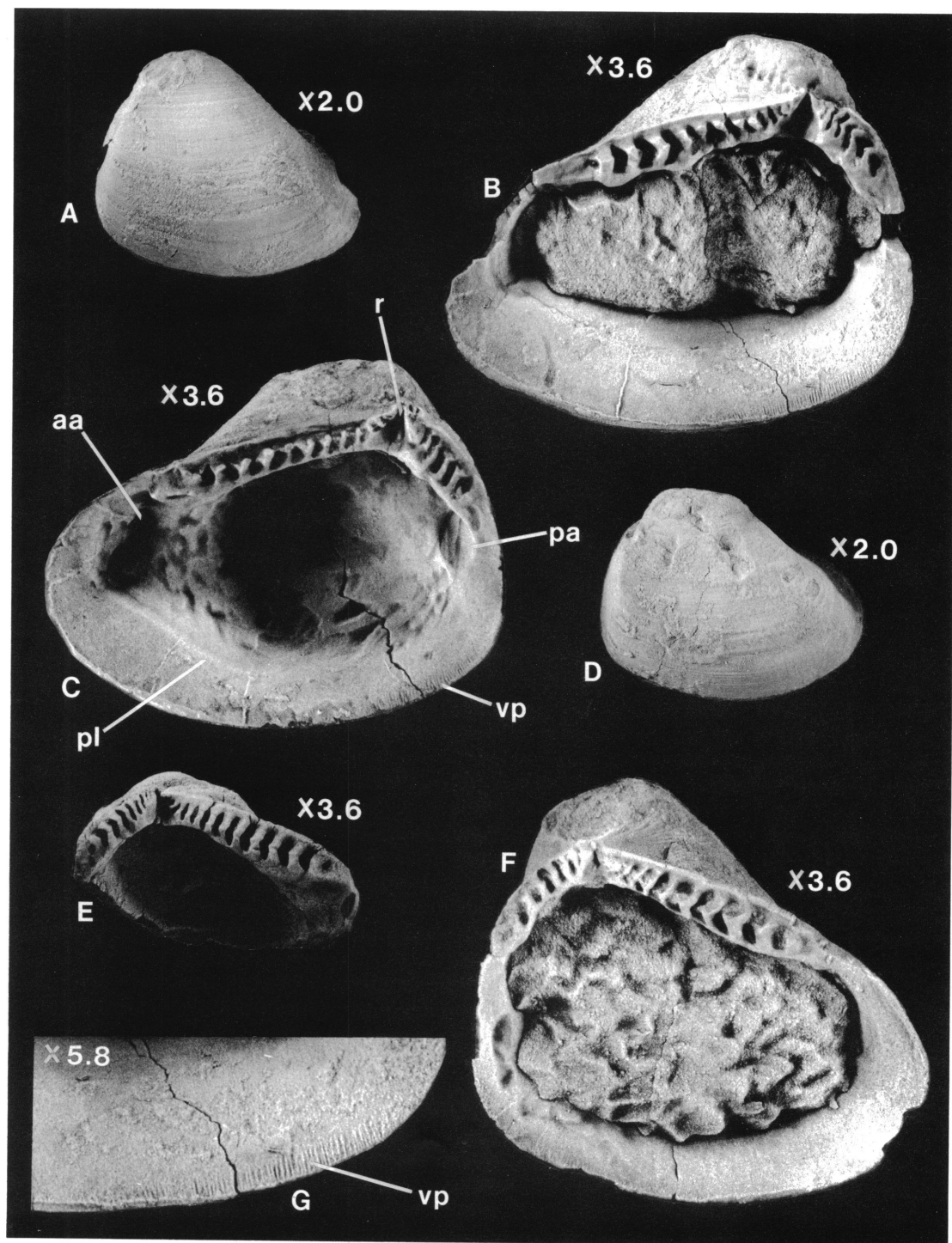


FIG. 26. *Nuculoidea deceptiformis*, new species (var. "A"). A, B, G. Holotype, a right valve (AMNH 36202) from AMNH loc. 3013. A. Exterior. B. Interior with hinge. G. Enlargement of inner, postero-ventral margin. C, D. Paratype, a right valve (AMNH 36204) from AMNH loc. 3017. C. Interior with hinge. D. Exterior. E. Hinge of left valve fragment (AMNH 36203) from AMNH loc. 3017. F. Paratype, a left valve with hinge (AMNH 36237B) from AMNH loc. 3012.

Abbreviations: aa—anterior adductor scar, pa—posterior adductor scar, pl—pallial line, r—resilifer, vp—ventral pectenations.

vious than in var. "A" owing to the greater strength of the growth lines in var. "B."

Dentition taxodont, consisting of an anterior and a posterior hinge tooth row each diminishing in strength as they converge beneath the umbones. Fixed to a narrow hinge plate, the teeth number 12 or 13 anteriorly, and at least six or seven posteriorly (fig. 26B, C) or as many as 10 (fig. 26E). They are trigonal or chevron-shaped blades (with similarly shaped corresponding sockets), very pronounced and erect in the anterior row or only slightly reclining toward the umbones. In the posterior row they are less pronounced, lower, more rounded and more steeply reclining toward the umbones.

The resilifer is an erect, equilaterally triangular hinge plate space beneath the convergence of the anterior and posterior hinge tooth rows. The flat floor of the resilifer forms no visible excavation into the hinge plate. Additionally, the structure does not protrude, as in most other nuculids, into the valve interior, the ventral limits of the structure remaining flush with the ventral border of the hinge plate.

Pallial line simple, emphasized and often pustulose along its upward curve toward the posterior adductor; it may appear either smoothly curving (figs. 26B, 29B) or may be broadly flattened to faintly sinuous along its anterior length.

Along the inner valve margins is a series of fine, striate, microdenticulations or micropectenations (fig. 26G) especially well defined posteroventrally.

The adductor scars are ovoid, subequal to equal in size, often curvilinearly striated (fig. 29H) in the familiar bivalvian manner. Pairs of small, ovate or slightly trigonal, anterior protractor and posterior retractor scars are preserved on internal molds (figs. 29, 30) lying just above the anterior adductors and posterior adductors, respectively. In addition, at least three "anterior retractor" scars were seen along anterior umbonal slopes of internal molds though the number and relative positions of these may vary from valve to valve and from specimen to specimen. "Dorso-medial" and "ventromedial" muscle scars are sometimes visible (though often very poorly defined) on the tips of the umbones of internal molds; commonly these appear to

be fused into a composite, bilobate scar (fig. 30) in a manner shown in other nuculids elsewhere by Driscoll (1964).

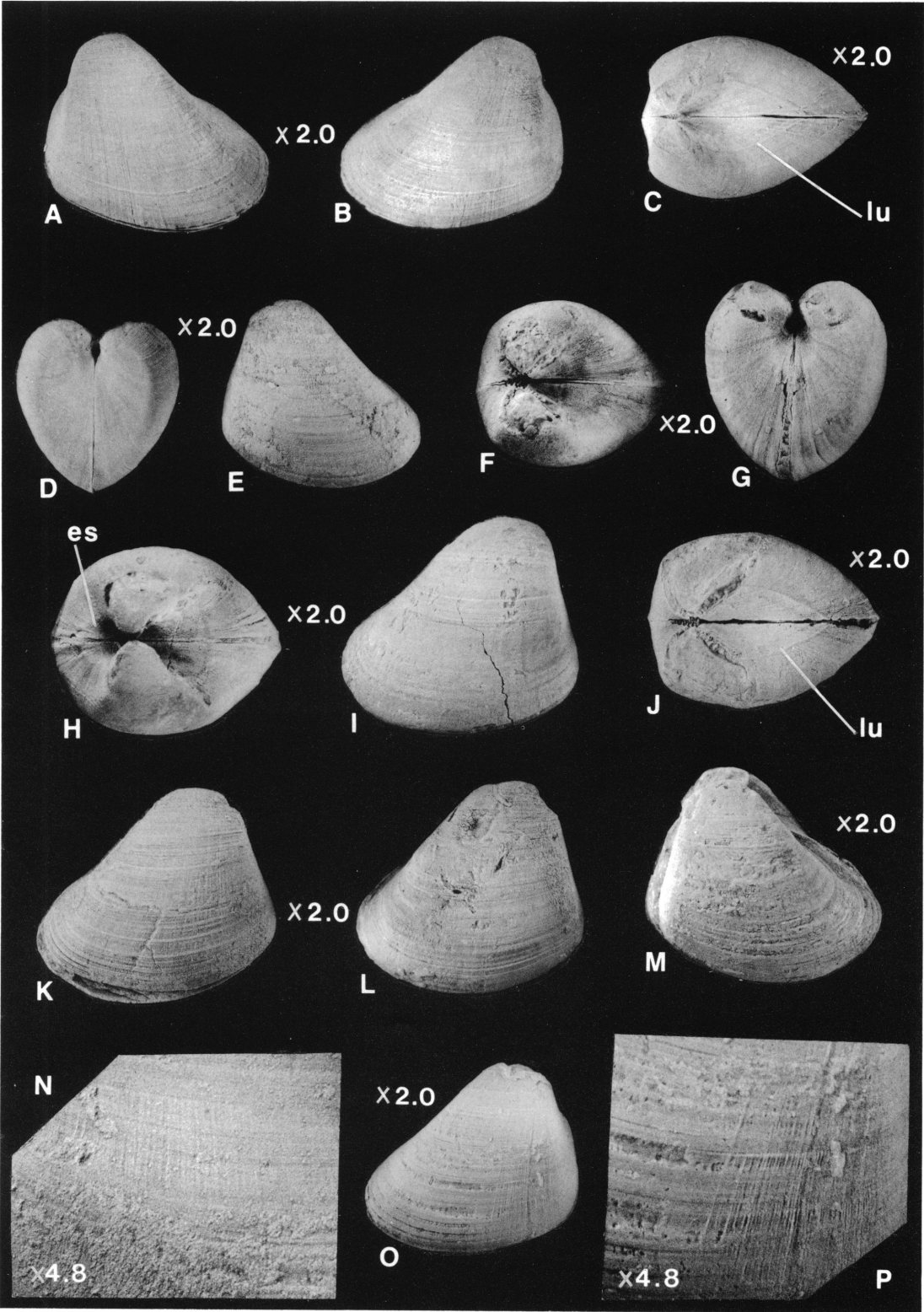
On internal molds a linear ridge (representing a weak groove on inner valve surfaces) extends diagonally in either valve from just below the juncture of the ventral margin of the posterior adductor scar and pallial line toward the umbonal region (fig. 29H). The ridge is subtle and can normally be seen only in low angle illumination; it has been consistently seen on several internal molds but may be absent in others.

Shell microstructure as described by Carter and Tevesz (1978b) consists of a nacreous layer composed of outer stacked nacre and inner simple nacre. Outer simple and fibrous prismatic layers are either absent or confined to earliest juvenile shell growth stages.

DISTRIBUTION: *Nuculoidea deceptriformis*, new species is apparently confined to the Solsville localities treated here.

REMARKS ON MORPHOLOGY: Many nuculoid families are superficially rather similar, but some, such as the Nuculanidae and Malletiidae, have posteriorly elongated shells, whereas others such as the Nuculidae are anteriorly elongate. Hence, valve orientation is critical for proper family placement. Confirmation that the elongated end of the valves in *N. deceptriformis* is truly the anterior is provided by three criteria. (1) Orientation can be determined by analogy to other nuculid species. (2) The teeth of the anterior hinge tooth row are longer, more erect and robust than those of the posterior tooth row. Bradshaw and Bradshaw (1971) showed that among palaeotaxodonts larger teeth are required anteriorly to maintain proper valve articulation during the extension of the foot which has the effect of increasing the dorsal gape in front of the umbones. (3) The position and arrangement of the dorsomedial, ventromedial, and anterior retractor scars along the anterior umbonal slopes of nuculid internal molds have been used by Driscoll (1964) in valve orientation; the muscular arrangements of *N. deceptriformis* seem homologous to those of Driscoll (but see Bradshaw, 1978).

The inner, marginal micropectenations and prosoponal radii are of similar strength, orientation, and spacing; moreover, both are



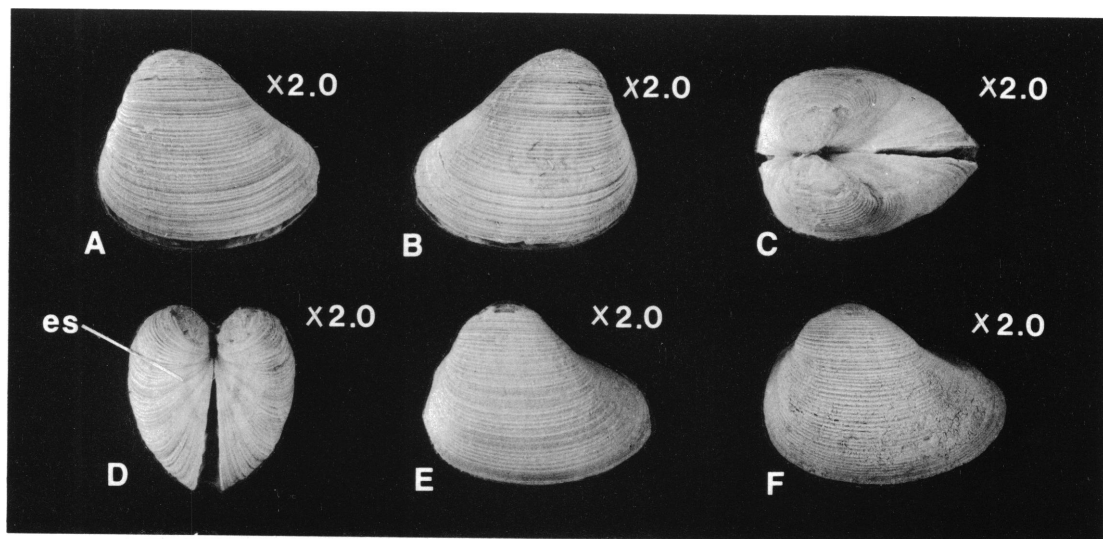


FIG. 28. *Nuculoidea decepitriformis*, new species (var. "B"). A–D. Paratype, gaping articulated specimen (AMNH 36241A) from AMNH loc. 3012. A. Right valve. B. Left valve. C. Dorsal view. D. Posterior view. E. Paratype, right valve of articulated specimen (AMNH 36241B) from AMNH loc. 3012. F. Paratype, right valve of articulated specimen (AMNH 36241C) from AMNH loc. 3012 showing rare form approaching *N. opima*.

Abbreviation: es—escutcheon.

emphasized posteriorly and reduced anteriorly in *N. decepitriformis*. This strongly suggests that both are merely different expressions of a single shell structural entity. That is, micropectenations are produced wherever prosoponal radii intersect shell margins. This is significant since the marginal micropectenations have been considered diagnostic of *Nuculoidea* (e.g., Vokes, 1949). But, since such delicate internal features are rarely preserved, the generic identity of many specimens would be difficult to confirm on this basis alone. The prosoponal radii, however, are commonly preserved in *Nuculoidea* and may be used as

evidence of the presence of micropectenations in the absence of preserved internal morphology.

The anterior sinuosity in the pallial line was observed on some internal molds of *N. decepitriformis* but not on others. A similar sinuosity has also been observed by the writer occasionally on internal molds of *N. opima* and *N. lirata* in the USNM collections (normally the pallial lines of the last two species are also smoothly curving). The significance of the sinuosity is uncertain; perhaps it is associated with some accommodative aspect

FIG. 27. *Nuculoidea decepitriformis*, new species (var. "A"). A–D. Paratype, an articulated specimen (AMNH 36237A) from AMNH loc. 3012. A. Right valve. B. Left valve. C. Dorsal view. D. Posterior view. E, F. Articulated specimen (AMNH 36206) from AMNH loc. 3012. E. Right valve. F. Dorsal view. G–I. Paratype, an articulated specimen (AMNH 36207) from AMNH loc. 3017. G. Posterior view. H. Dorsal view. I. Left valve. J. Paratype, dorsal view of articulated specimen (AMNH 36219) from AMNH loc. 3013. K. Left valve of articulated specimen (AMNH 36208) from AMNH loc. 3013. L. Left valve of articulated specimen (AMNH 36209) from AMNH loc. 3012. M. Right valve slightly approaching var. "B" of an articulated specimen (AMNH 36210), miscellaneous Solsville. N. Enlargement of prosopon of holotype (AMNH 36202) showing radial and concentric elements. O. Left valve approaching var. "B" of an articulated specimen (AMNH 36205) from AMNH loc. 3012. P. Posteroventral enlargement of prosopon of AMNH 36205 showing radial and concentric elements.

Abbreviations: es—escutcheon, lu—lunule.



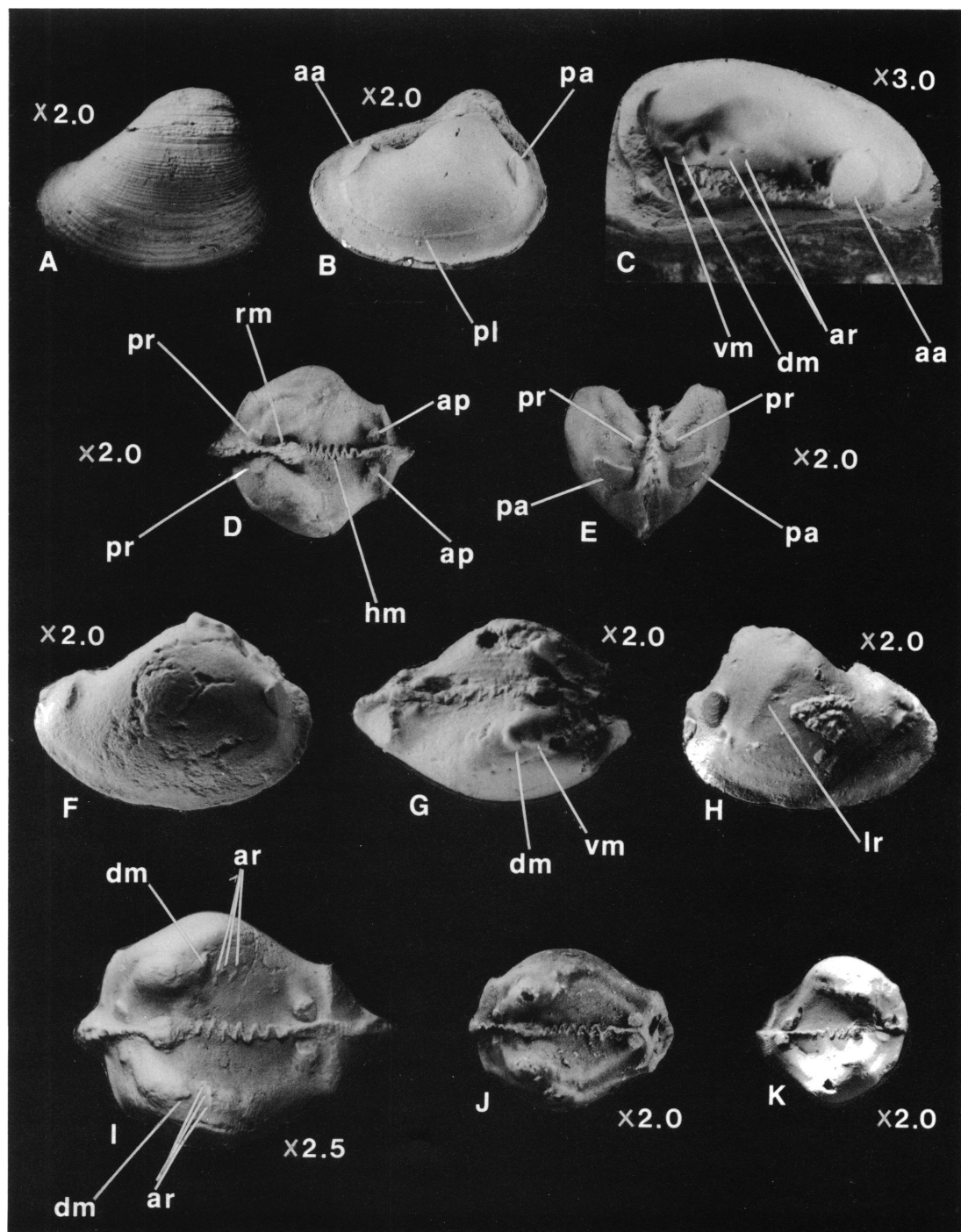


FIG. 29. *Nuculoidea deceptriiformis*, new species from AMNH loc. 3013. A–C. Paratype (AMNH 36164A, B), articulated specimen with internal mold (var. “B”). A. Left valve. B. Left view of internal mold, same valve removed. C. Dorsoanterior view of same internal mold. D, E. Paratype (AMNH 36165B), internal mold. D. Dorsal view. E. Posterior view. F, G. Internal mold (AMNH 36211). F. Left view. G. Left dorsolateral view. H. Paratype (AMNH 36165D) internal mold, right view. I. Paratype (AMNH 36165E), internal mold, dorsal view. J. Paratype (AMNH 36165A), internal mold, dorsal view. K. Paratype (AMNH 36165C), internal mold, dorsal view.

**Abbreviations:** aa—anterior adductor scar, ap—anterior protractor scar, ar—“anterior retractor” scar, dm—“dorsomedian” scar, hm—hinge tooth series mold, lr—lateral ridge, pa—posterior adductor scar, pl—pallial line, pr—posterior retractor scar, rm—resilifer mold, vm—“ventromedian” scar. See comments on accessory musculature in figure 30.



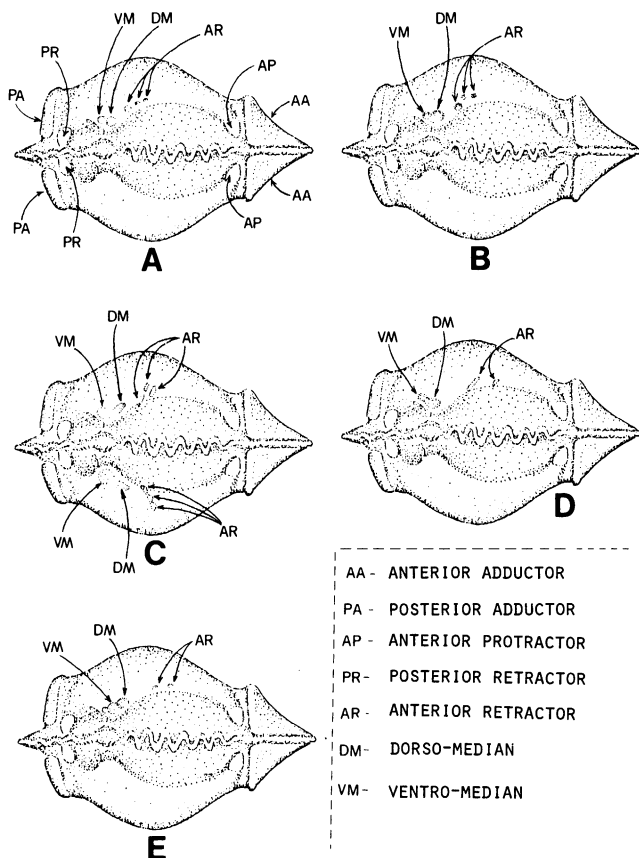


FIG. 30. *Nuculoidea deceptriformis*, new species. Variation in musculature attachment based upon various Solsville internal molds. Dorsal outlines of the molds shown are idealized. DM, VM, and AR are provisionally identified. Bradshaw (1978) considers scars like AR to be anterior visceral floor muscles. Occurrence of both DM and VM near summit of umbonal cavity (VM slightly forward of DM) is suggested by figures of Driscoll (1964). Both (esp. VM) are placed more laterally (off summit) in many post-Paleozoic genera.

of pedal retraction and extension in certain large-footed individuals.

Function of the dorsomedian and ventro-median muscles has been regarded as uncertain. Heath (1937) and Driscoll (1964) suggested that they are related to control of the foot. Bradshaw (1974) considered them to be pericardial muscles but more recently (1978) has linked them with attachment of the floor of the visceral cavity.

Prosopon varieties "A" and "B" are likely to be genetic or, perhaps to an extent, environmental; they are not the result of differential preservation since both varieties are found among comparably well-preserved specimens. Var. "A" is quite distinct from other Devonian nuculids; var. "B," however, approaches the morphology of *N. opima* although the latter remains distinctive in its greater anterior elongation, smaller, lower umbones, less truncate posterior and normally more strongly developed growth var-

ices. One var. "B" specimen (fig. 28F), nevertheless, shows a shell form bridging the gap between *N. opima* and var. "B." These morphological similarities strongly suggest that *N. deceptriformis* is a local species derived from the more widespread *N. opima*.

COMPARISONS: Of the various species described in the literature, *N. deceptriformis*, new species is most nearly similar to the type species, *N. opima*. However, it can be readily distinguished from the latter by its taller, more inflated, subangular umbones; its relatively shorter length, abruptly truncated posterior, and more strongly trigonal outline; its lack of any appreciable anterodorsal marginal flange; its more nearly continuous radial ornament and more poorly developed growth lines and growth varices; and its lack of outer simple and fibrous prismatic shell layers reported in *N. opima* by Carter and Tevesz (1978b).

The results of simple bivariate statistical

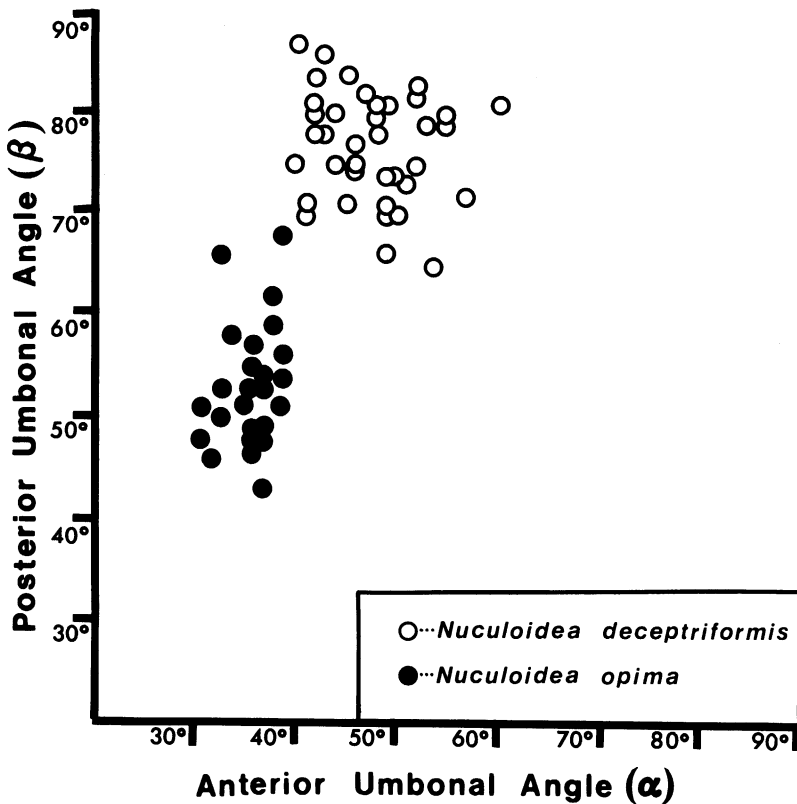


FIG. 31. Bivariate statistical comparisons of anterior and posterior umbonal angles in Solsville *Nuculoidea deceptriiformis*, new species and the type species, *N. opima* (Hall) from the USNM collections.

comparisons are shown in figures 31 and 32. The group of randomly selected *N. opima* specimens with which *N. deceptriiformis* was compared are from several lots from the Hamilton (Delphi) of New York in the collections of the National Museum of Natural History (USNM nos. 101711–101714 and 226024). Good statistical separations were obtained through analysis of variance using both *t* and *F* statistics and through regression analysis.

Besides *N. deceptriiformis*, only two or possibly three other morphologically well represented species are known from North America. These are:

1. *Nuculoidea opima* (Hall), 1843. (= *Nucula randalli* Hall and Whitfield, 1869). Lectotype: AMNH 5284/1 and 2a. Paratypes: AMNH 5284/1 and 2b, 5284/1 and 2c as designated by McAlester (1968). A larger, more ovoid species often with anterodorsal commissural flange, pronounced fasciculate growth lines,

discontinuous prosoponal radii, rounded posterior, enlarged, elongated anterior, and small, low, posteriorly placed umbones. A common species widely distributed in Middle Devonian (Hamilton) shales in eastern North America. Interior described by Vokes (1949) as earlier noted. Possibly conspecific, at least in part, with several German Lower Devonian forms figured by Beushausen (1895, pl. 4) which are obviously oversplit: "*Nucula*" *forficata* Goldfuss, "*Nucula*" *pelmensis* Beushausen, "*Nucula*" *sandbergeri* Beushausen and "*Nucula*" cf. *lodanensis* Beushausen.

2. *Nuculoidea corbuliformis* (Hall and Whitfield), 1869. Hall's (1883, 1885) figured specimens of this species are AMNH 5282/1: 46-29, 5281/1: 46-32, 5281/1: 46-35, 36; and NYSM 2843–2850. Shells equilaterally sub-trigonal with prominent, almost middorsally placed umbones and fasciculate growth lines. The most common and most widely distributed species. Middle-Upper Devonian of eastern and midwestern North America. Interior undescribed in the literature; a fine specimen

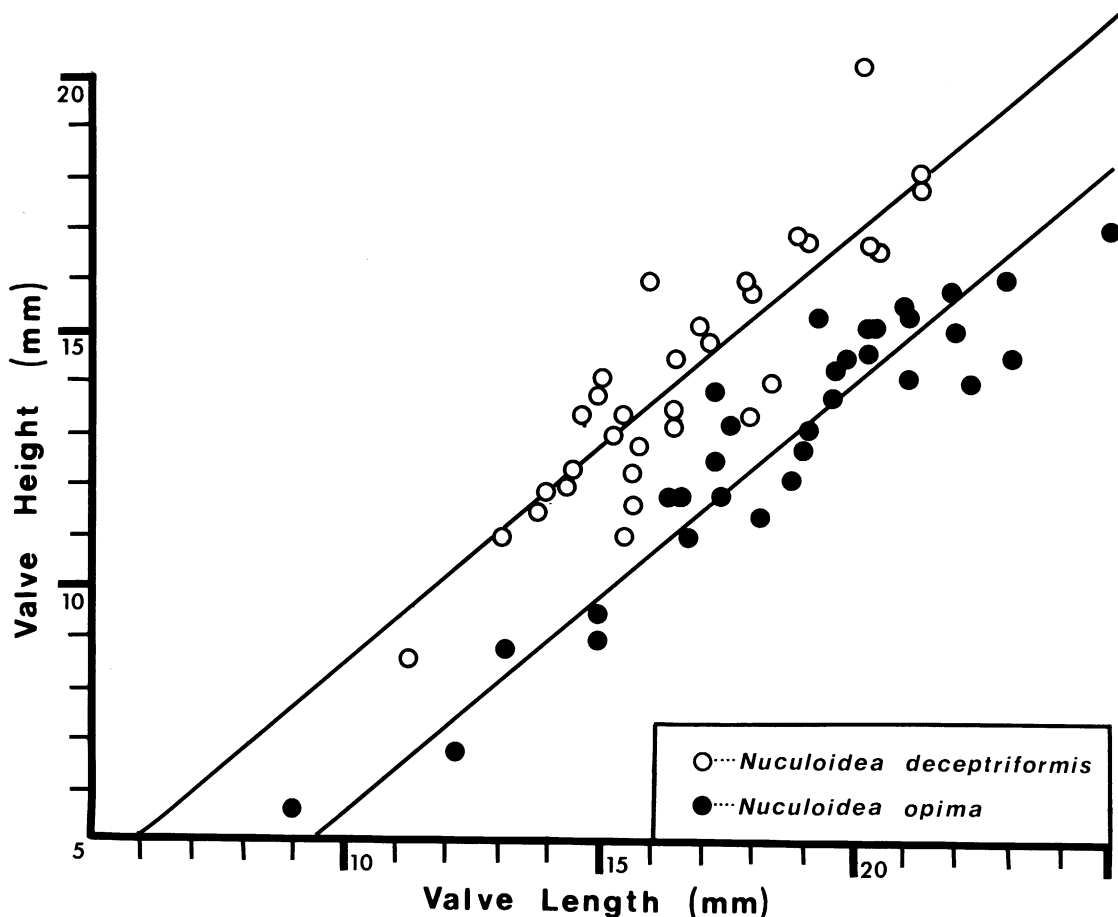


FIG. 32. Bivariate statistical comparisons of valve lengths and heights in Solsville *Nuculoidea deceptriformis*, new species and the type species, *N. opima* (Hall), from the USNM collections.

from the Skaneateles of New York shows the characteristic hinge and resilifer. Probably conspecific with the Middle and Lower Devonian German species: "*Nucula*" *aquisgranensis* Beushausen (Givetian), "*Nucula*" *triгона* Spriestersbach (Emsian), and "*Nucula*" *macrorhyncha* Spriestersbach (Emsian).

3. *Nuculoidea lirata* (Conrad), 1842. Hall's (1883, 1885) figured specimens of this species are AMNH 5282/2: 45-11, AMNH 5281/1: 45-5, and NYSM 2856-2861. Tentatively recognized. Identical to *N. opima* except for coarsely lirate, normally nonfasciculate growth lines. However, many specimens are intermediate between *N. opima* and *N. lirata* suggesting a morphocline. Perhaps *N. lirata* is merely a prosopon variety of *N. opima*; if so, the former deserves priority. Common in Middle Devonian Hamilton shales.

Other Devonian species either mistakenly assigned to *Nucula* or *Nuculoidea* or too poorly preserved for recognition include:

1. "*Nucula*" *varicosa* Hall and Whitfield, 1869, "*Nucula*" *bellistriata* (Conrad), 1841; "*Nucula*" *subelliptica* Hall, 1883; "*Nucula*" *umbonata* Hall, 1883; and "*Nucula*" *globularis* Hall, 1885. Hinges and internal molds show these species to be carydiids, not nuculids (Bailey, 1979a, and ms).
2. "*Nucula*" *diffidens* Hall, 1885. Upper Devonian (Chemung), New York. Based on composite molds lacking hinge data. Two syntypes (AMNH 42068, 42069) were originally figured as part of *Nucula randalli* (= *Nuculoidea opima*) by Hall (1883, pl. 45, figs. 12, 14). One (AMNH 42069) suggests *N. opima*, but both are similar to elongated examples of *N. cor-*

- buliformis* seen occasionally (e.g., McAlester, 1962a, pl. 3, figs. 16, 17).
3. "*Nucula*" *hanoverensis* Kindle, 1901 from the Jeffersonville Limestone of Indiana. The large holotype (USNM 62190) is an internal mold showing taxodont hinge and inner features; no other specimens known. This species is a ctenodontid not a nuculid; here assigned to *Praectenodonta* Philip, 1962.
  4. "*Nucula*" *lamellata* Hall, 1883. One Chemung specimen of *Nuculoidea corbuliformis* was evidently mislabeled by Hall (1885, pl. 45, fig. 13) as *Nucula lamellata*. All of Hall's other figures (1885, pl. 51, figs. 18–21, pl. 93, fig. 7) show a small, lirate, nonnuculid Hamilton species with unknown hinge; a probable ctenodontid assignable to *Praectenodonta*. Syntypes: AMNH 5183/1: 51-20, 6119/1: 45-13; NYSM 2852–2855.
  5. "*Nucula*" *niotica* Hall and Whitfield, 1872, and "*Nucula*" *neda* Hall and Whitfield, 1872 from the Sellersburg near Louisville, Kentucky. Poorly preserved, known mostly from internal and composite molds; hinge and accessory musculature show nuculid affinities. Figured by Hall (1883, 1885). One specimen of "*N.*" *neda* (in Hall, 1885, pl. 45, fig. 2) is posteriorly truncate like *N. deceptriformis* but the prosopon seems more lirate. All other figures of Hall suggest the form of *N. corbuliformis*. Plesiotypes of "*N.*" *niotica* (USNM 51301) and "*N.*" *neda* (USNM 51374) support the conclusion that both are junior synonyms of *N. corbuliformis*.
  6. "*Nucula*" *herzeri* Nettleroth, 1889 from the Sellersburg near the Falls of the Ohio River. Nettleroth's poorly preserved syntypes (USNM 51300) strongly suggest the form and prosopon of *N. corbuliformis*.
  7. "*Nucula*" *rescuensis* Walcott, 1884 from the Middle Devonian Nevada Limestone of Nevada. Known from a single specimen. Probably not a nuculid; no hinge data preserved. *Eoschizodus*?
  8. "*Nucula*" *snyderensis* Branson, 1924 from the Upper Devonian (Fingerlakesian-Chemungian) Snyder Creek Shale, Missouri. Known from internal molds which are posteriorly elongate and sinupalliate; McAlester (1963) correctly identified these as *Palaeoneilo constricta* (Conrad).
  9. I have examined the holotypes of several early Devonian (Helderbergian) species from the Chapman Sandstone of Maine described by Williams and Breger (1916) including "*Nuculoidea*" *bellatula* Williams and Breger (USNM 59783), "*Nuculoidea*" *aquisgranensis* (Beushausen) (USNM 59785), "*Nuculoidea*" *trigonale* Williams and Breger (USNM 59786) and "*Nuculoidea*" *cordata* Williams and Breger (USNM 59784). In each case preservation is too poor for generic or even superfamilial determination.
  10. "*Nucula*" *manitobensis* Whiteaves, 1892 from the Middle Devonian (Cazenovian) of Lake Winnipegosis, Manitoba, Canada. Hinge and interior unknown. Shape as in "*N.*" *varicosa-bellistriata* above. Varices weak; shape more trapezoidal. Probably not a nuculid. A carydiid?

**AUTECOLOGY:** Broad tolerances of substrate, temperature, pressure and salinity are indicated among Recent nuculids which are all nonsiphonate, infaunal deposit feeders. Among the most significant factors influencing their present distribution are temperature and substrate, a preference for temperate to cold subtidal muddy bottoms being reported. Bruun (1957) found *Nucula* in abyssal muds of Pacific Ocean trenches at hostile temperatures and pressures. Sanders (1958), however, noted that *Nucula* is common in the cool, shallow (11 m.), brackish muds of Buzzards Bay. Morris (1973) reported the distribution of *Nucula* to extend as far south as Florida, and Mexico although cooler, deeper waters seem preferred in the lower latitudes. Temperature and depth preferences of modern *Nucula* thus contrast sharply with those of *Nuculoidea* which was evidently confined mostly to warm, shallow marine environments (see Paleoecology section of present paper).

Despite apparent preferences for soft muds, nuculid occurrences in coarser substrates are common. *Nuculoidea deceptriformis*, for example, is common in both the argillaceous and sandy/silty facies of the Solsville although abundances in the latter are diminished. "*Nucula*" (= *Nuculoidea*) has been reported in greywacke sandstones (Beushausen, 1895) as well as limestones (Nettleroth, 1889; Kindle, 1901; Yang, 1939; LaRocque, 1950). Yonge (1939) reported the occurrence at Plymouth, England, of large species of *Nucula* in shell gravels, smaller species in muddy sand mixed with gravel, and the smallest species in muddy sand or silt.

Stanley (1970) using X-ray techniques determined that in aquaria living *Nucula* frequently does not assume the posture traditionally attributed to it, i.e., umbones up, commissure vertical and hinge line horizon-

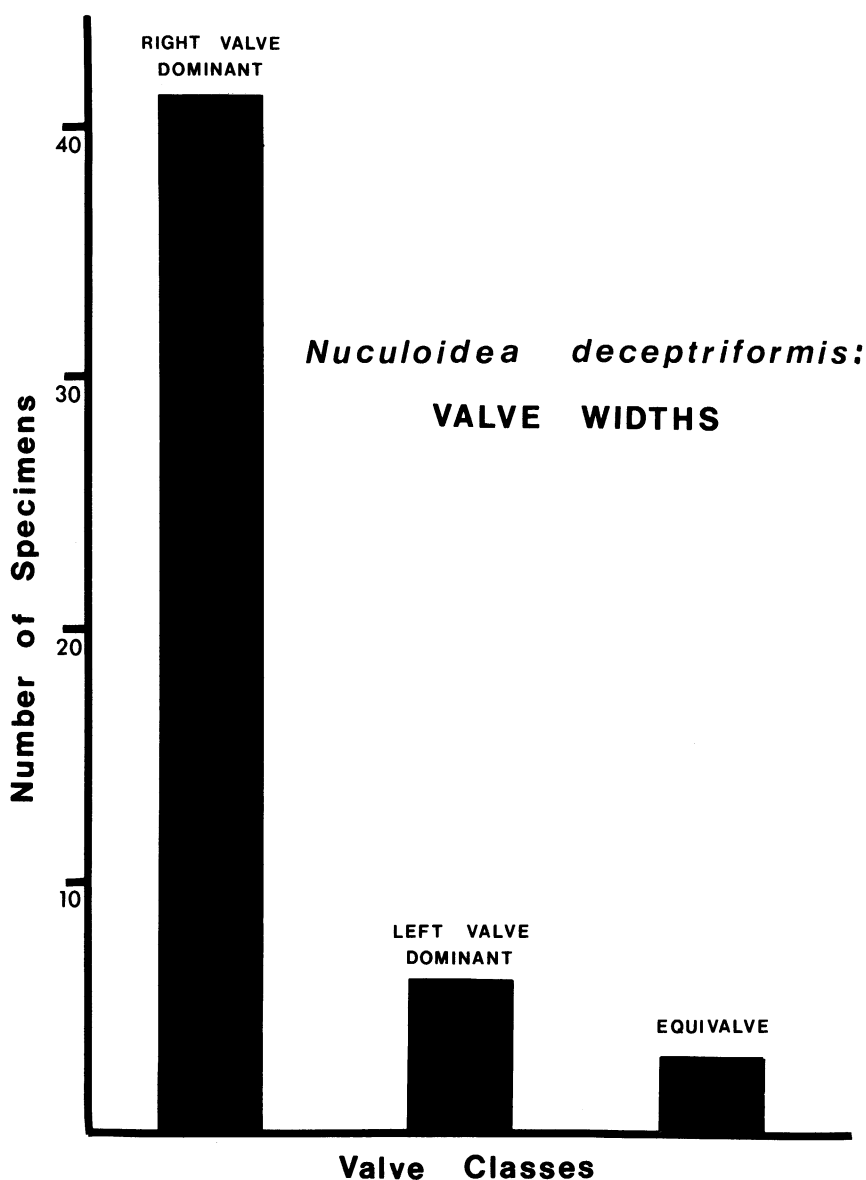


FIG. 33. *Nuculoidea deceptriiformis*, new species. Valve width asymmetry.

tal (see fig. 2 of Yonge, 1939). Instead, Stanley discovered that *Nucula* often reclines on one valve or the other. Bradshaw (1974) described "*Nuculoidea*" *vespa* and "*Nuculoidea*" *umbra*<sup>3</sup> from the Devonian of New Zealand as being slightly inequivalved (though

<sup>3</sup> Generic names are placed in quotation marks because I believe there to be some doubt about the suitability of applying *Nuculoidea* to these species since both lack radial markings and micropectenate inner margins.

one particular valve was not apparently favored over the other) and attributed this inequality to a typically reclining life position (see Bradshaw's fig. 16). Very slight valve asymmetry is also noted here in *N. deceptriiformis*, new species. It would, however, appear unlikely that this condition is the result of a reclining mode of life because virtually all the articulated specimens of *N. deceptriiformis* I personally collected were apparently in life position, and the valve orientation was

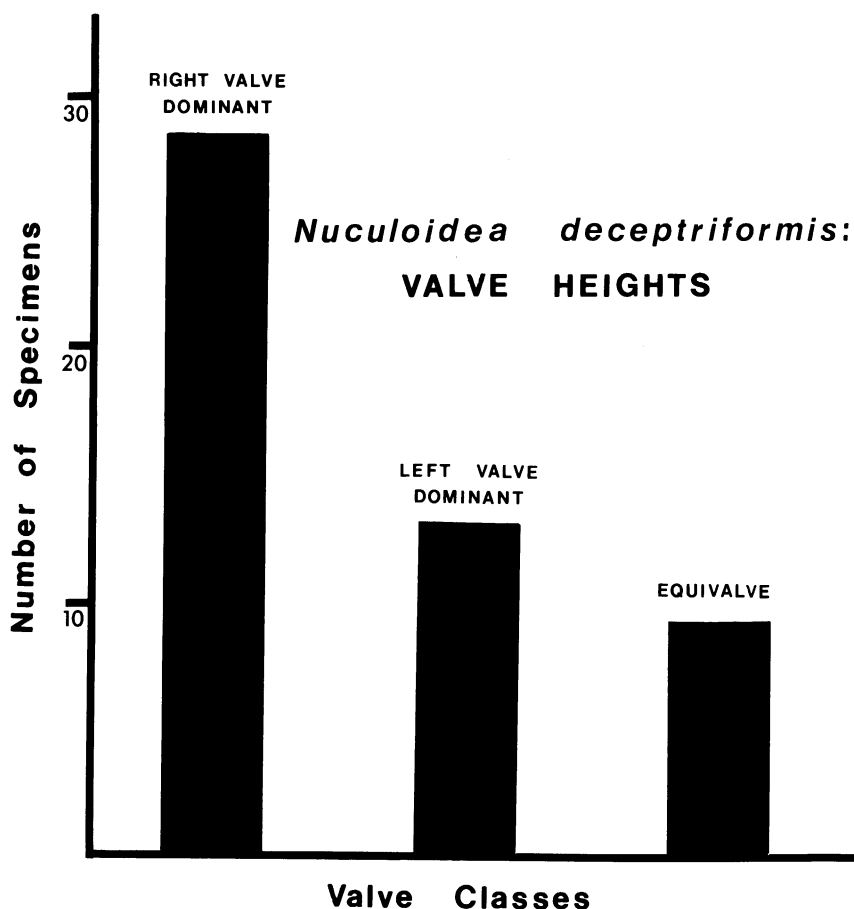


FIG. 34. *Nuculoidea deceptriformis*, new species. Valve height asymmetry.

similar to the "typical" nuculid position of Yonge (1939) described above. Furthermore, a number of these as well as specimens of *N. opima* in the USNM and NYSM collections exhibit evidence of dorsoventral crushing due to diagenetic compaction suggesting a vertical commissure, umbones upward as a common *in situ* attitude of the shells. As indicated in figures 33–35, the right valve appears to be favored in both *N. deceptriformis* and *N. opima*. Conceivably this asymmetry reflects the arrangement of internal organs. One possible explanation for this condition is the displacement of the intestine into the right valve, a condition common among all members of the Nuculidae (Yonge, 1939). Pelseneer (1891) believed the coiling to the right side of the gut was primitive, an indication of the fundamental asymmetry he ascribed to prim-

itive molluscs although Stempell (1898) believed it to be secondary. Drew (1901) showed that the gut bends to the right during embryonic development. Such development, if pronounced enough, might be sufficient to induce the right valve to be secreted with a slightly greater convexity than the left.

SUPERFAMILY NUCULANACEA  
ADAMS AND ADAMS, 1858  
FAMILY MALLETIIDAE  
ADAMS AND ADAMS, 1858  
GENUS *NUCULITES* CONRAD, 1841

TYPE SPECIES: *Nuculites oblongata* Conrad, 1841 (= *N. oblongatus* of later authors) by subsequent designation of Hall (1885; Hall in the same work designated *N. cuneiformis* Conrad as an alternate type species) and Mil-

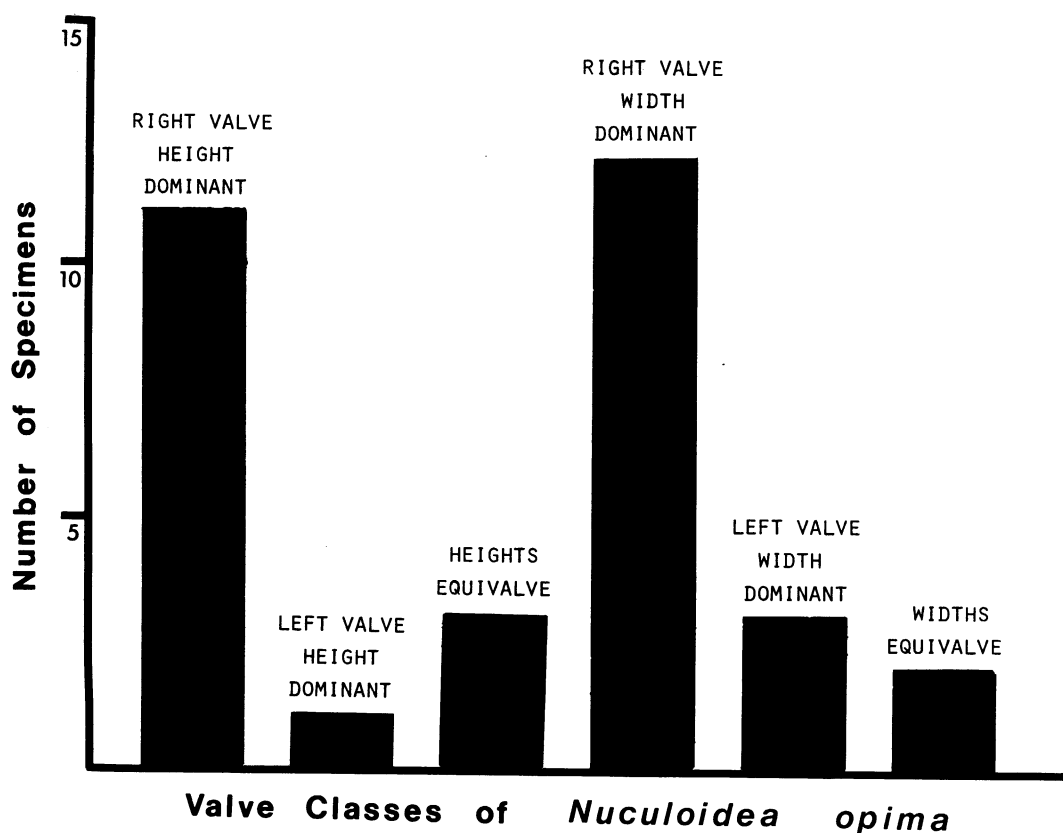


FIG. 35. *Nuculoidea opima* (Hall). Valve asymmetry. From the USNM collections.

ler (1889) from the "Sherburne Group" near Smyrna, Chenango County, New York. Cooper (1934), Cooper et al. (1942), and Oliver et al. (1969) show the Sherburne Mbr., Genesee Formation, to be Upper Devonian (Fingerlakesian) in age; McAlester (1968) maintained that the "Sherburne Group" was equivalent to the Middle Devonian Hamilton of modern nomenclature.

**GENERIC USAGE:** *Nuculites* Conrad, 1841 (= *Cleidophorus* Hall, 1847, *Cucullella* M'Coy, 1851, and *Pyrenomoeus* Hall, 1852), following McAlester's (in Moore, 1969) usage, is applied here to nuculoids like *Palaeoneilo* Hall and Whitfield but with a pronounced, internal, anterior clavicle or septum. According to Pohl's (1929) diagnosis, *Nuculites*, unlike *Palaeoneilo*, has both a septum and a resilifer. However, neither the Solsville material, the literature (e.g., McAlester, 1968) nor even Pohl's own figures support the existence of a resilifer in *Nuculites*. Some *Pa-*

*laeoneilo* in the literature show a short, broad, incipient clavicle like that of *Nuculites*, but it is never so narrowly elongate.

*Ditichia* is a Lower Devonian Rheinisch genus proposed by Sandberger (1891) for small, *Nuculites*-like shells bearing two internal septa. Unfortunately, Sandberger's sole species (i.e., the type species by monotypy), *Ditichia mira* (= *Leda? mira* Beushausen, 1884), is invalid as it is a *Ctenodonta*-like shell showing none of the diagnostic features attributed to *Ditichia* (e.g., see the photos of the holotype in McAlester, 1968, pl. 2, figs. 1-3 and McAlester, fig. A1,6 in Moore, 1969; see also remarks of Williams and Breger, 1916, p. 168, and Solle, 1936, p. 193). Described material closest to Sandberger's diagnosis are the small, ovate, taxodont shells with twin septa figured as *Cucullella elliptica* Maurer (= *Nuculites ellipticus* of later authors) by Beushausen (1895, pl. 5, figs. 12-14) who considered *Ditichia* to be the young of *Cucullella* and, hence, ge-



nerically synonymous. I reject Beushausen's conclusion on the following basis: (1) The holotype of *N. ellipticus* (Maurer) in Maurer (1902, pl. 51, fig. 18) is very small (a probable juvenile) but shows the same shell form and single septum as the adults. (2) Beushausen's supposed juveniles are almost identical (except for his pl. 5, fig. 15) with two specimens with twin septa called *Ditichia* cf. *elliptica* by Clarke (1909, pl. 16, figs. 7, 8) from the Moose River Sandstone (Lower Devonian) of Maine. While preserving the form of Beushausen's "juveniles," Clarke's specimens are much larger, attaining the length of average adults of described specimens of *N. ellipticus* and *N. oblongatus* and, hence, are not juveniles.

On these grounds *Ditichia* would seem to be a separate genus after all but lacks a type species. Therefore, a neotype is here nominated: plate 5, figure 12 of Beushausen (1895), originally designated *C. elliptica* Maurer. Since Solle (1936) suggested the name *Nuculites persulcatus* for the same specimen, the emended new type species is here designated *Ditichia persulcata* (Solle).

*Nuculites oblongatus* Conrad, 1841

Figures 5E, 6H, 36–37,  
39 (nos. 16, 17, 19, 20), 43B

*Nuculites oblongata* Conrad, 1841, p. 50, fig. 8. Hall and Whitfield, 1869, p. 4. Hall, 1883, pl. 47, figs. 1–12. Williams, 1917, p. 30. Willard, 1939, p. 476, pl. 26, figs. 15, 16.

*Nuculites oblongatus* Conrad. Miller, 1877, p. 198; 1889, p. 496. Hall, 1885, p. 324, pl. 47, figs. 1–12. Lesley, 1889, p. 475, fig. 3. Grabau, 1899, p. 254, fig. 170; 1906, p. 330. Whitfield and Hovey, 1900, p. 292. Clarke and Ruedemann, 1903, p. 465. Grabau and Shimer, 1909, p. 398, fig. 509a–c. Prosser and Kindle, 1913, pp. 107, 231, pl. 25, figs. 17–19 [not fig. 20]. Stauffer, 1916, p. 477. Williams, 1917, p. 30. Stumm, 1942, p. 557. Shimer and Shrock, 1944, p. 377, pl. 146, figs. 13, 14. Ellison, 1965, p. 121, pl. 14, figs. 16–20, [?] pl. 14, fig. 28, labeled *Palaeoneilo constricta*. Babin, 1966, p. 103; 1973, p. 42. Palmer and Brann, 1966, pl. 15, figs. 14–16. McAlester, 1968, p. 37, pl. 28, figs. 1–17; 1969, p. N233, fig. A5,7 (in Moore). Bailey, 1975, p. 167, pl. 12, figs. 1–15, text-figs. 25–27; 1978a, p. 121. Wilson, 1975, p. 126. Carter and Tevesz, 1978b, p. 865.

*Cucullella oblongata* (Conrad). Beushausen, 1895, p. 105.

[?] *Nuculites* cf. *N. oblongatus* (Conrad). Cooper and Cloud, 1938, pp. 445, 452, pl. 55, fig. 3.

[?] *Nuculites* cf. *oblongatus* Conrad. Clarke, 1909, pl. 111, pl. 28, fig. 11.

*Nucula? oblonga* Hall, 1843, p. 197, fig. 78, no. 3; 1885, p. 234. [= *Nuculites oblonga* Hall. Whiteaves, 1892, p. 302. Stumm, 1951, p. 32. = *Nuculites oblongus* Hall. Miller, 1877, p. 198. Kindle, 1912, p. 89. Williams and Breger, 1916, p. 174. = *Cleidophorus oblongus* Hall. Miller, 1877, p. 187. Lesley, 1889, p. 133.]

† *Nuculites milwaukeeensis* Cleland, 1911, p. 100, pl. 20, fig. 5. [In part = *Palaeoneilo milwaukeeensis* (Cleland). Pohl, 1929, p. 32, pl. 3, fig. 17 (not figs. 16, 18–25).] [Not *Palaeoneilo* cf. *plana*. Cleland, 1911, p. 104, pl. 20, figs. 15, 16 (=synonym of Pohl, 1929, p. 32).]

†[?] *Nuculites modulatus* Kindle, 1912, p. 89, pl. 7, figs. 13, 14.

†[?] *Cleidophorus perovalis* Williams and Breger, 1916, p. 161, pl. 25, figs. 2, 10.

†[?] *Palaeoneilo plana* Hall [and Whitfield]. Clarke and Swartz, 1913 [in part], p. 621, pl. 61, figs. 1, 3 [not fig. 2]. [Not *P. plana* Hall and Whitfield, 1869, p. 7. Hall, 1883, pl. 48, figs. 21–28; 1885, p. 334, pl. 48, figs. 21–28.]

*Cucullella elliptica* Maurer, 1886, p. 15; 1902, p. 51, pl. 15, fig. 18. Beushausen, 1895 [in part], p. 104, pl. 5, figs. 9–11, 15[?], [not] figs. 12–14. [In part of various other authors. See other ref. in Maillieux, 1937, pp. 189–190.]

*Cucullella* (*Cleidophorus*) *elliptica* (Maurer) [sic]. Williams and Breger, 1916, p. 395 [in part]. [This is *C. elliptica sensu* Beushausen.]

*Nuculites ellipticus* (Maurer). Kegel, 1913, p. 73. [In part of various authors. See other ref. in Maillieux, 1937, p. 190. Babin, 1966, p. 97, pl. 3, fig. 8[?]; 1973, p. 43, pl. 1, fig. 5 and esp. 7, pl. 2, figs. 6–9 [esp. fig. 8]. See other ref. in Babin, 1973, p. 44.]

*Nuculites* (*Ditichia*) *ellipticus* Maurer [sic]. Viëtor, 1919, p. 395 [in part]. [This is *C. elliptica sensu* Beushausen.]

[?] *Nuculites* cf. *oblongatus* Conrad and *ellipticus* Maurer [sic]. Clarke, 1907, p. 364; 1909, p. 111, pl. 28, fig. 11.

†[?] *Nuculites ellipticus longus* Mauz, 1933, p. 285, fig. 9; 1935, p. 57. [= *Nuculites longus* (Mauz). Solle, 1936, pp. 195, 197, fig. 4.] Dahmer, 1942, p. 284, figs. 16–18.

*Nuculites ellipticus ellipticus* Solle, 1936, pp. 195, 196, fig. 1. [= *N. beushauseni beushauseni* Mauz.] [Not *N. ellipticus ellipticus* Mauz, 1935. = Beushausen, 1895 [in part], pl. 5, fig. 12. = *N. persulcatus* Solle, 1936, pp. 195, 197, fig. 5. = *Ditichia* cf. *elliptica* (Maurer) Clarke, 1909, p. 78, pl. 16, figs. 7, 8.]

- Cucullella beushauseni* Fuchs, 1912, p. 67.  
*Nuculites beushauseni* (Fuchs). Wolf, 1930, p. 43.  
 Mauz, 1933, p. 284. [= *C. elliptica* Maurer of Beushausen, 1895 (in part), pl. 5, fig. 9. = *N. beushauseni beushauseni* Mauz.]  
 †[?] *Nuculites beushauseni expansus* Mauz, 1933, p. 285, fig. 10; 1935, p. 57. Solle, 1936, p. 195, fig. 2.  
 [?] *Nuculites beushauseni brevis* Mauz, 1933, p. 285, fig. 11a, b; 1935, p. 57. [= *N. ellipticus brevis* (Mauz). Solle, 1936, p. 195, fig. 3.] [Synonym of *N. ellipticus* (Maurer) according to Babin, 1966, pp. 97–98.]  
*Nuculites beushauseni beushauseni* Mauz, 1935, p. 57. [= *N. beushauseni* Fuchs, 1912. = *N. ellipticus ellipticus* Solle not Mauz.] Maillieux, 1937, p. 188, pl. 10, fig. 14[?] [labeled *N. beushauseni beushauseni* (Kegel) [sic].]  
 †[?] *Cucullella Vaissierei* Leriche, 1912a, p. 39, pl. 6, figs. 5, 6; 1912b, p. 32, text-fig. 2, pl. 2, figs. 1–3. [= *Nuculites vaissierei* (Leriche). Maillieux, 1937, p. 187, fig. 8. See also Maillieux's later ref.]  
 †[?] *Nuculites affinis* (Beushausen). Babin, 1966, pl. 3, fig. 1. [Not *N. affinis* (Beushausen), 1889, p. 217, pl. 4, fig. 8; 1895, p. 108, pl. 5, figs. 21, 22.]  
 [not] *Ditichia mira* Sandberger, 1891, p. 104 [= *Leda? mira* Beushausen, 1884, p. 90, pl. 3, fig. 15. Synonym of *C. elliptica* in Beushausen, 1895, p. 104, and Maurer, 1902, p. 51. But see Williams and Breger, 1916, p. 168 and McAlester, 1968, pl. 2, figs. 1–3.]

**DESCRIPTION:** Shells thin, medium-sized, equivalve, posteriorly elongate, laterally compressed. Shell shape variable; moderately to eccentrically elliptical, the major axis oriented anteroposteriorly. Posterior margin gently curving to subrectangular, sometimes with a faint sinuosity (also evident on internal molds).

Umbones weak, anteriorly placed, faintly elevated above the dorsal shell margins.

Prosopon variable, consisting of fine, concentric growth lines (often poorly defined) with variably developed, concentric lirae or weak to moderate undulaform rugae. The prosopon is often so faint and amorphous, even among specimens with well-preserved shell remnants (fig. 36H, K, M), that shells appear smooth and almost featureless. Other specimens, however, may possess a somewhat more irregularly lirate and rugose ornamentation (fig. 36P, O).

Internal molds and two shell interiors indicate a strong, narrow, gently arcuate, internal clavicle or septum extending vertically downward or obliquely forward just in front of the umbones. It is sharply defined dorsally, becoming progressively less defined ventrally where it faintly curves posteriorly.

Two hinges (fig. 36A, G) show a narrow hinge plate which anteriorly becomes briefly expanded downward to meet the septum. Dentition is taxodont consisting of two tooth rows which almost imperceptibly merge beneath the umbones to form a continuous series. The posterior row consists of narrowly cylindrical, vertically parallel teeth which become shorter and thicker posteriorly and taller and thinner anteriorly. Several anterior-most teeth of the posterior row become obliquely truncated by the hindmost tooth of the anterior tooth row which consists of long, thin, slightly radiating vertical teeth. Here teeth are longest and most divergent in the downward expansion of the hinge plate just above the septum. In both tooth rows teeth are more robust near each extremity and become exceedingly fine beneath the umbones. Resilifer absent.

The adductor scars are subequal and situated just beneath each extremity of the hinge plate. The posterior scar is narrower and more elongated than the anterior scar. The anterior scar is situated in a deep notch just in front of the internal septum. The posterior scar is vaguely defined except along its dorsal and dorsolateral circumference where it is deeply impressed.

A pair of posterior retractor scars is indicated on internal molds by a small elongate pustule just above and forward of each posterior adductor followed by a larger linear ridge farther forward (fig. 36D). These features are also visible inside a left shell (fig. 36A) where they are represented by a small, elliptical pit followed by a linear furrow, both positioned on the underside of the hinge plate.

An oblique row of at least four umbonal muscles (fig. 36A, E), probably anterior pedal retractors and pedal protractors, are situated near the apex of the umbonal interior just behind the septum. An interpretation of the restored pedal musculature is offered in figure 43B.

Ligament external, opisthodontic, parivincular. Probable ligamental insertional areas consist of (1) a plumose, beveled area near the posterior extremity of the hinge line (fig. 36I, J, L); and (2) small, inconspicuous furrows just outside of and parallel to the hinge plate (fig. 36I, J).

Pallial line variably impressed, more strongly so anteriorly; more deeply recessed posteriorly. The posterior upward curve of the pallial line is flattened or faintly sinuous.

Original microstructure described by Carter and Tevesz (1978b).

**REMARKS ON MORPHOLOGY:** Though abundant in the sandy/silty Solville facies where it occurs mostly as internal molds, this species is more commonly found among the argillites as near complete individuals with thin remnants of shell preserved. Here width of the valves is often undervalued due to diagenetic compaction; in other specimens, presumably those with an erect infaunal life position, height has become diagenetically compressed and width correspondingly exaggerated.

Aside from a few additional features noted by Hall (1885) and McAlester (1968), descriptions of shell morphology among past studies are generally limited to shape, pro-sopon, and septum. Previous ligamental data on *Nuculites* seem especially lacking in the literature.

The dentition of *Nuculites* was previously regarded as a single, continuous taxodont series. Two specimens here, however, reveal two separate tooth series, a posterior row of vertically parallel teeth truncated by an an-

terior row of slightly radiating teeth. A similar dental arrangement is figured in plate 3, figure 9a of Babin (1966) in *Nuculites subrectangularis*, a somewhat similar species from the European Upper Devonian.

In several articulated specimens (e.g., fig. 36I, J, L) the hinge line portion of the valves normally covered by the ligament is slightly gaping behind the umbones; i.e., hinge teeth and sockets are not in mutual contact except toward the hinge extremities. Since the remainder of the valve margins are closely appressed, the gape is undoubtedly natural. Maintenance of valve articulation in typical individuals of this species would have thus relied largely upon the ligament, many of the hinge teeth having become functionally vestigial except near hinge line extremities.

An internal mold (fig. 36E) shows a row of three pustuliform scars aligned vertically just in front of the septal position and in seeming continuity with the pallial line and/or the edge of the anterior adductor. These appear to be points of insertion of muscle fiber bundles of either the adductor or pallial line and do not, I believe, represent points of attachment of any other accessory muscles.

Recrystallized shell remnants show the valves to have been especially thin near the posterior extremity where shell material is often broken away. However, growth lines of better specimens sometimes indicate either a flattening or a faint re-entrant along the upward curve of the posterior shell margin. A similar flattening or sinuosity is especially pronounced on or near the pallial line of in-

---

FIG. 36. *Nuculites oblongatus* Conrad. A. Left valve interior (AMNH 36212) from AMNH loc. 3017. B-D. Internal mold (AMNH 36214B) from AMNH loc. 3017. B. Left view. C. Right view. D. Dorsal view. E. Partial right internal mold (AMNH 36213) from AMNH loc. 3017. F. Internal mold and shell, dorsal view (AMNH 36214C) from AMNH loc. 3017. G. Hinge of left valve (AMNH 36215) from AMNH loc. 3013. H, I. Articulated specimen (AMNH 36217A) from AMNH loc. 3017. H. Right valve. I. Dorsal view. J, K. Articulated specimen (AMNH 36217B) from AMNH loc. 3017. J. Dorsal view. K. Left valve. L. Dorsal view of articulated specimen (AMNH 36220) from AMNH loc. 3012. M. Left valve of articulated specimen (AMNH 36217C) from AMNH loc. 3017. N. Right internal mold (AMNH 36239) from AMNH loc. 3013. O, P. Articulated specimen (AMNH 36214A) from AMNH loc. 3017. O. Right valve. P. Left valve.

**Abbreviations:** aa—anterior adductor scar, apr—anterior pedal retractor scar, c—clavicle (septum), lg—ligamental area, pa—posterior adductor scar, pl—pallial line, pp—pedal protractor scar, ppr—posterior pedal retractor scars.

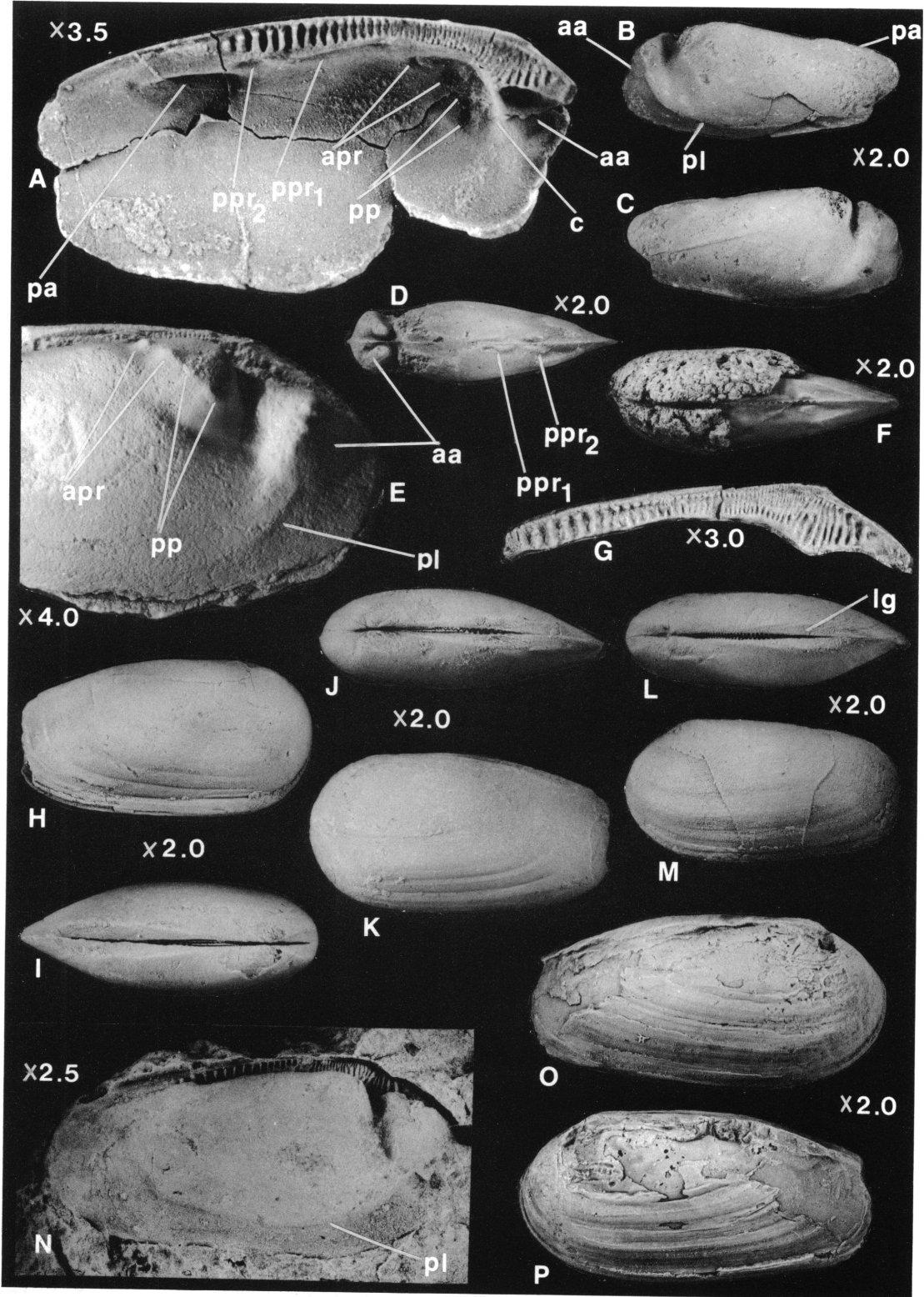


TABLE 7  
Measurements (in Millimeters) of *Nuculites oblongatus* Conrad

Locality	Length	Height	Width <sup>a</sup>
AMNH 3017	25.6	13.0	8.0
	23.0	11.9	7.3
	24.0	11.7	7.8
	27.1	12.4	8.5
	24.5 <sup>c</sup>	11.2	8.5
	21.7 <sup>c</sup>	11.4	7.7
	26.4 <sup>c</sup>	15.3	6.3
	27.3	11.8	9.8
	22.9 <sup>b</sup>	9.3 <sup>b</sup>	6.6 <sup>b</sup>
	24.9 <sup>c</sup>	13.2	9.3
Miscellaneous Solsville	27.9	14.4	4.6 <sup>d</sup>
	26.4	15.1	8.3
	24.2 <sup>c</sup>	13.5	7.9
	26.1 <sup>c</sup>	11.3	10.7
	25.0 <sup>c</sup>	14.6	5.8 <sup>d</sup>
	26.8 <sup>c</sup>	13.6	7.9
	27.7	13.5	7.2

<sup>a</sup> Total width, both valves articulated.  
<sup>b</sup> Internal mold.  
<sup>c</sup> Specimen broken at thin, posterior extremity.  
<sup>d</sup> Laterally crushed.

ternal molds (e.g., fig. 36B, C, N; see also pl. 28, figs. 3, 4 of McAlester, 1968) suggesting an exhalant opening (probably the longer, dorsal lobe) and an inhalant opening below. The same seems true for *Palaeoneilo* as well. This evidence, coupled with the fact that the pallial line is more deeply recessed from the posterior shell margin (see fig. 36N and McAlester, 1968, pl. 28, figs. 3, 4) suggest the presence of extensible siphons.

COMPARISONS: The Solsville specimens agree with those described and figured as *N. oblongatus* by past authors including Conrad (1841), Hall (1885), and Prosser and Kindle (1913).

This species was restudied by McAlester (1968) who could locate neither Conrad's original types nor further topotypic materials, basing his evaluation on a series of specimens, which I have also personally examined, from a gray-brown siltstone of the Skaneateles Formation (Butternut Mbr.?) collected by C. S. Prosser west of Brookfield, Madison County, New York (USNM no. 101678). Despite their higher stratigraphic occurrence, they seem indistinguishable al-

lowing for infraspecific and diagenetic variation (fig. 37).

In addition to these, the Solsville specimens seem identical with several other lots of specimens in the National Museum of Natural History. These include:

- USNM no. 14086: *Nuculites oblongatus* Conrad. Devonian (Hamilton), Moravia, New York.
- USNM no. 101685: *Nuculites oblongatus* Conrad, Hamilton, Earlville, New York. Two specimens.
- USNM no. 101692, Acc. 116983: *Nuculites oblongatus* Conrad. Hamilton, Cardiff, Pecksport, Morrisville Qd., New York. Eight specimens, mostly internal molds in siltstone.
- USNM no. 16112: *Nuculites oblongatus* Conrad. Hamilton, Brookfield, New York. One specimen.
- USNM no. 101716: *Nuculites oblongatus* Conrad. Hamilton, Fultonham, Schoharie County, New York. Two specimens.
- USNM no. 101684: *Nuculites oblongus* Conrad. Hamilton (Delphi), Onondaga County, New York. Three specimens.
- USNM no. 100939: *Nuculites oblongatus* Conrad. Hamilton, Fultonham, Schoharie County, New York. One specimen.
- USNM no. 101680: *Nuculites oblongatus* Conrad. Moscow, Lower Windom, Moore's Gully, 1½ mile N.E. of Georgetown, New York. One specimen.
- USNM no. 101682 503A<sub>6</sub>: *Nuculites oblongatus* Conrad. Hamilton, Pittsfield, Oswego County, New York. Two specimens.
- USNM no. 14086: *Nuculites oblongata* Conrad. Hamilton, Moravia, New York. Four specimens.

The literature abounds with different specific names applied to figured North American and European specimens which do not seem significantly different from *N. oblongatus*; many of these are surely junior synonyms. Past authors have also noticed these similarities. Solle (1936) pointed out that some intergrade. Babin (1973), emphasizing the need for exhaustive restudy, has suggested that many of these "species" are little more than diagenetic variants. Williams (1917), who would have called them "metamorphic species," similarly noticed that much of the variation among his Silurian *Nuculites* specimens was the result of postdepositional events. Such a view is supported here in both *N. oblongatus* and *N. triqueter* by the ob-

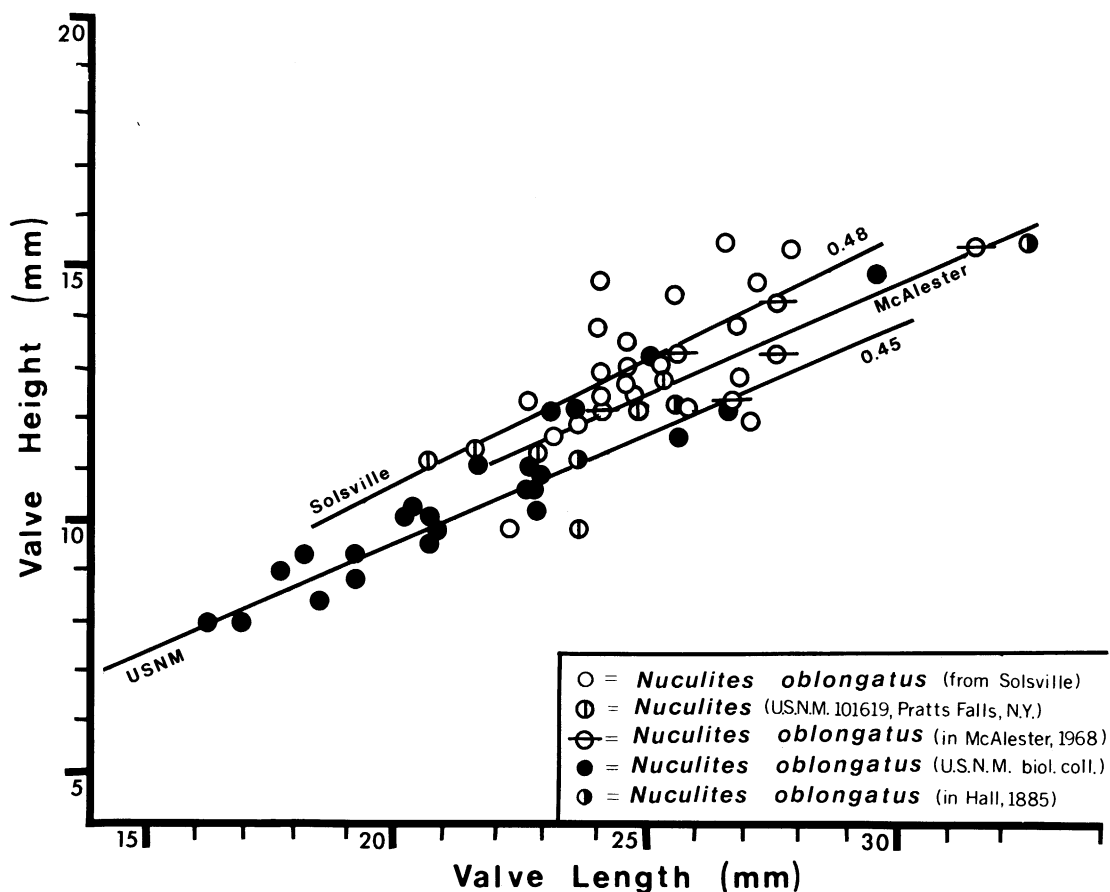


FIG. 37. *Nuculites oblongatus* Conrad. Bivariate comparisons of various samples.

served thinness of the shells which would be readily deformed by sedimentary compaction. Although a thorough revision is presently not feasible, a partial assessment of some of these conspecific or similar species is offered below (see also Babin, 1966).

1. "*Nucula*?" *oblonga* Hall, 1843 [= *Nuculites oblongus* (Hall) of Miller, 1877 and Lesley, 1889]. Middle Devonian, New York. Placed in synonymy with *N. oblongatus* by Hall (1885). Hall's original figure (1843, fig. 78-4), though generalized, shows the elliptical outline and internal septum of *N. oblongatus*.
2. *Nuculites branneri* Clarke, 1899 (1900, p. 73, pl. 8, figs. 6-8). Devonian, Pará, Brazil. A more trigonally rounded species somewhat similar to *N. beushauseni brevis* Mauz (1933, fig. 11a). Viëtor (1919) thought it might be conspecific with *N. oblongatus* and *N. ellip-*

*ticus*. *Nuculites* sp. of Saul et al. (1963, pl. 137, figs. 1-7) from the Devonian of Ghana is probably *N. branneri*; it will probably prove to be a valid Gondwana species.

3. *Nuculites milwaukeeensis* Cleland, 1911 [= *Palaeoneilo milwaukeeensis* (Cleland) of Pohl, 1929]. Middle Devonian (Milwaukee Fm.), Wisconsin. A subjective junior synonym of *N. oblongatus* based upon a single internal mold with hinge and septal groove. Cleland compared it with *N. oblongatus*. Pohl's reassignment to *Palaeoneilo* is puzzling. Evidently he did not observe the obvious septum; moreover he erroneously assumed *Nuculites* to be resiliated. Pohl also inaccurately placed Cleland's *Palaeoneilo* cf. *plana* Hall and various other specimens in synonymy with his "*P. milwaukeeensis*"; many of these are probably *P. filosa*.
4. *Nuculites modulatus* Kindle, 1912. Onondaga of Pennsylvania, Virginia, and Maryland.

Morphologically close to *N. oblongatus* but, perhaps, not conspecific. The form seems relatively shorter in Kindle's two figured specimens and three measured specimens.

5. *Nuculites perovalis* (Williams and Breger), 1916. Lower Devonian (Chapman Sandstone), Maine. Based on two internal molds. Compared by Williams and Breger to *N. ellipticus* as figured by Beushausen (1895, pl. 5, figs. 9–11). Specimens show an outline and septum similar to *N. oblongatus* but are too poorly preserved to verify.
6. *Nuculites ellipticus* (Maurer), 1886. Widespread. Lower Devonian (Siegenian-Emsian) of Europe. Excellent accounts of the complicated and confusing history of this species name have already been given by Solle (1936) and Babin (1966). Because it has been used in different senses by different authors and has been repeatedly split and recombined, the name has become practically meaningless. Most of the confusion stems from two sources. (1) Shell and septal variation are remarkable, but Babin (1966) showed that the variants intergrade and are largely the result of diagenetic distortions. (2) Beushausen's (1895) erroneous conclusion that small forms with strong double septa (*Ditichia persulcata*; see above) are juveniles of *N. ellipticus*. The posterior septum of the juveniles, Beushausen and later authors had supposed, atrophied during growth while the anterior septum increased. In the adult the posterior septum either vanished, or its remains were expressed on internal molds as a faint groove in front of a callosity in each valve. Solsville *N. oblongatus* suggest that, in reality, the callosity is a natural mold of the posterior adductor scar which is occasionally so deeply impressed along its anterior edge that it produces a short, steplike elevation. The supposed septal groove among the Solsville specimens is not a groove at all but merely the lower lying edge of the step representing a weak marginal buttress along the anterior edge of the posterior adductor in the original shell. This feature is hardly to be compared with a second septum and, like adductor morphology in many other bivalve taxa, is too variable (and frequently absent) to be regarded as potentially useful in differentiating species.  
*Nuculites ellipticus, sensu stricto* is regarded here as a subjective junior synonym of *N. oblongatus*. The close similarities of the two were noted by Beushausen (1895); Clarke (1909) speculated that the two are conspecific as did Viëtor (1919). The holotype of *N. ellipticus* as originally described by Maurer (1886) and later figured by the same author (1902, pl. 15, fig. 8) has the same elongated elliptical outline and single septum of *N. oblongatus* but is too small for satisfactory comparisons. Larger, better topotypes accepted as *N. ellipticus* by Maurer but illustrated by Beushausen (1895, pl. 5, figs. 9–11) seem identical with *N. oblongatus* as do the more recent figures of Babin (1973).
7. *Nuculites beushauseni* (Fuchs), 1912. Objective junior synonym of *N. ellipticus* (Maurer) and subjective junior synonym of *N. oblongatus*. Fuchs designated Beushausen's (1895, pl. 5, figs. 9–11 [= *N. ellipticus, sensu stricto*]) as types. Mauz (1933), who compared it to *N. oblongatus*, designated Beushausen's pl. 5, fig. 9, as lectotype (a photo of the lectotype is given by Solle, 1936, fig. 1). Mauz (1933, figs. 10, 11) designated two other specimens from Maurer's collection as *N. beushauseni expansus* and *N. beushauseni brevis*. These were shown by Babin (1966) to be orthogonally deformed variants of the same species group. *Nuculites beushauseni beushauseni* of Mauz (1935) refers to the lectotype of *N. beushauseni* (Fuchs).
8. *Nuculites ellipticus longus* (Mauz), 1933 [= *N. longus* (Mauz) of Solle, 1936]. Probable subjective junior synonym of *N. oblongatus*. Holotype is a laterally flattened internal mold (fig. 9 of Mauz and fig. 4 of Solle) drawn from Maurer's collection. It does not have a true second septum as supposed, but a slight posterior adductor buttress here deemed insignificant as similar variants are seen among *N. oblongatus*.
9. *Nuculites ellipticus ellipticus* Solle, 1936. An objective junior synonym of *N. beushauseni beushauseni* and, hence, of *N. ellipticus, sensu stricto*. Both subspecies share the same lectotype. *Nuculites ellipticus ellipticus* Mauz, 1935 (and Maillieux, 1937) is a junior homonym used in an opposite sense in reference to the biseptate "juvenile" *N. ellipticus, sensu lato* of Beushausen (1895, pl. 5, figs. 12–14). Solle rejected this usage pointing out that biseptate forms were not what Maurer originally had in mind. He proposed that *N. ellipticus ellipticus* would restore the original sense if it superseded *N. beushauseni beushauseni*. The "juveniles," Solle argued, should be placed in a separate species which he designated *N. persulcatus*.
10. *Nuculites vaissieri* (Leriche), 1912a. Lower Devonian (Gedinnian), France and Germany. A possible subjective junior synonym of *N.*



*oblongatus*. Leriche's (1912a, pl. 6, figs. 5, 6; 1912b, pl. 2, figs. 1–3) photos show small internal molds practically identical with *N. oblongatus*. His text-fig. 2 (1912b), a drawing of the hinge, is remarkably like the two Solsville hinges shown here (fig. 36A, G).

11. *Nuculites affinis* (Beushausen), 1889 *sensu* Babin, 1966. *Nuculites affinis sensu* Beushausen has a distinctive, crescentic shell shape. However, Babin's (1966, pl. 3, fig. 1) Middle Devonian (Eifelian) internal mold from France seems identical with McAlester's (1968, pl. 28, figs. 3, 4) internal mold of *N. oblongatus* except that the latter is more completely preserved beyond the pallial line. The short, upward, dorsoposterior curve of Babin's specimen suggestive of a crescentic shape is probably caused by the deeply impressed posterior adductor scars in that position as shown by McAlester's figures.
12. Williams (1917) described 19 badly oversplit new species of *Nuculites* from the Silurian of Washington County, Maine. McAlester (1962a, p. 11) called this work an "ultimate extreme of nomenclatural enthusiasm." Many of Williams's species show clear relations to Devonian *Nuculites* and should be restudied.

AUTECOLOGY: See *Palaeoneilo*.

*Nuculites triqueter* Conrad, 1841

Figures 5J, 38, 39 (nos. 1, 4–6, 8, 10)

*Nuculites triqueter* Conrad, 1841, p. 50. Hall and Whitfield, 1869, p. 4. Miller, 1877, p. 198. Hall, 1883, pl. 47, figs. 17–24; 1885, p. 326, pl. 47, figs. 17–28, pl. 93, figs. 8–10. Lesley, 1889, p. 475, 3 figs. Kindle, 1896, p. 42. Whiteaves, 1898, pp. 398, 416. Grabau, 1899, p. 255, fig. 72. Whitfield and Hovey, 1900, p. 294. Shimer and Grabau, 1902, p. 156. Clarke and Ruedemann, 1903, p. 466. Cleland, 1903, p. 62. Grabau, 1906, p. 330. Grabau and Shimer, 1909, p. 398, fig. 509d–f. Stauffer, 1909, p. 166; 1915, pp. 226, 235; 1916, pp. 477, 483. Prosser and Kindle, 1913, pp. 107, 232, pl. 26, figs. 1–5. Williams and Breger, 1916, pp. 160–161. Williams, 1917, p. 30. [not] Willard, 1939, p. 476, pl. 26, fig. 17. Stumm, 1942, p. 557, pl. 81, fig. 29. Shimer and Shrock, 1944, p. 377, pl. 146, figs. 15, 16. LaRocque and Marple, 1955, p. 85, fig. 91. Stumm and Wright, 1958, pp. 93, 117. Ellison, 1965, p. 122, pl. 14, figs. 21, 22, [?]23. Babin, 1966, pp. 100–101; 1973, p. 43. Palmer and Brann, 1966, pl. 15, fig. 12. Wilson, 1975, p. 126.

- [?] *Nuculites* cf. *triqueter* Conrad. Babin, 1973, p. 42, pl. 2, fig. 2.

*Nuculites triquetra* Conrad. Hall and Whitfield, 1872.

*Cucullella triquetra* Conrad [sic]. Beushausen, 1895, p. 102.

[?] *Cucullella* cf. *triquetra* Conrad [sic]. Beushausen, 1895, p. 102, pl. 5, figs. 2, 3. [= *N. dahmeri* Solle, 1936, p. 191.]

*Nuculites triquetrus* Conrad. Clarke, 1908, pp. 85, 233, pl. 24, figs. 7–10. Bailey, 1975, p. 164, pl. 12, figs. 16–18; 1978a, p. 121.

†*Nuculites nyssa* Hall and Whitfield, 1869, p. 5. Hall, 1883 [in part], pl. 47, figs. 25–30; 1885, p. 328, pl. 47, figs. 29, 30. Whitfield and Hovey, 1900, p. 292. Merrill, 1905, p. 44.

†*Nuculites cuneiformis* Conrad. Hall, 1885 [in part], pl. 47, fig. 16.

†[?] *Nuculites doto* Clarke, 1909 [in part] p. 140, pl. 33, fig. 6.

†*Nuculites laphami* Cleland, 1911, p. 101, pl. 20, fig. 4. Pohl, 1929, p. 31, pl. 3, fig. 13.

†[?] *Cucullella truncata* Steininger, 1853, p. 52, pl. 4, fig. 2. Maurer, 1886, p. 25. Beushausen, 1895, p. 101 [in part] pl. 5, figs. 5–7 [esp. fig. 6], [not] fig. 4. [Later ref. in Maillieux, 1937, p. 192.]

†[?] *Nuculites truncatus* (Steininger). Kegel, 1913, p. 74. [= *N. (Cucullella) truncatus* (Steininger). Viëtor, 1919, p. 395.] Maillieux, 1937, p. 192, fig. 9 [see also Maillieux's later ref.]. Dahmer, 1942, p. 266. Babin, 1966, p. 101; 1973, p. 42, pl. 2, figs. 1, 3–5.

†*Cucullella posthuma* Beushausen, 1895, p. 103, pl. 5, fig. 1. [= *N. posthumus* (Beushausen). Babin, 1966, p. 100, pl. 3, figs. 6–8.]

†[?] *Cucullella longiuscula* Beushausen, 1895, p. 103, pl. 5, fig. 8. [= *N. longiusculus* (Beushausen). Dahmer, 1940, p. 267, figs. 11, 12.] [= *N. truncatus* (Steininger) according to Babin, 1973, p. 42.]

DESCRIPTION: Shells thin, small- to medium-size, equivalve, moderately well inflated, nuculiform, trigonally rounded; length from one-third to one-fourth greater than height.

Umbones at anterior third or fourth, broad, prominent, inflated, prosogyrous, arching above the hinge line. Posterior umbonal slope gibbous to straight and subangular, sometimes carinate; posterior umbonal angle fairly gentle to moderately steep. Anterior umbonal slope short, concave anteriorly; anterior umbonal angle steep.

Ventral margin smoothly curving. Anterior margin sharply rounded, obliquely truncate to subtruncate. Posterior margin gently rounded, often becoming obliquely straight

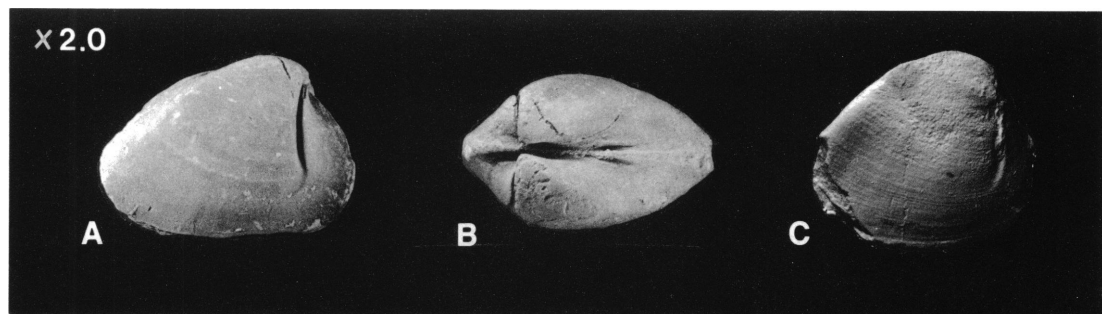


FIG. 38. *Nuculites triqueter* Conrad. A, B. An internal mold (AMNH 36222) from AMNH loc. 3012. A. Right view. B. Dorsal view. C. Right view of a composite mold with prosopon (AMNH 36221) from AMNH loc. 3017.

posterodorsally. A posterodorsal flange along the commissure behind the umbones may be variably developed to absent.

Hinge line short, slightly elevated posteriorly descending lower anteriorly, gently arcuate. Teeth finely taxodont forming a continuous, uninterrupted row of crenulations between the umbones on internal molds. Nonresiliated.

A strong, vertical, clavicle or septum is positioned in each valve just in front of the umbones and is represented on internal molds and composite molds by a narrow cleft or furrow which is dorsally very deep and sharply defined. It curves gently forward, ventrally becoming progressively less defined and (?) merging finally into the anterior limb of the pallial line.

Pallial line and internal muscle scars obsolescent.

Prosopon consisting of very fine, indistinct, nonfasciculate growth lines; no radial elements, varices or rugae are apparent. A few, very slight, concentric undulations on inner shell surfaces are suggested by a few faint ridges on an internal mold (fig. 38A).

Ligament unknown. Original microstructure and mineralogy unknown.

REMARKS ON MORPHOLOGY: Two specimens of *N. triqueter* were recovered from the Solsville, a composite mold (*sensu* McAlester, 1962b) with superimposed internal and external shell features from the argillaceous facies (fig. 38C), and an internal mold from the silty/sandy facies (fig. 38A, B). This species can easily be differentiated from *Nuculites oblongatus* in the same strata by its

shorter, more trigonal form, more gibbous umbones, and generally greater inflation.

As in *N. oblongatus*, the shell here was originally very thin in contrast to other thick-shelled nuculoids in the fauna (i.e., *Nuculoida deceptiformis* and *Palaeoneilo filosa*). So thin are the shells of *N. triqueter* that elsewhere it is commonly represented only by internal molds showing the characteristic septal cleft in each valve. Prosopon is rarely seen except in composite molds; here the cleft is also clearly visible (theoretically, in a purely external mold, no evidence of the internal septum would be visible). The ease of diagenetic distortion on such thin shells is probably, in part, responsible for the great shape variability which has resulted in the proliferation of species synonyms (Babin, 1966, 1973). Diagenetic flattening likely also exaggerates or underestimates the acuity of the umbonal ridge or carina, a feature which past authors have considered of diagnostic importance at the specific level.

Hall (1885) indicated more than 20 teeth in the taxodont hinge series which is illustrated in his plate 47, figure 24. In a Solsville internal mold, however, they are evident only as a series of fine crenulations along the dorsal line of commissure (fig. 38B). The absence of a resiliifer may be deduced by the lack of a resiliifer mold punctuating the crenulations as seen in nuculid internal molds.

The internal mold (fig. 38A, B) shows no clear indication of internal muscular features; only the anteriormost part of the pallial line is visible. Considering the preservation quality here, if these features had been even mod-

erately impressed into the inner shell surfaces, they would surely be visible; evidently they were only weakly impressed in the original shell.

**MEASUREMENTS:** The specimen in figure 38C has a length of 13.8 mm. (not truly representative since the posterior extremity is broken away) and a height of 11.3 mm. of the left valve (the right valve is a bit taller but has been diagenetically deformed); the total width of the articulated valves is 7.2 mm.; and the posterior umbonal angle from near the venter to about half way up the umbonal slope measures about 55°. The specimen in figure 38A, B, is 16.9 mm. in length, 12.4 mm. in height, and 10.1 mm. in total width (both valves); the posterior umbonal angle measures about 45° up to the midway point (beyond this region the curve of the umbonal slope makes objective angular measurement impossible).

**COMPARISONS:** The shells of *N. triqueter* are strongly nuculid-like and seem especially comparable in shape to "*Nucula*" (= *Carydium*; see Bailey, 1978a, 1979a, and MS) *varicosa* Hall and Whitfield, "*Nucula*" (= *Carydium*; references as above) *bellistriata* Conrad and some *Nuculoidea corbuliformis*, but the internal septum and indistinct non-fasciculate growth lines are distinguishing features.

*Nuculites triqueter* has considerable stratigraphic range having been reported from rocks as old as the early Devonian (Onesquethawan) Gaspé Sandstone of east Canada (Clarke, 1908) [similar shells have also been described in the Oriskany Sandstone of New York (Clarke, 1909) and the early Devonian of Germany] to rocks as young as the later Devonian (Fingerlakesian) Ithaca Mbr., Genesee Formation, of New York (Prosser and Kindle, 1913).

Descriptions and figures of past authors indicate few or no differences between *N. triqueter* and several other species:

1. *Nuculites cuneiformis* Conrad (1841) from the Hamilton of New York. A rare, longer species of uncertain validity showing a sharp, cuneiform posterior extremity (diagenetically distorted *N. triqueter*?). A smaller specimen of Hall (1885, pl. 47, fig. 6) closely approaches *N. triqueter*. See *N. longiusculus* (below).
2. *Nuculites nyssa* Hall and Whitfield (1869) from the Hamilton of New York. This species, originally distinguished only by its more ovate form, seems identical with *N. triqueter* from the same beds and is here regarded as a junior synonym. Even Hall equivocated; so great are the similarities that many specimens he earlier (1883) assigned to *N. nyssa* he later (1885) placed in *N. triqueter* after observing the intraspecific variation in larger collections.
3. *Nuculites laphami* Cleland (1911) from the Middle Devonian (Milwaukee Formation), Wisconsin. Based on a single internal mold described as showing a less trigonal shape and less distinct umbonal ridge than *N. triqueter*. However, the specimen was indicated as being "much weathered." Since no real basis for distinction seems evident in Cleland's drawing and Pohl's (1929) photograph, the species is here considered a probable junior synonym of *N. triqueter*.
4. *Nuculites doto* Clarke (1909) from the Lower Devonian Oriskany Sandstone of New York. Probably a valid species. Clarke's plate 33, figures 5, 7-10, shows internal molds uniquely possessing a slight, posterior clavicular cleft in addition to the typical anterior cleft. However, his figure 6, labeled *N. doto*, is probably *N. triqueter*.
5. *Nuculites truncatus* (Steininger), 1853, from the Lower Devonian (Siegenian-Emsian) of Germany. Beushausen's (1895) observation that this species is morphologically very similar to Hall's illustrations of *N. triqueter* is further supported by most of his figures, plate 5, figures 5-7 (his fig. 4 is not *Nuculites* but, perhaps, *Goniophora*). *Nuculites truncatus* is probably, for the most part, a junior synonym. Babin (1973) has also noted the close similarities but has not fully accepted synonymy of the two because of age difference and skepticism of Hall's figures. However, age difference does not seem significant since many other Rheinisch-Appalachian Devonian bivalve species show an earlier occurrence in Europe than in North America as I have indicated. Moreover, while it is true that Hall's figures are occasionally fanciful, most of Hall's original specimens I have examined closely agree with his figures.
6. *Nuculites* cf. *triqueter* (Beushausen), 1895 from the Lower Devonian (Emsian) of Germany. Beushausen noted no significant differences in shell form between the Rheinisch specimens and *N. triqueter*. His figures show two internal molds which have a gently arcuate posterior dorsal margin, a feature found in some American specimens but supplanted in others by a straighter margin. The variability is probably due in large part to diagenetic differences. One distinction of seeming importance is that the

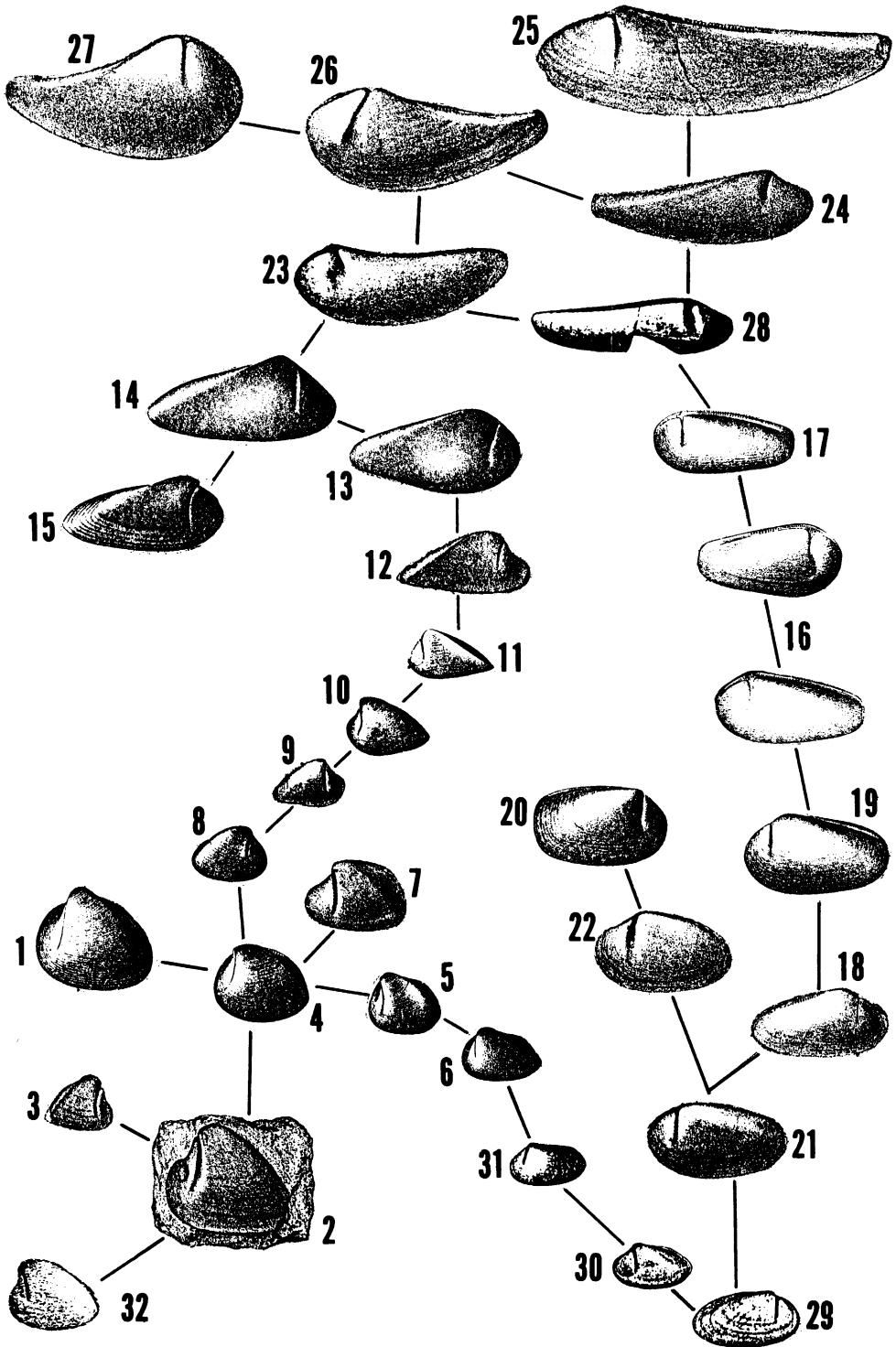


FIG. 39. *Nuculites* Conrad. Morphologic variation as figured by different authors. 1, 4–6, 8, 10. *N. triqueter* Conrad in Hall (1885, pl. 47: 1—fig. 22, 4—fig. 23, 5—fig. 19, 6—fig. 27, 8—fig. 18, 10—fig. 17). 2, 3. *N. truncatus* (Steininger) in Beushausen (1895, pl. 5: 2—fig. 6, 3—fig. 5a). 7. *N. cf. triqueter*

taxodont tooth row is characteristically uninterrupted in the American species but separated into anterior and posterior rows in the German forms. Solle (1936) considered this sufficient basis for calling Beushausen's specimens by a separate name, *N. dahmeri*. Oddly enough, the enlargement of the tooth row of *N. cf. triqueter* (Beushausen's pl. 5, fig. 2A) does not show the tooth row separation he described.

7. *Nuculites posthumus* (Beushausen), 1895 from the Middle Devonian (Eifelian) of Germany. Beushausen compared this species with *N. truncatus* except for its absence of a sharp, umbonal keel, less curving beaks and flatter form. His single figure, however, seems identical with *N. triqueter*. Babin (1966) regarded *N. posthumus* as a separate species noting that *N. posthumus* lacks the diagonal keel and straighter posterodorsal margin of *N. triqueter*. Individuals, he maintained, sometimes look similar to *N. triqueter* as a result of slight mechanical deformation. His plate 3, figure 6, however, shows an internal mold nearly identical to the Solsville figure 38A.
8. *Nuculites longiusculus* (Beushausen), 1895 from the Lower Devonian (Emsian) of Germany. Originally based upon a single internal mold (Beushausen, 1895, p. 103, pl. 5, fig. 8) like *N. triqueter* but more cuneiform, approaching *N. cuneiformis* Conrad (1841) (see Hall, 1885, pl. 47, figs. 13–16) as remarked by Beushausen. Two topotypic specimens of *N. longiusculus* later figured by Dahmer (1940, figs. 11, 12) as well as Beushausen's holotype were considered by Babin (1973) to be distorted specimens of *N. truncatus* found in the same beds.

AUTECOLOGY: See *Palaeoneilo*.

#### GENUS PALAEONEILO

HALL AND WHITFIELD, 1869

TYPE SPECIES: By subsequent designation of Hall (1885), *Nuculites constricta* Conrad, 1842, from the Middle Devonian (Hamilton)

near Moravia, Cayuga County, New York. Similar shells have been reported in North America from Lower Devonian–Lower Mississippian deposits by other authors.

GENERIC USAGE: *Palaeoneilo* was diagnosed by McAlester (in Moore, 1969; see same source for a list of generic synonyms) as malletiids with a faint, posterior, radial sulcus or groove, concentric prosopon and no internal clavicle (septum). Since an incipient "septum" (in reality little more than a shell thickening or buttress along the rear edge of the anterior adductor; hardly a true septum) is evident among occasional individuals in several species (including the type species), *Palaeoneilo* is here diagnosed as like *Nuculites* Conrad but internal septum absent or incipient only.

#### *Palaeoneilo constricta* (Conrad), 1842

Figures 5I, 6F, 40D, 44P

*Nuculites constricta* Conrad, 1842, p. 249, pl. 15, fig. 8.

*Palaeoneilo* [sic] *constricta* (Conrad). Hall and Whitfield, 1869, p. 7. Whitfield, 1882, p. 355, pl. 26, figs. 13, 14.

*Palaeoneilo constricta* (Conrad). Miller, 1877, p. 199. Hall, 1883, pl. 48, figs. 1–15; 1885, p. 333, pl. 48, figs. 1–16, pl. 51, fig. 17. Whitfield, 1883, p. 369. Lesley, 1889, p. 580, 2 figs. Kindle, 1896, p. 42. Grabau, 1899, p. 256, fig. 173; 1906, p. 330. Whitfield and Hovey, 1900, p. 294–296. Clarke and Ruedemann, 1903, p. 474. Cleland, 1903, p. 64; 1911, p. 102, pl. 20, figs. 9, 19–22; 1916, p. 459, fig. 432E. Clarke, 1904, p. 311, pl. 15, figs. 9–13. Slocum, 1906, p. 265. Prosser and Kindle, 1913, p. 235, pl. 26, figs. 9–12. Clarke and Swartz, 1913, p. 620, pl. 61, figs. 7–10. Williams and Breger, 1916, p. 163, etc. Willard, 1939, p. 477, etc. Shimer and Shrock, 1944, p. 377, pl. 146, figs. 20, 21. McAlester, 1962a, p. 17, pl. 1, figs. 1–18; 1963a, pp. 1211, 1221, figs. 2, 9; 1963b, p. 989, tabs. 1, 2, pl. 121, figs.

←  
Conrad in Beushausen (1895, pl. 5, fig. 3a). 9. *N. posthumus* (Beushausen) 1895, pl. 5, fig. 1. 11, 13–15. *N. cuneiformis* Conrad in Hall (1885, pl. 47: 11—fig. 16, 13—fig. 13, 14—fig. 14, 15—fig. 15). 12. *N. longiusculus* (Beushausen), 1895, pl. 5, fig. 8, 16, 17, 19, 20. *N. oblongatus* Conrad in Hall (1885, pl. 47: 16—fig. 3, 17—fig. 2, 19—fig. 1, 20—fig. 10). 28 in Prosser and Kindle, 1913, pl. 25, fig. 20. 18, 21, 22. *N. ellipticus* (Maurer) in Beushausen (1895, pl. 5: 18—fig. 11, 21—fig. 9, 22—fig. 10). 23. *N. solenoides* (Goldfuss) in Beushausen, 1895, pl. 5, fig. 17. 23–25. *N. solenoides* var. *cultrata* (Sandberger) in Beushausen (1895, pl. 5: 23—fig. 17, 24—fig. 19, 25—fig. 18). 26, 27. *N. affinis* (Beushausen) in Beushausen (1895, pl. 5: 26—fig. 22, 27—fig. 21). 29, 30. *N. neglectus* (Hall) in Ulrich (1897, pl. 42: 29—fig. 25, 30—fig. 22). 31. *N. sp.* Clarke (1908, pl. 24, fig. 11). 32. *N. tortus* Barrois (1891, pl. 1, fig. 10b).

- 1-18, pl. 122, figs. 1-17; 1968, p. 41, pl. 15, figs. 1-15; 1969, p. N233, fig. A5, 9 in Moore. Ellison, 1965, p. 124, pl. 14, figs. 27-37. Palmer and Brann, 1966, pl. 1, fig. 13, pl. 15, figs. 4, 13. Bailey, 1975, p. 201, pl. 15, fig. 5, text-figs. 30, 31; 1978a, pp. 120, 121.
- Palaeoneilo* cf. *constricta* (Conrad). Clarke, 1908, p. 233, pl. 24, fig. 6. Kindle, 1912, p. 87, pl. 7, fig. 10 [see also Kindle's exhaustive ref. list]. Pohl, 1929, p. 34, pl. 4, figs. 2-15. Cooper and Cloud, 1938, p. 452, pl. 55, fig. 2.
- [?] *Palaeoneilo* sp. aff. *P. constricta* (Conrad). Wilson, 1975, p. 127, pl. 72, fig. 20.
- Palaeoneilo constricta* (Conrad) var. *flexulosa* Hall, 1883, pl. 48, figs. 16-20; 1885, p. 334, pl. 48, figs. 17[?], 18-20. Whitfield and Hovey, 1900, p. 296.
- Ctenodonta constricta* Conrad [sic]. Beushausen, 1895, p. 91.
- [?] *Nuculites maxima* Conrad, 1841, p. 50. [= *Tellina ovata* Hall, 1843, p. 196, fig. 6. = *Palaeoneilo maxima* (Conrad), Hall and Whitfield, 1869, p. 9. = *Palaeoneilo maxima* (Conrad), Hall, 1883, pl. 48, figs. 29-38; 1885, p. 335, pl. 48, figs. 29-38. Whitfield and Hovey, 1900, p. 296.] [See also McAlester, 1962a, p. 17.]
- Nucula bellatula* Hall, 1843, p. 197, fig. 78, no. 7. [= *N. bellula* [sic] Hall. Clarke, 1904, p. 311. [not] *Nuculoidea bellatula* Williams and Breger, 1916, p. 174, pl. 19, fig. 4.] See additional ref. in Kindle, 1912, p. 87. [Synonym also of McAlester, 1962a, p. 17.]
- Palaeoneilo* [sic] *plana* Hall and Whitfield, 1869, p. 7. [= *Palaeoneilo plana* Hall [and Whitfield]. Hall, 1883, pl. 48, figs. 21-28; 1885, p. 334, pl. 48, figs. 21-28. = *P. cf. plana* Hall [and Whitfield]. Cleland, 1911, p. 104, pl. 20, figs. 15, 16. [not] *P. plana* Hall [and Whitfield]. Clarke and Swartz, 1913, p. 621, pl. 61, figs. 1, 2[?], 3. [in part] *P. plana* Hall [and Whitfield]. Willard, 1939, p. 477, etc., pl. 26, fig. 28, [not] fig. 29.] [Provisional synonym of McAlester, 1962a, p. 17.]
- [?] *Palaeoneilo* [sic] *brevis* Hall and Whitfield, 1869, p. 10. [= *Palaeoneilo brevis* Hall [and Whitfield]. Hall, 1883, pl. 50, figs. 24-33; 1885, p. 342, pl. 50, figs. 24-33. [not] *P. brevis* Beushausen, 1884, p. 79, pl. 3, fig. 13a, b.] [Provisional synonym also of McAlester, 1962a, p. 17.]
- †[?] *Palaeoneilo bedfordensis* Meek, 1875, p. 298, pl. 15, fig. 3a-c. [= *Palaeoneilo* [sic] *bedfordensis* Meek. Lesley, 1889, p. 580.]
- Palaeoneilo petila* Clarke, 1904, p. 311, pl. 15, figs. 1-8. [?] Clarke and Swartz, 1913, p. 624, pl. 60, fig. 24. [Provisional synonym of McAlester, 1962a, p. 17.]
- [??] *Palaeoneilo* cf. *petilla* [sic] Clarke. Butts, 1941, p. 203, pl. 120, fig. 12.
- †[?] *Palaeoneilo mainensis* Clarke, 1907a, p. 230. 1909, p. 110, pl. 28, figs. 24-30. [= *P. (Ditichia) mainensis* Clarke. Williams and Breger, 1916, p. 168, pl. 19, figs. 10[?], 12[?], 19[?], pl. 25, figs. 6, 9, 11, 13.]
- †*Palaeoneilo* (*Nuculites*) *folles* Clarke, 1907a, p. 232; 1909, p. 36, pl. 7, figs. 1-3.
- †[?] *Palaeoneilo orbignyi*. Clarke, 1909, p. 109, pl. 28, figs. 20-23. [not] Clarke, 1899 (1900), p. 74, pl. 8, figs. 14-17.
- Nucula snyderensis* Branson, 1924, p. 112, pl. 25, figs. 17, 18. [= *N. cf. lirata* (Conrad), Branson, 1924, p. 112, pl. 25, figs. 13, 14.] [Synonym also of McAlester; see especially 1963b, p. 989.]
- †[?] *Palaeoneilo dentata* Pohl, 1929, p. 34, pl. 4, figs. 16-25. [= *P. brevis* Hall [and Whitfield]. Cleland, 1911, p. 101, pl. 20, figs. 6, 7. = *Palaeoneilo* sp. Cleland, 1911, p. 105, pl. 20, fig. 8.]
- †[?] *Palaeoneilo* sp. Caster, 1930, p. 74, pl. 40, fig. 12.
- †[?] *Ctenodonta krotonis* Roemer, 1850 [= *Cucullella tenuirata* Sandberger and Sandberger, 1850-1856, p. 276, pl. 29, fig. 4.] Beushausen, 1895, p. 72, pl. 5, figs. 24, 25.
- †[?] *Ctenodonta crassa* Beushausen, 1895, p. 77, pl. 6, figs. 4, 5. Maillieux, 1937, fig. 6. [See other ref. in Maillieux, p. 179.] [not *Palaeoneilo crassa* Clarke and Swartz, 1913, p. 625, pl. 61, figs. 14, 15.]
- †[?] *Ctenodonta* aff. *crassa* Beushausen. Maurer, 1902, p. 43, fig. 10a [not 10b].
- †[?] *Ctenodonta gemündensis* Beushausen, 1895, p. 80, pl. 5, figs. 26[?], 27.
- †[?] *Ctenodonta elegans* Maurer, 1886, p. 14. Beushausen, 1895, p. 81, pl. 7, fig. 6. [See other ref. in Maillieux, 1937, p. 175.]
- †*Ctenodonta daleidensis* Beushausen, 1895, p. 85, pl. 6, fig. 6.
- †*Ctenodonta demigrans* Beushausen, 1895, p. 90, pl. 6, figs. 1, 2.
- †*Ctenodonta* sp. aff. *demigrans* Beushausen. Babin, 1966, p. 64, pl. 1, figs. 16-19.
- †*Ctenodonta planiformis* Beushausen, 1895, p. 91, pl. 6, fig. 3, pl. 7, fig. 5. Dahmer, 1942, figs. 19, 20. [See other ref. in Dahmer, p. 288.]
- †[?] *Ctenodonta* (*Palaeoneilo*) aff. *planiformis* Beushausen. Kegel, 1913, p. 83, pl. 4, fig. 7.
- †[?] *Ctenodonta* (*Palaeoneilo*) *maureri* var. *obsoleta* Kegel, 1913, p. 79, pl. 4, fig. 8.
- †[?] *Ctenodonta* (*Palaeoneilo*) *candida* Kegel, 1913, p. 82, pl. 4, fig. 9.

DESCRIPTION: See recent redescrptions of McAlester (1962a, p. 17; 1963b, p. 989; 1968, p. 41).

REMARKS ON MORPHOLOGY: The single right valve (fig. 44P) shows the typical, faint, posteroventral embayment or sinus in the

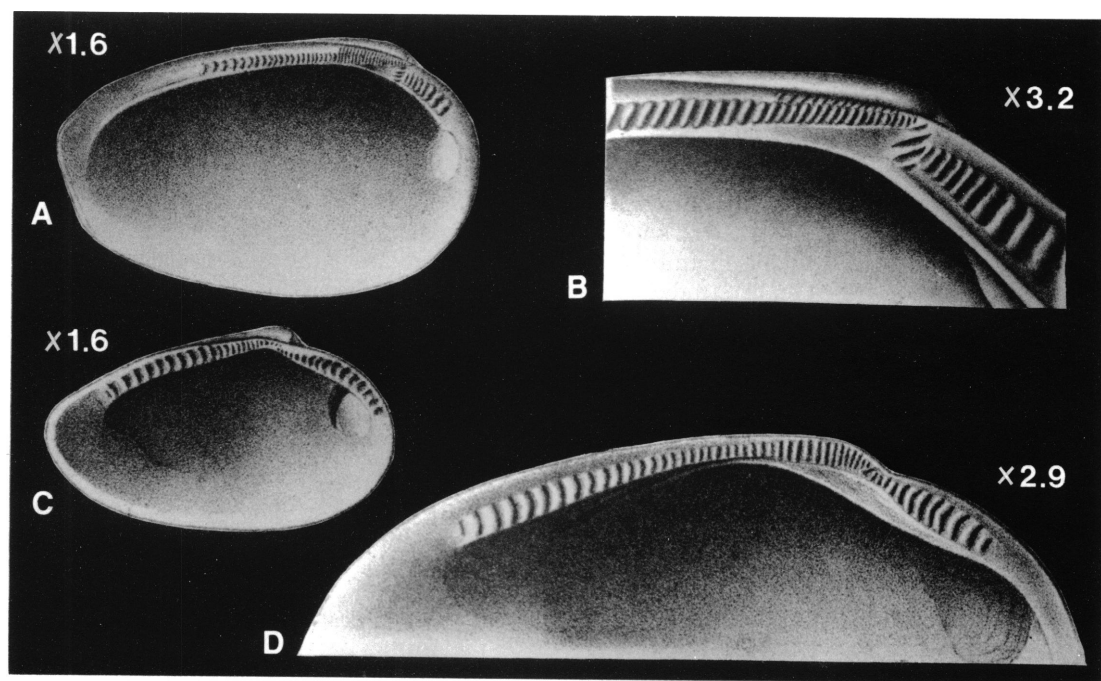


FIG. 40. *Palaeoneilo* Hall and Whitfield hinges as figured by Hall (1885). A, B. *P. secunda* in Hall (pl. 49: A—fig. 21, B—fig. 22). C. *P. plana* in Hall (pl. 48, fig. 26). D. *P. constricta* in Hall (pl. 48, fig. 15).

shell margin, a feature which also shows up in the growth lines near the same region. The sinus is associated with a broad, faint, radial sulcus in the shell extending from the umbo toward the posteroventral margin. Since this feature is subtle, it can best be seen under low-angle, high-contrast illumination.

Along shell margins (especially the anteroventral and posterodorsal margins), a thin commissural flange or brim is visible; this has probably resulted from diagenetic flattening. It seems likely that shell inflation and relief of the radial sulcus have been reduced by the same process.

Dentition of this species is poorly known. Here only the posterior portion of the taxodont tooth row is visible. Individual denticles are uniform, each possessing a short, vertically cylindrical shape, often with a slight tubercular swelling at upper and lower tooth extremities. The teeth decrease in strength toward the umbo. As illustrated by Hall (see fig. 40C, D), anterior and posterior tooth rows of *P. constricta* appear to thin and merge almost imperceptibly beneath the umbones

without the major interruption or deflection as seen in other species.

McAlester (1962a, 1963b, 1968) has observed that typical populations of *P. constricta* were polymorphic with respect to shell shape and prosopon. In the Solsville specimen prosopon consists of very fine, regular, concentric growth lines numbering as many as or more than eight lines per mm. Relief is very low on these, and they cannot be clearly discerned without optical aid. Neither radial elements, concentric undulations, nor growth varices are evident. Several of McAlester's (1962a, pl. 1, figs. 1–18) specimens show the same fine growth line pattern observed here; some of his others show variably developed concentric growth varices.

Marked shell shape variation exists among McAlester's *P. constricta* samples with respect to umbonal position and posterior elongation. In some individuals (e.g., McAlester, 1962a, pl. 1, fig. 17), umbones are almost middorsally placed; in most others they are more anteriorly located. Some individuals approach a suborbicular shape (e.g., Mc-



Alester, 1968, pl. 15, fig. 6) with a weak posteroventral sinus, whereas others (e.g., same pl., fig. 5) are more posteriorly elongate with prominent sinus and sulcus. Since the shell was probably thin as in *Nuculites*, inherent shape variability is no doubt aggravated by the relative ease of diagenetic distortion.

Many internal shell features are well known. The adductor and accessory musculature were described by McAlester (1963b). In the same work his plate 121, figures 2, 5, 8, 14, 18, and plate 122, figures 12–15, 17, show a posteriorly recessed pallial line with a small, distinct, posterior pallial sinus like *Nuculites*. Evidently *P. constricta* had small, extensible siphons.

One seemingly neglected shell feature variably developed in this species is an incipient internal anterior septum as shown in several of McAlester's (1962a, pl. 1, figs. 4, 6, 11, 12, 14) composite molds. In his figure 12 the "septum" appears to be little more than a strong rim of the anterior adductor scar (diagenetically exaggerated?). Others in his sample show little or no evidence of this feature.

**MEASUREMENTS:** The specimen measures 19.0 mm. in length and 12.5 mm. in height, slightly larger than the lectotype (from the Hamilton Group near Moravia, New York) which, according to McAlester (1968), measures 18 mm. in length and 12 mm. in height. His (1962a) 101 measured specimens had a median length of 16 mm. with shell height ranging from 41 to 86 percent of length. A similar size range is indicated by Hall (1885) with the largest specimen 25 mm. in length and 18 mm. in height.

**COMPARISONS:** Evaluations of several *Palaeoneilo* species occurring in the Upper Devonian are given in McAlester (1962a).

*Palaeoneilo constricta* is readily distinguishable from *P. filosa* found in the same beds. The former is smaller, more thin-shelled with less inflation and finer, more uniform prosopon; the posterior marginal sinus is more ventrally directed than in *P. filosa*, and the radial sulcus is weaker. The uniform, vertical, "dumbbell"-shaped denticles in *P. constricta* are seen in *P. filosa* near the umbones only; the remaining teeth in *P. filosa* are robust, chevron-shaped denticles.

Failure of early authors to recognize the broad variation of both prosopon and shell

form in normal populations of *P. constricta* has resulted in the proliferation of synonyms many of which seem, at best, polymorphic or diagenetic variants. The incipient, variably developed to absent septum has generated further confusion because past authors have accorded generic significance to its presence or absence. Thus, while one member of a population lacking it might be placed in *Palaeoneilo*, another member with the structure might be mistakenly assigned to *Nuculites* or *Cucullella*.

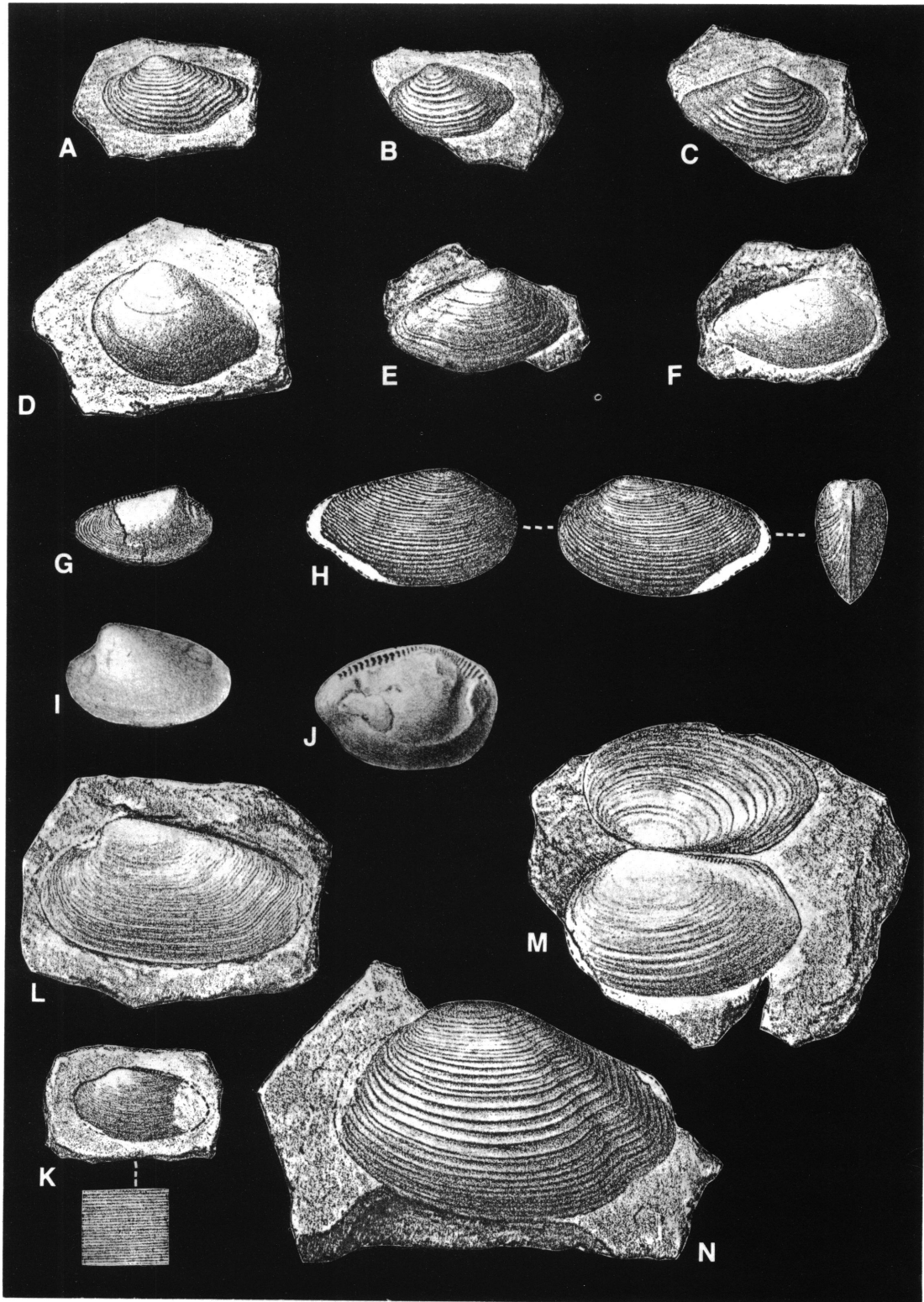
Descriptions and figures of past authors indicate few or no differences between *P. constricta* and several other species:

1. *Palaeoneilo maxima* (Conrad), 1841. Middle-Upper Devonian, New York. Poorly preserved material similar to *P. constricta*. McAlester (1962a) suspected that *P. constricta* is a junior synonym of the earlier *P. maxima* but advocated suspension of priority since the former is the morphologically well-grounded type species of *Palaeoneilo* and the material basis of the latter is poor. Adherence to priority, he maintained, would seriously undermine the diagnostic clarity of genus *Palaeoneilo*.
2. "*Nucula*" *bellatula* Hall, 1843. Devonian, New York. Hall's original figure, though generalized, is a clear example of *P. constricta* showing the fine lirae, sulcus, and taxodont hinge. Although Miller (1877) and Lesley (1889) erroneously placed Hall's species in synonymy with "*Nucula*" *bellistriata* Conrad (= *Carydium bellistriatum*; see Bailey, 1978a, 1979a), Hall (1885) himself considered it synonymous with *P. constricta*, and McAlester (1962a) agreed.
3. *Palaeoneilo plana* Hall and Whitfield, 1869. Middle Devonian (Hamilton), New York. A junior synonym of *P. constricta* applied to elongate variants with more subcentrally placed umbones and delicate prosopon. Hall (1885) compared it to *P. constricta*; his figures show only minor differences well within the range of observed variation. Placed in tentative synonymy with *P. constricta* by McAlester (1962a).
4. *Palaeoneilo brevis* Hall and Whitfield, 1869 (not *P. brevis* Beushausen, 1884). Upper Devonian (Chemung), New York-Pennsylvania. Needs restudy. Hall (1885) allied this species to *P. constricta*; McAlester (1962a) also placed it in tentative synonymy. Some of Hall's figures of this species agree with *P. constricta*; others do not. Hinge taxodont.

5. *Palaeoneilo bedfordensis* Meek, 1875. Lower Mississippian (Bedford Shale) of Ohio. Meek compared it to *P. brevis* Hall. The shell outline, prosopon, sulcus, and hinge shown in his figure 3b are convincingly similar to *P. constricta*. If conspecific it represents the latest known occurrence of the species.
6. *Palaeoneilo petila* Clarke, 1904. Upper Devonian (Sonyea Formation), New York. A probable junior synonym applied to small, elongated variants of *P. constricta*. Clarke compared this species to *P. constricta*; McAlester (1962a) placed it in tentative synonymy. Clarke's figures, especially his plate 15, figures 5–8, confirm McAlester's conclusion. Hinge taxodont.
7. *Palaeoneilo mainensis* Clarke, 1907a. Lower Devonian (Chapman Sandstone), Maine. Possible junior synonym. Shell form and dentition agree with *P. constricta*; incipient septum. Clarke compared it to *P. orbigny*, another possible synonym in part.
8. *Palaeoneilo folles* Clarke, 1907a. Lower Devonian (Helderbergian) Dalhousie Shale, New Brunswick. Possible junior synonym. Hinge unknown. Incipient septum? Clarke's three specimens are similar to *P. constricta*; one clearly shows the marginal sinus and radial sulcus.
9. *Palaeoneilo orbigny* in Clarke, 1909 (not *P. orbigny* Clarke, 1899, 1900). Lower Devonian (Chapman Sandstone), Maine. One of Clarke's (1909, pl. 28, fig. 23) specimens resembles *P. constricta*; hinge unknown. Affinities of other Maine specimens to Clarke's South American species, *P. orbigny*, uncertain. Williams and Breger (1916) regarded *P. orbigny* as synonymous with the European *Ctenodonta crassa* Beushausen, a species likely, in part, to be *P. constricta* (see below).
10. *Palaeoneilo crassa* Clarke and Swartz, 1913. Upper Devonian (Jennings Formation), Maryland. Based on an internal mold with continuous tooth row, musculature, and pallial line. McAlester (1962a) did not recognize this species due to lack of external morphology. The form and hinge are like *P. constricta*.
11. "*Nucula*" *snyderensis* Branson, 1924. Upper Devonian (Snyder Creek Shale), Missouri. Based mostly on internal molds. McAlester's (1963b) restudy leaves little doubt that this species, as well as "*N.*" cf. *lirata* of Branson, are synonymous with *P. constricta*.
12. *Palaeoneilo dentata* Pohl, 1929. Middle Devonian (Milwaukee Fm.), Wisconsin. Based on several small composite molds showing the hinge, shell outline and marginal sinus. Appears identical with *P. constricta*.
13. "*Ctenodonta*" *krotonis* Roemer, 1850. Middle Devonian (Eifelian), Germany, and Upper Devonian (Frasnian), France. Beushausen (1895) reproduced and Sandbergers' (1850–1856) figure of "*Cucullella*" *tenuiarata* and placed it in synonymy with "*C.*" *krotonis*. Beushausen's figures strongly resemble variants of *P. constricta* with delicate, regular prosopon, taxodont hinge, and poorly defined marginal sinus and sulcus (cf. fig. 44P). Babin (1966) placed it in synonymy with "*Ctenodonta*" sp. aff. *demigrans* (see below).
14. "*Ctenodonta*" *gemuendensis* Beushausen, 1895. Lower Devonian (Siegenian-lower Emsian), Germany. Hinge taxodont. A possible candidate for synonymy but too poorly known for confirmation.
15. "*Ctenodonta*" *elegans* Maurer, 1886. Lower Devonian (Emsian), Germany. Taxodont hinge. Maurer's (1902, pl. 4, fig. 12) specimen, designated lectotype by Mauz (1935), is a badly deformed internal mold, affinities unknown. But Beushausen's (1895) figure resembles a variant of *P. constricta* with more subcentral umbones, fine, regular prosopon and typical marginal sinus and radial sulcus.
16. "*Ctenodonta*" *daleidensis* Beushausen, 1895. Lower Devonian (Emsian), Germany. Hinge unknown but holotype profoundly resembles *P. constricta*. A probable synonym.
17. "*Ctenodonta*" *demigrans* Beushausen, 1895. Lower Devonian (Gedinnian? and Emsian), Germany and France. Lectotype designated by Mauz (1935) is Beushausen's, 1895, plate 6, figure 1. Hinge unknown. Probable synonym. Beushausen observed the extraordinary similarity to *P. constricta*; kinship seems especially pronounced in the lectotype. Babin's (1966) "*C.*" sp. aff. *demigrans* (Upper Devonian Frasnian of France) are internal molds with well-preserved hinges; the form is of *P. constricta* with incipient septum. Babin (1966) considered it very similar if not identical to *P. petila* Clarke (see above).
18. "*Ctenodonta*" *planiformis* Beushausen, 1895. Lower Devonian (Emsian), Germany. Lectotype designated by Mauz (1935) is Beushausen's, 1895, plate 6, figure 3. Beushausen noted the similarities of this species to *P. plana*, a probable synonym of *P. constricta*. The lectotype is a composite mold with partial hinge. Similarities to *P. constricta* are strong.
19. "*Ctenodonta*" *maureri* Beushausen, 1895. Lower Devonian (Emsian), Germany. Probable junior synonym of *P. emarginata* (Conrad), 1841. Hinge taxodont. Very similar to weaker variants of *P. emarginata* (Middle-Upper Devonian, New York) as illustrated by

- Hall (1885, pl. 50, figs. 4–6) and Cleland (1911, pl. 20, figs. 11, 12; = *P. corrugata* Pohl, 1929, pl. 4, figs. 26–33). Also similar in part to *P. sulcatina* (Conrad) of Hall (1885, pl. 50, fig. 43) and in part to *P. constricta* var. *flexulosa* of Hall (1885, pl. 48, fig. 17). The shells are like *P. constricta* but the prosopon is more coarsely lirate and sinus/sulcus more sharply defined. Variants in populations of *P. constricta* approach this morphology but are uncommon. Beushausen described nine subspecies of “*C.*” *maureri*; all need restudy. Mauz (1935) designated lectotypes of “*C.*” *maureri maueri* Beushausen and “*C.*” *maureri dunensis* Beushausen. Kegel’s (1913, pl. 4, fig. 8) “*C.*” (*Palaeoneilo*) *maureri* var. *obsoleta* Beushausen is probably *P. constricta*.
20. “*Ctenodonta*” *megaptera* Beushausen, 1895. Lower Devonian (Emsian), Germany. Hinge unknown. Similar to “*C.*” *maureri*.
  21. “*Ctenodonta*” *primaeva* Steininger, 1853. Lower Devonian (Emsian), Germany. Lectotype designated by Mauz (1935) is plate 3, figure 9a of Steininger. Beushausen’s specimens are internal molds with taxodont hinge and external ligament. Has the general form of *P. constricta* but sinus/sulcus (?) absent. See also remarks of Babin (1966, p. 66).
  22. “*Ctenodonta*” *crassa* Beushausen, 1895 (not *P. crassa* Clarke and Swartz, 1913). Lower Devonian (Emsian), Germany. Beushausen’s plate 6, figure 4, 4a, shows an internal mold similar to *P. constricta* with well-preserved taxodont hinge; but his plate 6, figure 5a, b, of the shell exterior does not seem to agree with the internal mold. Needs restudy.
  23. “*Ctenodonta*” (*Palaeoneilo*) *candida* Kegel, 1913. Lower Devonian (Siegenian), Germany. Although Kegel indicated that this species closely compares with *P. primaeva* Steininger, his figure shows a stronger resemblance to *P. constricta*.
- Other European species showing certain similarities to *P. constricta* but requiring further study include: “*Ctenodonta*” *laevis* Beushausen, 1884, plate 3, figure 10; *Palaeoneilo obovata* Beushausen, 1884, plate 3, figure 17; and “*Ctenodonta*” *hercynia*? Beushausen of Spriestersbach, 1915 (in part), plate 3, figures 14?, 16?, 17?, 18? (not figs. 15, 18a).
- Palaeoneilo filosa* (Conrad), 1842  
Figures 5G, 42, 43A, 44A–L
- Nuculites filosa* Conrad, 1842, p. 250, pl. 15, fig. 7.
- Palaeoneilo* [sic] *filosa* (Conrad). Hall and Whitfield, 1869, p. 10.
- Palaeoneilo filosa* (Conrad). Miller, 1877, p. 199. Hall, 1883, pl. 49, figs. 33–38; 1885, p. 343, pl. 49, figs. 33–38. Kindle, 1896, p. 43. Whitfield and Hovey, 1900, p. 296. Clarke and Ruedemann, 1903, p. 477. [not] Clarke and Swartz, 1913, p. 623, pl. 61, figs. 11, 12. [?] Willard, 1939, p. 477, etc., pl. 26, fig. 26. McAlester, 1962a, p. 16. Ellison, 1965, p. 127, pl. 15, fig. 6. Palmer and Brann, 1966, pl. 1, fig. 12.
- Palaeoneilo* [sic] *fecunda* Hall and Whitfield, 1869, p. 8. Whitfield, 1882, p. 357; 1883, p. 369.
- Palaeoneilo foecunda* [sic] Hall [and Whitfield]. Miller, 1877, p. 199.
- Palaeoneilo fecunda* Hall [and Whitfield]. Hall, 1883, pl. 49, figs. 13–24; 1885, p. 336, pl. 49, figs. 13, 15–24. Lesley, 1889, p. 581, 2 figs. Kindle, 1896, p. 43. Grabau, 1899, p. 257, fig. 175. Clarke and Ruedemann, 1903, p. 476. Cleland, 1903, p. 65. 1911, p. 103, pl. 20, figs. 13, 14. Grabau and Shimer, 1909, p. 399, figs. 510k, l. Prosser and Kindle, 1913, p. 239, pl. 26, figs. 18–21. [?] Willard, 1939, p. 477, etc., pl. 26, fig. 25. Shimer and Shrock, 1944, p. 377, pl. 146, fig. 23. McAlester, 1962a, p. 17. Ellison, 1965, p. 128, pl. 15, fig. 7. Bailey, 1975, p. 183, pl. 13, figs. 1–9, pl. 14, figs. 1–8, pl. 15, figs. 1–4, text-figs. 27b–31; 1978a, p. 121. [Not *P. fecunda* (Hall), Pojeta, 1971, pl. 1, figs. 1–8 (= *Ctenodonta fecunda* (Hall) Ulrich, 1894, 1897, p. 595; = *Nucula* (*Tellinomya*) *fecunda* Hall, 1862, p. 55).]
- Palaeoneilo* [sic] *tenuistriata* Hall and Whitfield, 1869, p. 9.
- Palaeoneilo tenuistriata* Hall and Whitfield. Whitfield and Hovey, 1900, p. 296.

FIG. 41. European *Palaeoneilo* Hall and Whitfield as figured by Beushausen (1895). A. “*Ctenodonta*” *megaptera* Beush. (pl. 7, fig. 29). B, C. “*C.*” *maureri* Beush. (pl. 7: B—fig. 24, C—fig. 18). D. “*C.*” *demigrans* Beush. (pl. 6, fig. 1). E, F. “*C.*” *planiformis* Beush. (E—pl. 6, fig. 3, F—pl. 7, fig. 5). G. “*C.*” *krotonis* Roemer in Beush. (p. 5, fig. 25). H. “*C.*” *daleidensis* Beush. (pl. 6, fig. 6). I. “*C.*” *primaeva* Steininger in Beush. (pl. 5, fig. 29). J. “*C.*” *crassa* Beush. (pl. 5, fig. 4b). K. “*C.*” *gemuendensis* Beush. (pl. 5, fig. 26). L. “*C.*” *beushauseni* Kegel (= “*C.*” *oehlerti* Beush. not Barrois) in Beush. (pl. 7, fig. 2). M. “*C.*” *bertkaui* Beush. (pl. 6, fig. 17). N. “*C.*” *unioniformis* Sandberger in Beush. (pl. 6, fig. 12). All figures  $\times 1$  of Beushausen.



- Palaeoneilo tenuistriata* Hall [and Whitfield]. Miller, 1877, p. 199. Hall, 1883, pl. 49, figs. 1–12; 1885, p. 336, pl. 49, figs. 1–12, 14, pl. 93, fig. 13. Lesley, 1889, p. 583, 2 figs. Grabau, 1899, p. 257, fig. 174; 1906, p. 330. Clarke and Ruedemann, 1903, p. 479. Cleland, 1903, p. 65. Grabau and Shimer, 1909, p. 399, fig. 510c. Prosser and Kindle, 1913, p. 242, pl. 27, figs. 7–9. [not] Willard, 1939, p. 477, etc., pl. 26, fig. 30. McAlester, 1962a, p. 17. Ellison, 1965, p. 126, pl. 15, fig. 3. Palmer and Brann, 1966, pl. 15, figs. 7, 8. Bailey, 1975, p. 183; 1978a, p. 121.
- †*Palaeoneilo* cf. *plana* Hall [and Whitfield]. Cleland, 1911, p. 104, pl. 20, figs. 15[?], 16. [Not *P. plana* Hall and Whitfield, 1869, p. 7.]
- †*Palaeoneilo grandis* Butts, 1926, pl. 160, fig. 26.
- †*Palaeoneilo pulchella* Pohl, 1929, p. 37, pl. 4, figs. 46–51, pl. 5, fig. 1. [= *P. fecunda* Hall [and Whitfield]. Cleland, 1911, p. 103, pl. 20, figs. 13–14.]
- †[?] *Palaeoneilo milwaukeensis* (Cleland). Pohl, 1929 [in part], pl. 3, fig. 16, figs. 18[?]-25[?] [not fig. 17, = *Nuculites milwaukeensis* Cleland, 1911].
- †[?] *Ctenodonta bertkaui* Beushausen, 1895, p. 80, pl. 6, fig. 17, pl. 7, fig. 8[?]. [= *C. (Palaeoneilo) bertkaui* Beushausen. Mauz, 1935, p. 54.] [See other ref. in Maillieux, 1937, p. 174.]
- †[cf.] *Ctenodonta unioniformis* Sandberger and Sandberger. Beushausen, 1895 [in part], p. 84, pl. 6, fig. 12. [= *C. (Palaeoneilo) unioniformis* Sandberger. Mauz, 1935, p. 53.] [?Not *P. unioniformis* (Sandberger). Maillieux, 1937, pl. 10, fig. 11. See other ref. in Maillieux, p. 173.]
- †[?] *Ctenodonta (Palaeoneilo) beushauseni* Kegel, 1913, p. 72. [= *Ctenodonta oehlerti* Beushausen, 1895, p. 82, pl. 7, figs. 1, 2. Not *C. oehlerti* Barrois, 1891, p. 184, pl. 1, fig. 5.] [See other ref. in Maillieux, 1937, p. 170, and in Babin, 1966, p. 78.]
- †[?] *Palaeoneilo?* cf. *beushauseni* Kegel [sic]. Babin, 1973, p. 45, pl. 1, fig. 8.
- †[?] *Ctenodonta moehrkei* Dahmer, 1934, p. 59, pl. 3, fig. 5; 1936, p. 22, pl. 5, figs. 1, 2.

**DESCRIPTION:** Shells thick, medium to large, equivalve, strongly to moderately inflated, posteriorly elongate. Shape smoothly curving, ovate; slight, variably developed posterior marginal sinus with faint radial sulcus. Umbones low, rising only slightly above hinge line, anteriorly placed.

Prosopon variable. Early growth stages with fine to moderately fine, regularly spaced, concentric growth lirae (fig. 42D) becoming irregular, variably defined, and progressively punctuated with irregular coarse lirae in later stages of growth. Shell surface often concen-

trically undulaform or rugose with strong growth varices in large adults. Very fine, faint radial lineations are variably developed to absent.

Ligament external, opisthodontic, parivincular; ligamental area bordered by a pair of linear insertional grooves.

Dentition taxodont, hinge plate narrow. As many as 40 teeth in the posterior row; as few as 10 in the anterior row. All teeth oriented with long axes perpendicular to shell dorsal margin. Posterior tooth row with two kinds of teeth: the first 13 or 14 hindmost teeth are large, robust, erect chevronal blades with deep intervening sockets; they diminish anteriorly and are replaced by finer, shorter, vertical teeth with low relief. These are cylindrical, often with dorsal, ventral or medial swellings resulting in a series of faint dumbbell shapes. Anterior tooth row with strong, erect, chevronal teeth and sockets diminishing toward the umbones and becoming more cylindrical. Beneath the umbones the tooth rows do not exactly meet but are visibly offset, the posterior row displaced upward. In the space between lies a small group of obliquely radiating teeth (these are faint—little more than striae) occupying a slightly depressed triangular area (resilifer?) beneath the umbones where the hinge plate noticeably widens.

Pallial line recessed, more deeply so posteriorly where it is faintly sinupalliate.

Adductors isomyarian, scars ovoid, placed directly beneath the hinge plate near each extremity. Each scar is more deeply impressed along its dorsal circumference, weakly impressed below. An internal mold indicates an oblique row of small umbonal muscle pits (pedal protractors and anterior pedal retractors). A long posterior groove beneath the hinge plate in each valve (seen in two specimens—not figured) probably represents the line of attachment of posterior retractor muscles.

A broad, short, internal buttress (i.e., incipient septum or clavicle) lying in each valve just behind the anterior adductor scar is seen inside a left valve and indicated on two internal molds by a broad notch in the same position.

Original shell microstructure and mineralogy unknown.

**REMARKS ON MORPHOLOGY:** Valves typically show great shape variability probably exaggerated by diagenetic flattening.

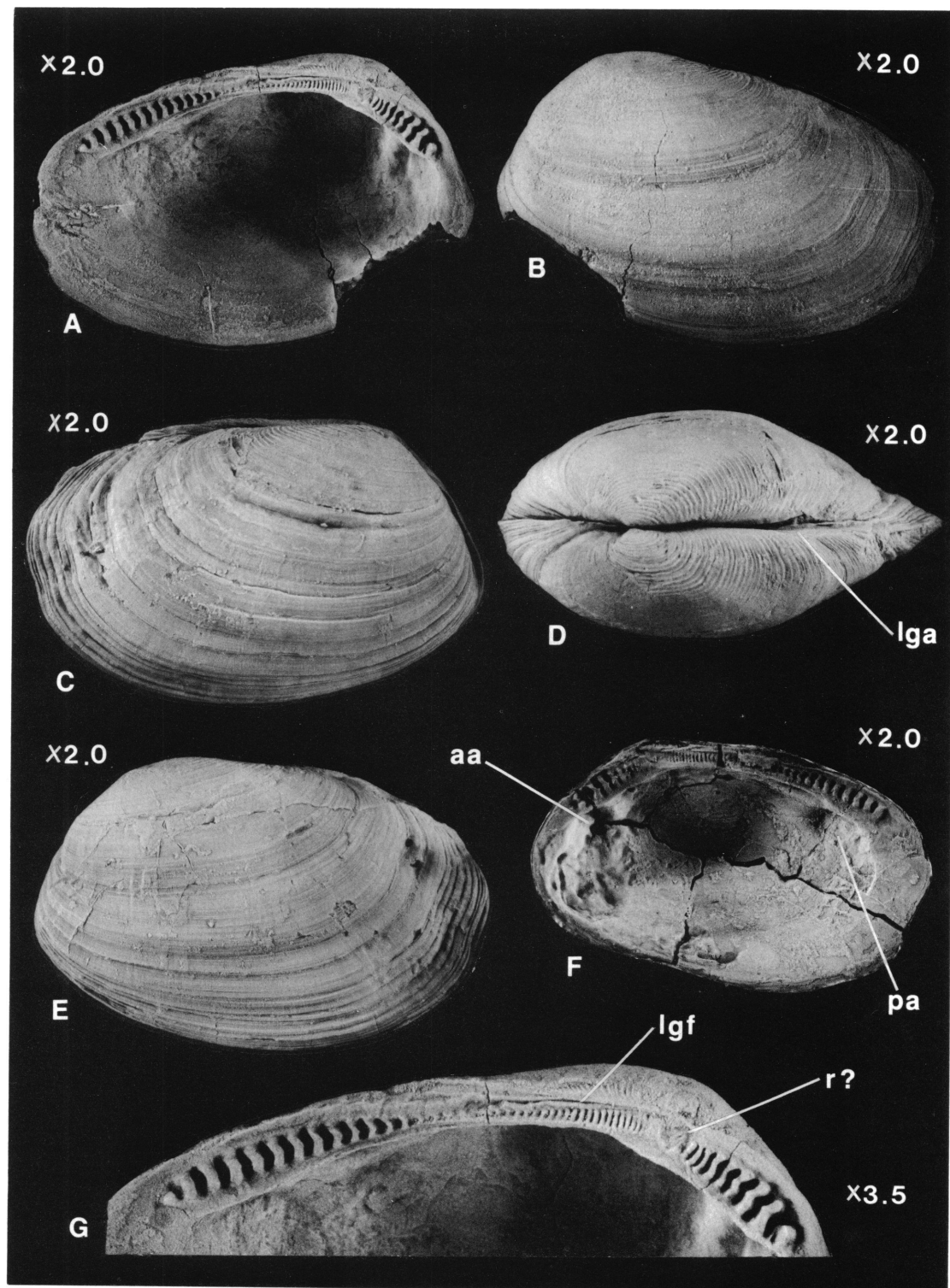


FIG. 42. *Palaeoneilo filosa* (Conrad). A, B, G. A left valve (AMNH 36233) from AMNH loc. 3017. A. Internal view. B. External view. G. Enlargement of hinge. C–E. Articulated specimen (AMNH 36244) from AMNH loc. 3012. C. Right valve. D. Dorsal view. E. Left valve. F. Broken left valve interior (AMNH 36225) from AMNH loc. 3013.

Abbreviations: aa—anterior adductor scar, lgf—ligamental furrow, pa—posterior adductor scar, r?—resiliifer?



TABLE 8  
Measurements (in Millimeters) of *Palaeoneilo  
filosa* (Conrad)

Locality	Length	Height	Width <sup>a</sup>
AMNH 3013	35.2	20.7	17.3
	34.6	20.0	19.5
AMNH 3014	38.0	24.9	—
AMNH 3017	30.3	19.4	18.0
	35.7	21.7	18.0
	34.6	18.9	14.5 <sup>b</sup>
	32.3	23.3	12.4 <sup>b</sup>
	32.0	20.7	—
	29.0	17.9	15.7
	30.7	18.8	—

<sup>a</sup> Total width, both valves articulated.  
<sup>b</sup> Laterally crushed.

The ligament of *Palaeoneilo* has been poorly known. However, figure 44B, D show two weathered, external, opisthodontic ligamental areas (nymphs) with short, close, obliquely parallel striations or lamellae. These cannot be growth lines which have a near tangential orientation along the hinge line. Similar striae are seen where the fibrous ligamental layer attaches to the nymph in many Recent taxa. Along the posterior outer borders of the nymph in each valve is a narrow groove (suture), probably for the insertion of an outer, (?)lamellar or (?)fusion ligamental layer. Another groove or furrow is visible between the nymph and the hinge plate in a left valve (*lgf* in fig. 42G) may also be related to ligamental insertion.

The dentition seen here is roughly similar to Hall's gutta percha impression of a lost internal mold of "*P. fecunda*" (= *P. filosa*) reproduced here in figure 40A, B. However, the cylindrical shapes of the forward members of the gutta percha anterior tooth row do not agree with the slightly chevronal teeth (like those in fig. 42G) of the internal mold on which it was supposedly based (i.e., Hall's 1885, pl. 49, figs. 19–21). Nevertheless, Hall's short, oblique tooth row connecting the offset, subumbonal terminations of anterior and posterior tooth rows do seem verified in Solsville figure 42G. But here they are faint, not so mutually parallel but slightly radiating, and set within a shallow, triangular depression which seems related to a ventral expansion

of the hinge plate just below. I earlier (1975) speculated that this trigonal depression is a resilifer and suggested that superposition of it and the small group of radiating teeth has perhaps resulted from an ontogenetic change from a nonresiliated to a resiliated condition, the (?)earlier, partially eradicated denticles on the "resilifer" floor serving as loci for later insertion of the resilium. However, the prominent external ligament here and apparent lack of resilia in other malletioid genera do not support a resilifer interpretation of this structure. But, since near-relatives, the nuculanids, may possess both resilifer and external ligament (e.g., see Tebble, 1966, p. 23), such an interpretation is not unreasonable. A second hinge (fig. 42F) is too poorly preserved to settle the question.

Hall's (1885) plate 49, figures 19, 20, 24 show an internal mold with two rows of umbonal accessory scars in a right valve; six in the upper row and two in the lower row. His left valve, however, shows only four such scars. The right Solsville internal mold (fig. 44H) shows a single row of five scars.

The posterior marginal embayment, radial sulcus, posterior sinuities in the growth lines and posteriorly recessed, faintly sinuous pallial line suggest extensible siphons in *P. filosa*.

COMPARISONS: I earlier (1975, 1978a) placed this Solsville species in *Palaeoneilo fecunda* Hall and Whitfield; I now regard them as *P. filosa*, a species originally described from the Upper Devonian (Chemung), near Ithaca, New York. Kindle (1896) early noticed the similarities of *P. filosa* and *P. fecunda*. McAlester (1962a) speculated that *P. filosa* would probably prove to be the senior subjective synonym of the *P. fecunda*–*P. tenuistriata* group. Conrad's original drawing (1842, pl. 15, fig. 7), like many of his others, is either a generalized composite attributable to no single specimen or based upon a single specimen now lost (see remarks of McAlester, 1962a, p. 18; 1968, p. 37). Conrad's figure and Hall's (1883, 1885) topotypic specimens of *P. filosa* appear to be nothing more than smaller growth stages of *P. fecunda*–*P. tenuistriata*. *P. filosa* of Clarke and Swartz (1913) is not *P. filosa* of Conrad and of Hall but should be referred to either *P. bisulcata* Hall and Whitfield (see McAlester, 1962a, p. 19) or *P. angusta* Hall and Whitfield.



The best Solsville specimens show ontogenetic loss of prosoponal regularity. Taxonomic confusion naturally results when small individuals with regular growth lines are contrasted with larger individuals showing numerous irregular lirae and varices. Size differences and prosoponal variation combined with diagenetically exaggerated shell shapes have resulted in the proliferation of several probable synonyms:

- 1, 2. *Palaeoneilo fecunda*—*P. tenuistriata* Hall and Whitfield. From many of the same localities in the Middle Devonian (Hamilton) of New York and Maryland. *Palaeoneilo fecunda* Hall and Whitfield is not to be confused with the Ordovician *P. fecunda* (Hall) *sensu* Pojeta (1971) which is a secondary homonym originally described as *Nucula* (*Tellinomya*) *fecunda* by Hall (1862) and later called *Ctenodonta fecunda* by Ulrich (1894, 1897).

Hall's (1885) descriptions and figures do not adequately delineate *P. fecunda* Hall and Whitfield from *P. tenuistriata*. McAlester (1962a) speculated that the two are synonymous. I have examined Hall's syntypes of both *P. fecunda* Hall and Whitfield (NYSM 2938, Hamilton, Skaneateles Lake, New York; NYSM 2939–2942, Hamilton, Cumberland, Maryland) and *P. tenuistriata* (NYSM 2954, 2955, 2958, Hamilton, Skaneateles Lake, New York; NYSM 2956, 2957, Hamilton, Pratt's Falls, New York; AMNH 5300, Hamilton, various localities, New York). The shape and prosopon in the syntypes are variable, and both sets broadly overlap or intergrade morphologically. The Solsville material compares favorably with either set. Some differences exist—e.g., a specimen in AMNH lot 5300, *P. tenuistriata*, Pratt's Falls, Onondaga County, New York (fig. by Hall, 1885, pl. 49, figs. 2, 3) shows finer, more regular growth lines and a less undulaform shell—but these differences are not marked. Among other specimens in the same lot, the dentition and single row of five umbonal muscles are similar to the Solsville specimens; the dentition is also similar to Hall's (1885, pl. 49, figs. 19–21) *P. fecunda* (whereabouts of this syntype unknown).

Solsville *P. filosa* are also closely similar to several lots of specimens in the USNM collections including:

USNM (uncatalogued) *Palaeoneilo*. Hamilton (Delphi). On U.S. 20, 1¼ mi E. of Pompey Center, New York (see fig. 45F, G, J).

USNM 101791 *P. tenuistriata*. Hamilton (Ludlowville), Kashong Creek, New York.

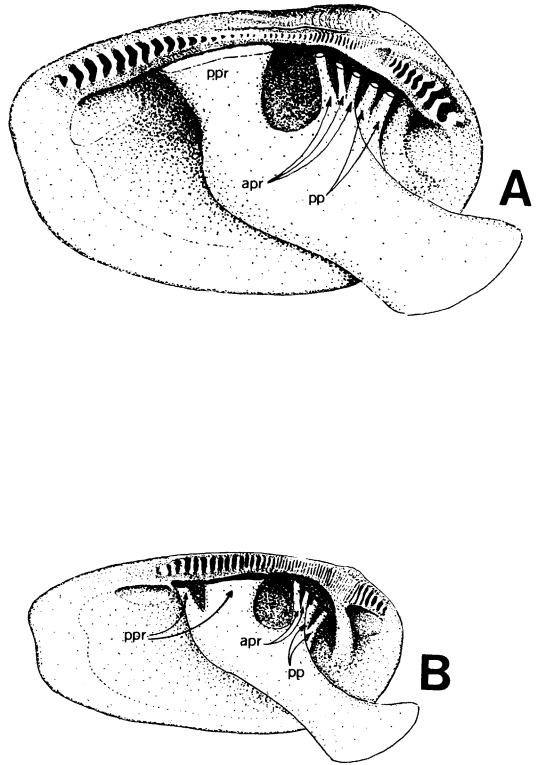


FIG. 43. Pedal musculature reconstruction in two Solsville nuculanaceans. A. *Palaeoneilo filosa* (Conrad). B. *Nuculites oblongatus* Conrad. Based on muscle scars observed here in homology to Recent *Yoldia* Møller (compare with fig. 31B of Cox et al., p. N30, in Moore, 1969).

Abbreviations: apr—anterior pedal retractor, pp—pedal retractor, ppr—posterior pedal retractor.

USNM 101793 *P. tenuistriata*. Hamilton (Moscow), Cayuga Lake, New York (see fig. 45L).

USNM 101835 *P. tenuistriata*. Hamilton (Ludlowville), Elma, New York.

USNM 10935 *P. tenuistriata*. Hamilton, Cayuga Lake, New York.

USNM (uncatalogued) *P. tenuistriata*. Hamilton (Ludlowville), Eighteen Mile Creek, New York.

Solsville *P. filosa* were statistically compared with USNM specimens above and with published dimensions of *P. fecunda* from Hall (1885) and Prosser and Kindle (1913) in Bailey (1975, text-fig. 29). Although the differences in slopes and y-intercepts of the regression lines are obvious, these differences are more apparent than real since: (1) too few

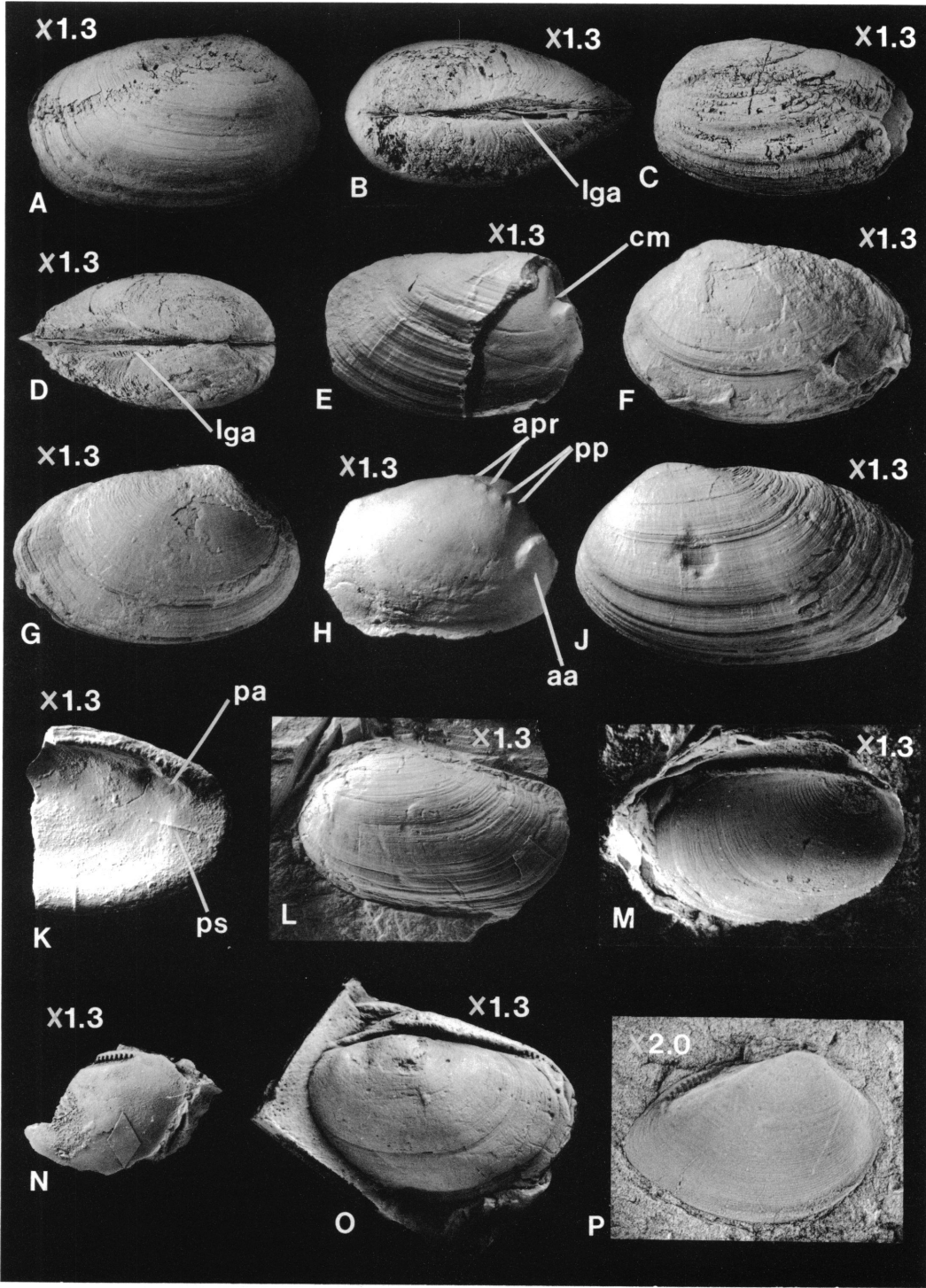


FIG. 44. A–N. *Palaeoneilo filosa* (Conrad). A, B. Articulated specimen (AMNH 36229) from AMNH loc. 3013. A. Right valve. B. Dorsal view. C, D. Articulated specimen (AMNH 36230) from AMNH loc. 3017. C. Left valve. D. Dorsal view. E. Right valve of articulated specimen with internal mold

specimens were available for a valid statistical sample; (2) the available USNM individuals are unfortunately from various Hamilton formations; (3) diagenetic differences among the specimens are evident; (4) only relatively large specimens were found among the Solsville samples; (5) the species commonly shows broad inherent variability.

3. *Palaeoneilo* cf. *plana* Hall [and Whitfield] of Cleland, 1911. Middle Devonian, Berthelet, Wisconsin. A probable synonym, at least in part. One of Cleland's figured specimens is a right (?) composite or internal mold with the outline of *P. filosa*; his other figured specimen is a better preserved right valve with shape and prosopon identical with *P. filosa*. Hinge unknown.
4. *Palaeoneilo grandis* Butts, 1926. Lower Devonian (Onesquethawan) Frog Mountain Sandstone, Odenville, Alabama. A probable synonym. Portions of a syntype and plastocotype (fig. 44M, O) show a size and shape similar to the moderately regular, undulaform varieties of Solsville *P. filosa* and *P. fecunda* (cf. AMNH 5300 fig. by Hall, 1885, pl. 49, figs. 2, 3). Compare with figure 44F, G of the present paper. Butts's other syntype (fig. 44N) is a fragment of an internal mold with partial hinge too incompletely preserved for identification.
5. *Palaeoneilo pulchella* Pohl, 1929. Middle Devonian Milwaukee Formation, Wisconsin. Cleland (1911) called the types of this species *P. fecunda* Hall and Whitfield. Pohl's photographs show the shell shape, prosopon, hinge, and internal mold. There is no basis for regarding this as a separate species.
6. *Palaeoneilo milwaukeeensis* (Cleland) of Pohl, 1929 (in part). Middle Devonian Milwaukee Formation, Wisconsin (not *Nuculites milwaukeeensis* Cleland). Several figured specimens of *P. milwaukeeensis*, *sensu* Pohl are likely to be *P. filosa*, especially his plate 3, figure 16. Others are diagenetically deformed and too poorly preserved for confirmation.
7. "*Ctenodonta*" *bertkaui* Beushausen (1895). Lower Devonian (Siegenian-Emsian), Germany and Belgium. Hinge taxodont; interior unknown. Lectotype, designated by Mauz (1935), is Beushausen's plate 6, figure 17. Of Beushausen's two figured specimens, the lectotype (reproduced here as fig. 41M) suggests *P. filosa* but the drawing is not clear enough to be certain.
8. "*Ctenodonta*" *beushauseni* Kegel (1913). Originally described as *C. oehlerti* Beushausen (1895), a primary homonym of *C. oehlerti* Barrois (1891). Lower Devonian (Siegenian-Emsian) of Germany, Belgium and France. Mauz (1935) designated Beushausen's plate 7, figure 2 as the lectotype. Hinge and interior unknown. Of Beushausen's two figured specimens, the lectotype is most like *P. filosa*. It shows similar outline and growth lines; the same posterior marginal sinus is visible in the prosopon.
9. "*Ctenodonta*" *unioniformis* Sandberger and Sandberger (1856). Lower Devonian (Siegenian-Emsian), Germany and Belgium. Mauz (1935) designated plate 29, figure 2, of Sandberger and Sandberger as lectotype. Hinge taxodont. Large palaeoneilos with sharply defined prosopon; probably a valid but closely related species. One individual figured by Beushausen (reproduced here as fig. 41N) closely approaches the prosopon and shape of *P. filosa* seen in figure 42E. Maillieux's (1937, pl. 10, fig. 11) photograph shows a modioloid or modiomorphoid shell shape and may not be this species.
10. "*Ctenodonta*" *moehrkei* Dahmer, 1936. Lower Devonian (Siegenian), Germany. Specimens with form and prosopon identical to Solsville *P. filosa* but larger. Aside from the size differences, the similarities seem convincing. Conspecific or very closely related.

AUTECOLOGY: *Nuculites* and *Palaeoneilo* are encountered in both Solsville facies. A single specimen of *P. constricta* was found in the arenaceous facies, and one specimen of *N. triqueter* was located in each of the facies.

(AMNH 36226) from AMNH loc. 3017. F, G. Lightly flattened articulated specimen (USNM uncatalogued), Hamilton (Delphi), Pompey Center, New York. F. Left valve. G. Right valve. H. Right internal mold (AMNH 36227) from AMNH loc. 3017. J. Left valve (USNM uncatalogued), Hamilton (Delphi), Pompey Center, New York. K. Partial right valve interior (AMNH 36228) from AMNH loc. 3013. L. Left valve (USNM 101793), Hamilton (Moscow), Cayuga Lake, New York. M-O. "*P. grandis*" Butts (= *P. filosa*). M. Syntype. External mold. N. Syntype. Partial internal mold. O. Plastocotype. Plastic cast of M. P. *Palaeoneilo constricta* (Conrad). Right valve (AMNH 36232) from AMNH loc. 3013.

Abbreviations: aa—anterior adductor scar, apr—anterior pedal retractor scar, cm—incipient clavicle (septum) mold, lga—ligamental area (nymph), pa—posterior adductor scar, pp—pedal protractor scar, ps—pallial sinus.

*Palaeoneilo filosa* and *N. oblongatus* inhabited both facies; however, they are considerably more abundant in the argillites in association with *Nuculoidea* indicating a preference typical of deposit feeders for softer, finer grained substrates.

Figures 5 and 6 show possible life positions in *Palaeoneilo* and *Nuculites* somewhat like those shown by Bowen, Rhoads, and McAlester (1974, fig. 11) for the same genera and by Thayer (1974, fig. 18G) and Levinton and Bambach (1975, figs. 11, 12) for *Nuculites*. Fairly similar life orientations are shown by Stanley (1970, pl. 2) in the Recent nuculanaceans *Yoldia limatula* (Say) and *Y. perprotracta* Dall, with the valves entirely buried in the mud, posterior extremity upward, the extensible siphons protruding slightly from the substrate.

The heavy shell with coarse prosopon elements and wide, subcircular cross-section in unflattened *P. filosa* specimens suggest sluggish, shallow burrowing habits. *Nuculites oblongatus* was probably a rapid, more deeply burrowing species as evidenced by the long, *Solen*-like shells. The narrow cross-sections and smooth prosopon would enable this species to penetrate the sediments quickly with minimal resistance. The shells of *P. constricta* and *N. triqueter* are intermediate in inflation suggesting burrowing rapidity somewhere between *P. filosa* and *N. oblongatus*. The tall umbones and inflated shells of *N. triqueter* are convergent on those of the Nuculidae, perhaps indicating similar shallow infaunal life positions (see Stanley, 1970).

The development of extensible siphons in *P. filosa*, *P. constricta*, and *N. oblongatus* is supported by the posterior elongation of the shell and sinuous pallial line moderately to deeply recessed from the posterior shell margins. Among these nuculanaceans, however, the pallial line is only faintly sinuous in contrast to the deeply embayed pallial sinus of Recent *Yoldia*. This suggests that the siphons of the fossil forms were proportionately shorter; hence they were probably shallow burrowers. Given the weaker pallial sinus in some *P. constricta* figured in the literature, its siphons were perhaps even shorter suggesting very shallow burial. Reliable pallial line data on *N. triqueter* is lacking.

It is likely that the near vertical shell pos-

ture (anteroposterior axis normal to sediment/water interface), shown here in figures 5 and 6 and the figures of Bowen, Rhoads, and McAlester (1974) and Thayer (1974), was not consistently maintained. Although steep shell angles are common for Recent taxa such as *Y. limatula* and *Y. perprotracta* in their native muds, the anteroposterior axis is often less than 40° and 30° respectively from the horizontal in aquaria (Stanley, 1970). Dorsoventral flattening of some probably *in situ* specimens of *P. filosa* with articulated valves suggest that often the anteroposterior axis may have likewise been oriented at some low angle near the horizontal. Several transversely flattened, articulated *N. oblongatus* and *P. filosa* were found reclining laterally. These may also be life positions since Stanley (1970) showed that members of the Nuculidae (e.g., *Nucula proxima*) occasionally depart from an upright orientation, adopting a reclining pose on either valve.

The *P. constricta* specimen is a disarticulated right valve, probably not *in situ* and, hence, provides no direct data on life position. Nevertheless, life position of this species was probably somewhat different from *P. filosa* since the posterior marginal embayment and radial sulcus are more ventrally placed in the former than in the latter. Because the embayment is a manifestation of the siphonal position, a much steeper growth position (anteroposterior axis near vertical) would be necessary in *P. constricta* to allow the short siphons to reach the substrate surface.

SUBCLASS ANOMALODESMATA DALL, 1889  
ORDER PHOLADOMYOIDA NEWELL, 1965  
SUPERFAMILY PHOLADOMYACEA GRAY, 1847  
FAMILY GRAMMYSIIDAE MILLER, 1877  
(=SANGUINOLITIDAE MILLER, 1877)  
GENUS GRAMMYSIOIDEA  
WILLIAMS AND BREGER, 1916

TYPE SPECIES: *Grammysia (Grammysioidea) princiana* Williams and Breger (1916) by original designation from the Lower Devonian Moose River Sandstone, Maine.

GENERIC USAGE: *Grammysia* and *Grammysioidea* include many large, thin-shelled species of variable shape with coarsely concentric prosopon corrugations. *Grammysioidea* was originally proposed as a subgenus

of *Grammysia* de Verneuil for species lacking radial prosoponal cinctures, while *Grammysia*, *sensu stricto* was reserved for species with either one or two cinctures. Although McAlester (1962a) suggested raising *Grammysioidea* to generic rank, Shimer and Shrock (1944) had already done so using Williams's and Breger's criteria as the basis for their diagnosis. McAlester (1962a) rejected these criteria noting they would effectively place closely related species such as *Grammysia arcuata* and *G. subarcuata* into separate genera. And, since a single cincture may be variably developed to absent within certain species, variants of the same population would likewise be generically subdivided. McAlester therefore tentatively redefined these genera pending a needed revision of the Grammysiidae, confining *Grammysia* to doubly cinctured species and *Grammysioidea* to singly cinctured or noncinctured forms. His diagnosis was accepted by later authors (e.g., Newell and LaRocque in Moore, 1969) and Runnegar (1974). But, Newell and Runnegar (1974) and Runnegar (1974) added that the external opisthodetic ligament in *Grammysioidea* characteristically splits anteriorly during growth, and the lunule is not as well defined as in *Grammysia*.

In support of the generic distinctiveness of *Grammysia* and *Grammysioidea*, McAlester (1962a) attempted to supply evidence that the two represent separate Middle-Upper Devonian phyletic lineages. In *Grammysioidea*, he stated, the Middle Devonian species (e.g., *G. arcuata*, *G. alveata*, etc.) were smooth, a single cincture first appearing among otherwise similar species (e.g., *G. subarcuata*) in the Upper Devonian. In *Grammysia*, he further noted, doubly cinctured species range from Middle Devonian to Upper Devonian rocks where they diminish in abundance and diversity. It is evident, however, that these supposedly separate lineages cannot be as neatly parceled as McAlester suggested. Bambach (1971), for example, described an early singly cinctured species, *Grammysioidea obliqua* (McCoy)<sup>4</sup> from the late Silurian Stonehouse Formation, Arisaig, Nova Scotia.

<sup>4</sup> Bambach called it *Grammysia obliqua*. The species is here placed in *Grammysioidea* because of its single cincture.

Moreover, Maillieux (1937) described both singly and doubly cinctured species from the Lower Devonian of Europe. Finally, a singly cinctured species, *Grammysioidea cf. elliptica*, is here reported from the Solsville.

*Grammysioidea alveata* (Conrad), 1841

Figures 5A, 45A–F

*Posidonia alveata* Conrad, 1841, p. 53.

*Grammysia alveata* (Conrad). Hall and Whitfield, 1869, p. 55. Miller, 1877, p. 192. Hall, 1883, pl. 57, figs. 1, 2, pl. 60, figs. 1–11; 1885, p. 370, pl. 57, figs. 1, 2, pl. 60, figs. 1–11. Whitfield and Hovey, 1900, p. 278. Clarke and Ruedemann, 1903, p. 395. Grabau, 1906, pp. 221, 331, fig. 172. Grabau and Shimer, 1909, p. 381, fig. 487. Cooper, 1930, p. 134. Bambach, 1971, p. 181, tab. 1.

*Grammysia* (*Grammysioidea*) *alveata* (Conrad). Williams and Breger, 1916, p. 134.

*Grammysioidea alveata* (Conrad). Shimer and Shrock, 1944, p. 371, pl. 144, fig. 22. McAlester, 1962a, p. 59. [?] Ellison, 1965, p. 118, pl. 14, fig. 8. Bailey, 1975, p. 87, pl. 9, figs. 1–4, 6, 7.

*Grammysia lirata* Hall and Whitfield, 1869, p. 57. Whitfield and Hovey, 1900, p. 278.

*Grammysia lirata* Hall [and Whitfield]. Miller, 1877, p. 192. Hall, 1883, pl. 59, figs. 6–12; 1885, p. 371, pl. 59, figs. 6–12. Clarke and Ruedemann, 1903, p. 401.

*Grammysia* (*Grammysioidea*) *lirata* [Hall and Whitfield]. Williams and Breger, 1916, p. 134.

†[?] *Grammysia subarcuata* Hall and Whitfield. Kindle, 1901, p. 684, pl. 15, fig. 3.

†[?] *Grammysia sylvaniensis* Wilson, 1975, p. 145, pl. 72, figs. 1–3, pl. 121, figs. 1–3.

**DESCRIPTION:** Shells large to medium, posteriorly elongate, equivalve, strongly inequilateral. Outline variably ovoid and fusiform except for abruptly truncate anterior margin. A posterodorsal flange or slight alation was evidently present but is broken away. Valves smoothly convex, strongly inflated; maximum inflation attained anterodorsally in the medial region of the umbones, decreasing abruptly upwards and gradually below, producing a cordate cross-sectional outline. Ventral margin smoothly curving, nonsinuate, with a prominent rudder-like anteroventral expansion. Articulated specimens show valves closely appressed anterodorsally, anteriorly, and ventrally. No byssal gape.

Prosopon concentric consisting of (1) very fine, obscure to obsolescent growth lines becoming ventrally more pronounced, and (2)

TABLE 9  
Measurements (in Millimeters) of  
*Grammysioidea alveata* (Conrad)

Locality	Length	Height	Width <sup>a</sup>
AMNH 3012	—	27 <sup>b</sup>	28.8
AMNH 3013	39.4	26.9	28.8
	35 <sup>b</sup>	27.5	26.7
	45.7	27.8	28.4

<sup>a</sup> Total width, both valves articulated.  
<sup>b</sup> Original dimensions inferred; specimen broken.

prominent, regular, coarse corrugations (plicae). Plicae are best defined anteriorly where the spacing is close; posteriorly and dorsally they are more widely separated, becoming poorly defined to obsolescent. No radial elements, cinctures, or sulci observed.

Lunular area prominent, cordate but not distinctly limited. Escutcheon large and prominent, occupying much of the dorsal margin and encompassed by two fine, closely parallel escutcheonal grooves.

A short, opisthodontic, barrel-shaped calcified ligament is preserved in four specimens. Behind the ligament the valves are visibly gaping. Hinge probably edentulous. Beneath and extending briefly behind the ligament is a narrow, thick plate (nymph?) with a narrow anteroposterior ligamental(?) groove in each valve.

Recrystallized shell remnants over much of the valve surfaces show that the original valves were extremely thin and fragile. They further indicate that the concentric prosoponal corrugations were plicae, i.e., expressed on both outer and inner shell surfaces. Other internal features not observed.

Original shell microstructure and mineralogy unknown.

REMARKS ON MORPHOLOGY: A similar barrel-shaped calcified ligament was observed by Bambach (1971) in Silurian *Grammysioidea obliqua*. As noted above the valves in *G. alveata* are narrowly gaping just behind the ligament. This is not completely apparent in my figures since the space between the valves is matrix filled. I regard the dorsal gape as natural since an articulated specimen (fig. 45A, B) shows the valves to be closely appressed elsewhere along the commissure (ex-

cept in the extreme dorsoposterior region where the shells are incomplete). The gape probably widened posteriorly into a permanent, posterodorsal, siphonal gape which was probably emphasized by posterodorsal, commissural flanges, here broken away. A similar dorsal gape was described in *G. obliqua* by Bambach who suggested that it may have been covered in life by a periostracal sheath for a short distance behind the ligament. Bambach further described a distinct byssal gape in his Silurian species. However, no such gape is present here; in two articulated specimens the valves are closely appressed in the byssal region.

Both *Grammysia* and *Grammysioidea* are regarded as edentulous (Newell and LaRocque in Moore, 1969; Runnegar and Newell, 1974; Runnegar, 1974). An edentulous hinge in *Grammysia* is clearly evident in figure 9G of Runnegar and Newell's study. The thickened, singly grooved plates along the hinge in *G. alveata* might be regarded as lamellar teeth. However, since these plates were not in mutual contact during life because of the dorsal gape, such an interpretation is unlikely. A clearer understanding of the hinge may be gained from the specimen shown in figure 45C. Much of the ligament is absent in this individual; evidently it was only weakly calcified in this case. Because of its absence, however, the pair of grooved plates below are exposed. It is evident that the edges of the ligament inserted into the grooves of the plates which might more properly be called nymphs. Moreover, since these nymphs are longer than the calcified ligaments seen in three other specimens, it seems probable that the portions of the nymphs behind the calcified ligament represent the position of insertion for noncalcified ligamental and periostracal tissues.

Hall (1885, p. 366, pl. 58, figs. 6, 12) described and figured a "thickened hinge plate bearing a single angular fold beneath the beak" in *Grammysioidea elliptica* (Hall and Whitfield). His figure 6, which has been diagenetically compressed judging from the sharp crease along the umbo, shows a short ridge below in the ligamental position. Although it superficially resembles a lamellar tooth, it is probably the flattened remains of the calcified

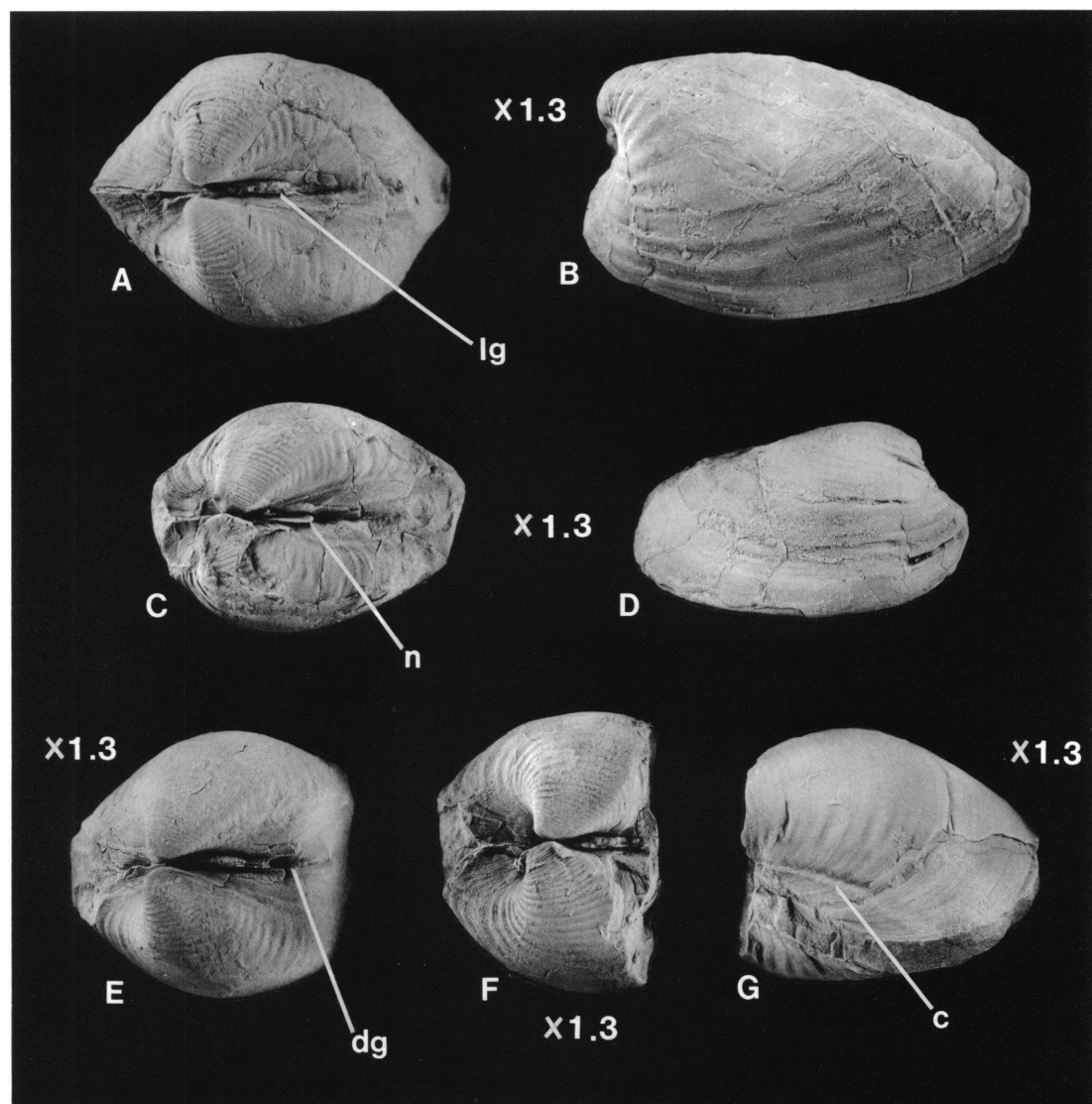


FIG. 45. A–F. *Grammysioidea alveata* (Conrad). A, B. Articulated specimen (AMNH 36197) from AMNH loc. 3013. A. Dorsal view. B. Left valve. C, D. Articulated specimen (AMNH 36200) from AMNH loc. 3013. C. Dorsal view. D. Right valve. E. Articulated specimen, dorsal view (AMNH 36198) from AMNH loc. 3013. F. Dorsal view of gaping articulated specimen (AMNH 36199) from AMNH loc. 3012. G. *Grammysioidea cf. elliptica* (Hall and Whitfield). Distorted articulated specimen (AMNH 36201) from AMNH loc. 3013.

Abbreviations: c—cincture, dg—dorsal gape, lg—ligament, n—nymph.

ligament. His figure 12 showing a broad, anterior cuneiform “tooth” is more difficult to interpret.

The interior morphologies of most species of both *Grammysia* and *Grammysioidea* are poorly known. Bambach (1971) reported verification by Runnegar of the morphology of

an internal mold of *Grammysia circularis* Hall and Whitfield (from the Hamilton of New York) as figured by Hall (1885, pl. 57, fig. 4) the salient features of which are reproduced in Bambach’s figure 7B and in figure 6B of Runnegar (1974). This anisomyarian specimen (AMNH and YPM 5328/2) shows a



large, lobate posterior adductor scar with indications of small pedal or byssal/pedal retractor musculature above the adductors and a simple pallial line which anteriorly degenerates into a series of small elongated pits resembling short striae. The intrapallial area is marked by numerous pallial punctae. An internal mold with essentially similar adductor and pallial features is shown by Prosser and Kindle (1913, pl. 23, figs. 1, 2) in another Hamilton *G. circularis* specimen. Both specimens show that the radial cinctures and prosoponal corrugations are expressed on the inner shell surfaces and, hence, are plicae.

Further data on grammysiid internal morphology are supplied by the internal mold designated *Grammysia marginata* Goldfuss figured by Beushausen (1895, pl. 23, fig. 1, 1a). The specimen, again, is strongly anisomyarian. However, the large posterior adductor scar is uniformly circular showing no lobation or extensions associated with the posterior byssal/pedal retractor scars as suggested by the figures of Runnegar and of Bambach. The mold is integripalliate and the pallial line, as before, is formed by a series of elongated pallial muscle pits. Anomalously, however, Beushausen's figure shows a double row of these, at least in the anteroventral region. The mold also shows two long radial ridges, an inner expression of the twin radial cinctures characterizing genus *Grammysia*.

The shell microstructure and mineralogy of the Grammysiidae are virtually unknown. However, a Pennsylvanian grammysiid from Oklahoma described by Bailey and Sandberg (1979, 1980, and MS) has an aragonitic shell with microstructure very similar to that of Recent *Pholadomya*, thus confirming past classification of the extinct grammysiids among the Pholadomyacea. It consists of an inner layer of sheet nacre and an outer layer of steplike "treppen nacre" (cf. Taylor, Kennedy, and Hall, 1973, pl. 12, fig. 4); but the thin outermost prismatic layer reported in *Pholadomya* is lacking.

COMPARISONS: As indicated by Newell and LaRocque (in Moore, 1969) the grammysiids probably constitute a heterogeneous, somewhat artificial grouping which, as McAlester (1962a) stated, are in need of extensive revision. Therefore assignment of these Solsville specimens to *Grammysioidea alveata* is,

at best, somewhat tenuous since this species may eventually prove to be conspecific with certain other species of genus *Grammysioidea* which, McAlester indicated, is comprised of the following forms: *G. alveata*, *G. arcuata*, *G. subarcuata*, *G. communis*, *G. undata*, *G. duplicata*, *G. hannibalensis*, and *G. plena*. Bambach (1971) speculated that *G. subarcuata* is a subspecies of *G. arcuata*. Comparisons are difficult since grammysiids exhibit an altogether remarkable degree of variation often aggravated by extreme diagenetic distortion. Due to their large, thin shells, grammysiids seem consistently among the most severely distorted of the bivalve taxa found among the faunas I have examined. Before most species differences can be seriously considered, natural variation and diagenetic effects among type materials must be more closely studied.

Somewhat tentative assignment of these Solsville grammysiids to *G. alveata* is based upon (1) lack of any radial cincture; (2) elongate form similar to *G. alveata* of Hall (1885, pl. 57, figs. 1 and especially 2; pl. 60, figs. 2, 8, 9); and (3) strong reduction or absence of the concentric prosoponal corrugations on the posterodorsal slope. But Hall's (1885) specimens of *G. alveata* from the Hamilton of Schoharie and Otsego counties and eastern New York are considerably larger than these Solsville grammysiids which compare dimensionally to Hall's *Grammysioidea arcuata* (Conrad) from the Hamilton shales of Schoharie County and central and western New York as well as above the "Corniferous Limestone" (=Jeffersonville Limestone; see Sutton and Sutton, 1937), of southern Indiana and northern Kentucky. Furthermore, these Solsville specimens are substantially similar to one specimen Hall (1885, pl. 93, fig. 27) perhaps mistakenly attributed to *G. arcuata*.

Hall (1885) stated that *G. alveata* differs from *G. arcuata* in its more erect form (*G. arcuata* was described as having a more elongated, more rounded posterior extremity) and the absence of the concentric corrugations on the posterior umbonal slope. The Solsville species appears to be close to *G. arcuata* in the variable properties of shape and size, but, significantly, it exhibits the prosopon of *G.*

*alveata*, *sensu stricto*. Both *G. arcuata* and *G. alveata* are probably very closely linked.

Other species which show some measure of similarity include:

1. "*Grammysia subarcuata* Hall?" of Kindle (1901). Middle Devonian (Sellersburg), southern Indiana. Hall and Whitfield (1869) reported *G. arcuata* above the Jeffersonville Limestone. Kindle could not find that species in his study of the Middle Devonian of southern Indiana in the beds Hall and Whitfield mentioned. Nevertheless, he did recover a single, broken specimen which he tentatively assigned to *G. subarcuata*. His drawing (1901, pl. 15, fig. 3) shows strong similarities to Solsville figure 45A, B. Indeed, greater agreement is apparent here than any other published illustrations I have examined. Although he mentioned a faint, radial cincture, it is not visible in his drawing. It is possible that he was confusing the escutcheon-al grooves with the radial cinctures. The specimen is not *G. subarcuata* which is a species of *Grammysioidea* bearing a prominent cincture recognized only in the Upper Devonian by McAlester (1962a, 1963a).
2. *Grammysia lirata* Hall and Whitfield (1869). Middle Devonian (Hamilton), New York. A junior synonym of *G. alveata*. Even though the prosoponal corrugations are often more continuous across the posterior umbonal slope in *G. lirata*, Hall (1885) considered it to be merely the juvenile stages of *G. alveata*. This view is supported by (1) the greater posterior continuity of the corrugations in the earlier ontogenetic stages of Solsville *G. alveata* (see fig. 45A, C, E, F), and (2), as Hall noted, by the occurrence of *G. lirata* in all of the same localities he cited for *G. alveata*.
3. *Grammysia gibbosa* Hall and Whitfield of Nettleroth (1889). Middle Devonian (Sellersburg), southern Indiana, and northern Kentucky. A possible candidate for synonymy, but Nettleroth's drawings are too stylized for serious comparisons. Nettleroth mentioned a broad, radial cincture not apparent in his drawings. Needs restudy.
4. *Grammysia sylvaniensis* Wilson, 1975. Middle Devonian (Silica Formation), Ohio. Wilson's figured specimens are diagenetically distorted, but his plate 72, figures 1 and 3 show the same general shape, the posteriorly diminishing prosoponal corrugations and obsolescent or missing cincture seen here in figure 45B. A probable synonym.

**AUTECOLOGY:** One of the four figured specimens was recovered from the argillaceous facies of the vertical road cut at AMNH loc.

3012, whereas the three other specimens, collected by Rollins from AMNH loc. 3013, appear to have been derived from the same facies judging from the associated matrix. Hence, it seems probable that this species preferred the soft substrata of low energy waters where the thin shell would remain sheltered from turbulence. The extreme inflation and thinness of the shells effectively increased their buoyancy in thixotropic muds. Further positional stability was provided by the dorsal placement of maximum shell width (producing a shape remarkably like the hull of a ship) as Stanley (1970) noted in characteristically semi-infaunal forms such as *Modiolus modiolus*, *M. americanus*, and *M. demissus*. The rudder-like, anteroventral shell expansion may have aided in lateral stabilization.

The concentric prosoponal corrugations, as noted, predominantly cover the anterior and ventral portions of the valves in contrast to the smoother, posterior and dorsal shell surfaces. The differential development of the corrugations is perhaps associated with the need for anterior and ventral gripping surfaces (Bambach, 1971) for shell stabilization in soft sediments. Similar ventrally pronounced corrugations have been noted by Stanley (1970) in Recent semi-infaunal and infaunal bivalve taxa inhabiting soft sediments where suspensory requirements are great. Another possible function of the corrugations will be suggested later.

Bambach (1971, p. 170) convincingly established the life position of *G. obliqua*; 74 percent of the specimens he examined *in situ* were oriented "with the plane of commissure at right angles to bedding and the anteroposterior length inclined 30° to 45° to bedding, anterior end down." These observations, shell shape data, probable lack of extensible siphons (as judged from integripalliate internal molds of grammysiids), permanent postero-dorsal gape, and manifestations of a byssal apparatus provide compelling evidence that the grammysiids were endobyssate, semi-infaunal filter feeders. Bambach indicated that the permanent posterodorsal gape must have remained exposed in life since sedimentary infilling of the shell would block respiratory water currents if the grammysiids were completely buried. Reconstructed life positions

of grammysiids are shown here in figure 5 (see also Bambach, 1971, fig. 11; Stanley, 1972, text-fig. 32; and Thayer, 1974, fig. 18E, G).

Bambach (1971), Stanley (1972), and others (e.g., Yonge, 1953; Pojeta, 1966, 1971) have demonstrated that the anisomyarian condition, as seen here among the grammysiids, strongly suggests byssal attachment. Furthermore, as Bambach has also indicated, lobation of the large posterior adductor scar of grammysiid internal molds implies posterior byssal retractor musculature. Additionally, Bambach noted an anteroventral byssal gape in *G. obliqua*, a feature seen neither in the Solsville specimens nor in several other articulated grammysiids figured by Hall (1885, including *Grammysia nodocostata*, pl. 55, fig. 1; *Grammysioidea alveata*, pl. 57, fig. 2, pl. 60, figs. 3, 10; *Grammysia obsoleta*, pl. 59, fig. 22; and *Grammysioidea arcuata*, pl. 61, fig. 7). Hence, it appears that a byssal gape was not very common among Devonian grammysiids though most were probably byssate.

One debatable aspect of the grammysiid mode of life is the mobility of the shells. Bambach (1971) reckoned that, except in the youngest individuals, calcification of the ligament in *G. obliqua* caused it to lose its normal spring function; instead it served solely for shell articulation, maintaining the shells tightly closed and immobile. This, he reasoned, would not be an impairment since permanent byssal and siphonal gapes were present. His conclusions were based largely on the perfect articulation and ventral apposition of all individuals except a juvenile whose valves were "butterflied" (i.e., sprung open widely but still dorsally attached). Bambach's conclusions probably do not apply to grammysiids in general for the following reasons: (1) Numerous specimens of various Solsville bivalve species were found in assorted attitudes though often near their original life positions. In spite of these varied orientations, the large percentage are found articulated with valves in near perfect ventral apposition. This fact, however, cannot be used to reasonably argue that these diverse taxa were all incapable of opening their shells. In most cases the closed valves are here the result of sedimentary compaction. (2) Although *G. obliqua* possesses a byssal gape and would therefore

require no ability to open the valves, byssal gape among many other grammysiids is lacking. If we are to reasonably assume that most were byssally attached, then at least some ability to open the valves seems necessary for byssal adjustment. (3) In several grammysiids figured by Hall (1885), the valves are "butterflied" indicating that the valves naturally opened at death (e.g., see Hall's figures of *Grammysia bisulcata*, pl. 54, figs. 10, 14, 15, 16; *Grammysia circularis*, pl. 57, fig. 3; *Grammysioidea obsoleta*, pl. 59, fig. 25; *Grammysioidea globbosa*, pl. 62, figs. 16–19). Most of these specimens appear to be large and could not be reasonably argued to be juvenile. Such ligamental elasticity could therefore not have been a solely juvenile condition among these grammysiids. Furthermore, although three specimens of *G. alveata* figured here have their valves closed, in a fourth undoubtedly an adult (fig. 45F), the valves are "butterflied." (4) Although one Solsville *G. alveata* with closely appressed shells (fig. 45C) shows incomplete ligamental calcification, the other three have ligaments which seem closely comparable in size and calcification to those of *G. obliqua*. Since such a ligament did not prevent the shells from opening in *G. alveata*, it may not have done so in *G. obliqua* either. It seems probable that in *G. alveata* the stiff, calcified ligament would have held the valves ajar. Contraction of the adductor muscles would have gently deformed or flexed the thin shells into a position, the concentric corrugations additionally serving to increase the strength, flexibility and elasticity of the shells during the deformation. Moreover, if the shell microstructure was similar to that described by Bailey and Sandberg (1979, etc.) in the aforementioned Pennsylvanian grammysiid, the steplike dislocations in the thick, treppen nacre layer may have further added to the flexibility of the shells during closure.

*Grammysioidea cf. elliptica*  
(Hall and Whitfield), 1869

Figures 5B, 45G

*Grammysia elliptica* Hall and Whitfield, 1869, p. 53. Whitfield and Hovey, 1900, p. 278. McAlester, 1962a, p. 60, pl. 25, figs. 10–12. 1963a, fig. 6, tab. 1; 1963b, tab. 1, text-fig. 2, p. 994, pl. 124, figs. 9–13. [?] Palmer and Brann, 1966, pl. 1, fig. 22.

*Grammysia elliptica* Hall [and Whitfield]. Miller, 1877, p. 192. Hall, 1883, pl. 58, figs. 1–12; 1885, p. 365, pl. 58, figs. 1–12. Lesley, 1889, p. 261, 2 figs. Clarke and Ruedemann, 1903, p. 400. Clarke and Swartz, 1913, p. 606, pl. 59, figs. 11, 12. Branson, 1924, p. 111, pl. 25, figs. 15, 16. [??] Willard, 1939, p. 474, etc., pl. 27, fig. 4. *Grammysioidea* cf. *elliptica* (Hall and Whitfield). Bailey, 1975, p. 100, pl. 9, fig. 5. *Grammysia chemungensis* Pitt, 1873, p. 199, pl. 6. [See also McAlester, 1962a, p. 60.] [?] *Grammysia magna* Hall and Whitfield. Hall, 1883 [in part], pl. 56, fig. 5. 1885 [in part], p. 362, pl. 56, fig. 5. [See also McAlester, 1962a, p. 60.]

**DESCRIPTION:** Shells medium size, thin, strongly inflated, subtrigonal, equivalve, strongly inequilateral. Umbones prominent, beaks strongly prosogyrous. Margins smoothly curving. Lunule and escutcheon unknown.

Prosopon consists of both fine, irregularly fasciculate growth lines and coarse, concentric corrugations, pronounced anteroventrally and obsolescent posterodorsally. A narrow, radial cincture is well defined near the anteroventral margin.

Valve interior, ligament, original microstructure and mineralogy unknown.

**REMARKS ON MORPHOLOGY:** *Grammysioidea elliptica* is elsewhere a poorly known Upper Devonian species. McAlester (1962a, 1963b) described three specimens from the Chemung of New York and two specimens from the Snyder Creek Shale of Missouri. Hinge, ligament, lunule, escutcheon, and internal features among these are unknown.

A single grammysiid tentatively referred to this species and measuring roughly 33 mm. in length and 25 mm. in height was found in the dark argillites of AMNH loc. 3012. The valves are closely appressed except for the anteroventral and dorsoposterior portions of the commissure where the valves are visibly gaping. The gapes seem similar in position to the permanent byssal and siphonal gapes described by Bambach (1971) in *G. obliqua*. But, in view of the obvious shell deformity of the Solsville specimen, it is uncertain whether the gapes are natural or merely the result of diagenetic stresses. No such gapes were noted by McAlester (1963b) in the two Snyder Creek specimens.

**DISCUSSION:** McAlester (1962a, 1963a,

1963b) placed this species in *Grammysia* de Verneuil noting that, while only a single radial cincture is usually evident, a second, obscure cincture is “probably” present. However, each of Hall’s (1885, pl. 58) *G. elliptica* shows only a single, long, anteroventral cincture except for his plate 58, figure 4 which exhibits two short, mid-umbonal cinctures. Because the cinctures differ in position as well as number, the latter likely represents a species different from the rest. Likewise, McAlester’s (1962a, pl. 25, figs. 11, 12) figures show essentially single-cinctured specimens. The subtly bipartite appearance of the feature in his figure 11 seems attributable to the faint ridge which bounds the cinctural groove on either side. However, his figure 10 of the same plate shows a specimen with two distinct cinctures; but, since the remaining morphology is so poorly preserved, there seems little reason to believe it to be conspecific with the others.

Should future study confirm McAlester’s suggestion that a variably developed to absent second cincture exists in *G. elliptica* populations, the primary diagnostic distinction between *Grammysioidea* and *Grammysia* would be dissolved. Pending such study *G. elliptica* is here provisionally placed in *Grammysioidea* since specimens previously referred to that species are predominantly singly cinctured.

**COMPARISONS:** McAlester (1962a) emphasized the uniqueness of *G. elliptica* noting that it is unlikely to be confused with other species. Although the valve distortion prohibits positive identification, the Solsville specimen seems comparable to those of Branson (1924) and McAlester (1962a, 1963b). The specimen is also reasonably similar to the *G. elliptica* figures of Hall (1885, pl. 58, figs. 2, 3, 5, 7, 9) but the growth lines are less fasciculate and the radial cincture more anteroventrally located than in Hall’s drawings. In view of the shell distortion and lack of additional specimens, these differences cannot presently be assessed.

*Grammysioidea* cf. *elliptica* is distinguished from *G. alveata* in the same beds by its (1) relatively shorter, taller, more trigonal form; (2) its single, radial cincture and (3) its less pronounced prosoponal corrugations.

McAlester (1962a) considered *G. elliptica* to be the senior subjective synonym of two

other Upper Devonian species, *Grammysia chemungensis* Pitt and probably *Grammysia magna* Hall and Whitfield (in part). It may be added that *Grammysia obscura* Beushausen (1895, pl. 21, fig. 3, pl. 22, figs. 4, 5) from the Lower Devonian (Emsian) of Germany seems superficially similar to *G. elliptica*, but further comparisons are needed.

One of Clarke and Swartz's (1913, pl. 59, fig. 11) Upper Devonian specimens labeled *Grammysia elliptica* seems more similar to *Grammysia circularis* Hall and Whitfield (1869) although the latter appears to possess two faint cinctures.

#### SUBCLASS PALAEOHETERODONTA

NEWELL, 1965

#### ORDER MODIOMORPHOIDA NEWELL, 1969

(=ACTINODONTA DOUVILLÉ, 1912;

ACTINODONTOIDA NEWELL, 1965)

#### SUPERFAMILY MODIOMORPHACEA

MILLER, 1877

#### FAMILY MODIOMORPHIDAE MILLER, 1877

(=MODIOLOPSIDAE FISCHER, 1887)

#### GENUS *MODIOMORPHA*

HALL AND WHITFIELD, 1869

TYPE SPECIES: *Modiomorpha concentrica* (Conrad), 1838, by subsequent designation of Hall (1885) from the Middle Devonian Hamilton beds of New York.

GENERIC USAGE: *Modiomorpha* is applied in general accordance with the diagnosis given by LaRocque and Newell (in Moore, 1969, p. N393) who also supply a list of generic synonyms. Study confirms their observation of a large, cuneiform cardinal tooth in the left valve and a corresponding socket in the right valve. Although they further indicate an absence of lateral dentition, weak laterals are evident in Solsville specimens of the type species.

The ligament of *Modiomorpha* has been the topic of a notable controversy among past authors. Although Hall (1885) described the ligament as external, Ulrich (1894, 1897) and Beushausen (1895) both maintained that the ligament was, in fact, internal. Williams and Breger (1916), after examining large numbers of New York Devonian *Modiomorpha* specimens (including *M. concentrica* and *M. mytiloides*), could find no evidence of an external ligament and likewise concluded that the lig-

ament must have been internal. LaRocque and Newell (in Moore, 1969), however, correctly implied that the ligament is external by placing the Modiomorphoidea within the Subclass Palaeoheterodonta. The question is here firmly settled by the exceptional hinge preservation in both *M. concentrica* and *M. mytiloides*; these clearly show the conclusions of Beushausen, Ulrich, and Williams and Breger to be incorrect.

As Newell (in Moore, 1969) indicated, the modiomorphoids are a heterogeneous assemblage grouped together for convenience. Although I have chosen to follow Newell's systematic placement of the Modiomorphidae, it should be noted that the morphology of *Modiomorpha* shows significant similarities to members of both the Carditacea Fleming, 1820 (e.g., *Pernophorous* Chavan, 1954; see Chavan in Moore, 1969, fig. E44, 1a, b) and the Crassatellacea Férussac, 1822 (e.g., *Hippopodium* Sowerby, 1819; see Cox in Moore, 1969, fig. E82, 1a-e).

#### *Modiomorpha concentrica* (Conrad), 1838

Figures 1B, 6C, 46A-I, 47, 49B

*Pterinea concentrica* Conrad, 1838, p. 116.

*Cypricardites concentrica* Conrad, 1841, p. 52.

*Cypricardites oblonga* Conrad, 1841, p. 52. Synonym of Hall, 1885, p. 275.

*Modiola concentrica* [(Conrad)]. Hall, 1843, p. 19, fig. 78, no. 9.

*Modiomorpha concentrica* (Conrad). Hall and Whitfield, 1869, p. 73. Miller, 1877, p. 196. Whitfield, 1882, p. 335, pl. 26, fig. 10; 1883, p. 369. Hall, 1883, pl. 34, figs. 9, 10, pl. 36, figs. 1-16 [17?, 18?]; 1885, p. 275, pl. 34, figs. 9, 10, pl. 35, figs. 1-5, pl. 36, figs. 1-16 [17?, 18?]. Nettleroth, 1889, p. 219, pl. 2, figs. 9-12, 14. Ulrich, 1894, 1897, pp. 503-504. Grabau, 1899, p. 250, fig. 165; 1906, p. 330. Whitfield and Hovey, 1900, p. 288. Clarke and Ruedemann, 1903, p. 448. Cleland, 1903, p. 70; 1911, p. 113, pl. 24, figs. 6[?], 7; 1916, p. 459, fig. 232b. Slocum, 1906, p. 264. Stauffer, 1909, p. 165. Prosser and Kindle, 1913, p. 266, pl. 32, figs. 5, 6 [7-9?]. Williams and Breger, 1916, p. 216, 218. Branson, 1924, pp. 114. Pohl, 1929, p. 65. Savage, 1930, pp. 10, 97, pl. 4, fig. 23; 1931, p. 232, pl. 3, fig. 8. Stumm, 1942, p. 557, [not] pl. 84, fig. 49. Shimer and Shrock, 1944, p. 409, pl. 164, fig. 2. LaRocque and Marple, 1955, p. 85, fig. 190. McAlester, 1962a, p. 44. Ellison, 1965, p. 141, pl. 16, figs. 4-6. Palmer and Brann, 1966, pl. 14, figs. 2, 3. LaRocque and

Newell, 1969, p. N393, fig. D1,1 (in Moore).  
Bailey, 1975, p. 135, pl. 7, figs. 1-7, text-fig. 18b; 1978a, p. 121, tab. 1. Wilson, 1975, p. 126.  
Carter and Tevesz, 1978b, p. 865, fig. 14.  
*Modiomorpha concentrica* Hall [sic]. Lesley, 1889, p. 414, 2 figs. Kindle, 1896, p. 43; 1901, p. 680, pl. 14, figs. 10, 11. Clarke, 1899, 1900, p. 53. Grabau and Shimer, 1909, p. 515, figs. 692d, 694d. [?] Stewart, 1927, p. 52, pl. 5, fig. 4. [?] Willard, 1939, p. 477, etc., pl. 25, fig. 19. Stumm and Chilman, 1967, p. 130.  
*Modiola (Modiomorpha) concentrica* Hall [sic]. Hall and Whitfield, 1872, p. 199.  
[not] *Modiolopsis concentrica* Hall and Whitfield, 1875, p. 86. Ulrich, 1894, 1897, p. 510, pl. 37, figs. 15, 16. Pojeta, 1971, pl. 13, figs. 16, 17. [An Ordovician species.]  
*Mediomorpha* [sic] *concentrica*. Kindle, 1901, pl. 14, fig. 11. Ellison, 1965, pl. 16, figs. 4-6.  
†*Modiomorpha saccula* Pohl, 1929, p. 65, pl. 10, figs. 8-15, pl. 11, figs. 2, 3. [= *M. concentrica* Conrad of Cleland, 1911 [in part], p. 113, pl. 24, fig. 7.]  
†[?] *Modiomorpha elongata* Pohl, 1929, p. 66, pl. 11, figs. 1, 4-10. [= *M. concentrica* Conrad of Cleland, 1911 [in part], p. 113, pl. 24, fig. 6.] [?= *Nyassa elongata* Cleland, 1911, p. 111, pl. 22, figs. 10-12. Synonym of Pohl, 1929, p. 66.]  
†[?] *Modiomorpha anulifera* Spriestersbach [in part]. 1925, p. 410, pl. 11, fig. 3. [not] 1919, p. 37, pl. 12, figs. 1-5.

DESCRIPTION: Shells medium- to large-size, equivalve, inequilateral, inflated. Shape variable, modioloid or mytiloid in outline. Umbones prosogyrous, anteriorly subterminal, rising but slightly above the straight to gently arcuate hinge line. Commissure somewhat flanged dorsoposteriorly with a faint, shallow sulcus between the flange and a broadly convex umbonal ridge which curves obliquely toward the posteroventer. The oblique ventral margin forms a gentle embayment or sinus which is often marked by a constriction (byssal notch) extending obliquely upward. Faintly defined by an oblique, preumbonal sulcus is a narrow, anteriorly terminal auriculate lobe beneath and in front of the umbones.

Prosopon consists of mostly regular, distinct, concentric lirae of high relief punctuated by a few undulatory growth varices. Radial elements lacking.

Ligament opisthodontic, parivincular; each nymph marked by a single, flanking insertional groove (suture).

TABLE 10  
Measurements (in Millimeters) of *Modiomorpha concentrica* (Conrad)

Locality	Length	Height	Width <sup>a</sup>
AMNH 3013	53	33	21.5
	38	28	17
	57	41	—
	36	27	—
	75 <sup>b</sup>	52 <sup>b</sup>	28.7
	44	37	22.7
	39	25	18
	53	44	—

<sup>a</sup> Total width, both valves articulated.  
<sup>b</sup> Original dimensions inferred; specimen broken.

Hinge plate middorsally narrow, widening and thickening forward. A single, robust, cuneiform cardinal tooth with an ovoid basal outline is obliquely placed in the left valve and a corresponding socket in the right valve. Internal anterior shell margin peripherally broadened by growth laminae forming a rugose forward continuation of the hinge plate and cardinal tooth/socket. Along the lower edge of the hinge plate, a weak lateral tooth and socket are developed behind the cardinal dental element in each valve. The lateral tooth of the left valve underlies that of the right valve.

Anterior adductor scar small, subcircular, strongly impressed; situated in the anterior auricle beneath the cardinal tooth/socket and forming a deep embayment in the hinge plate. Just behind and above is a small anterior byssal/pedal retractor muscle pit. Posterior muscular scar larger, more weakly impressed and composite: ventral lobe (posterior adductor scar) large, ovoid or subreniform and faint; dorsal lobe (posterior byssal/pedal retractor scar) small, phylloid and better defined.

Pallial line recessed, simple, encompassing numerous pallial punctae.

The valves are thick and especially so in the umbonal and auricular regions, thinning posteriorly. Original shell microstructure described by Carter and Tevesz (1978b).

REMARKS ON MORPHOLOGY: Lateral teeth have never been described in *Modiomorpha*, and I (1975) did not previously observe them. Past authors have regarded them as absent

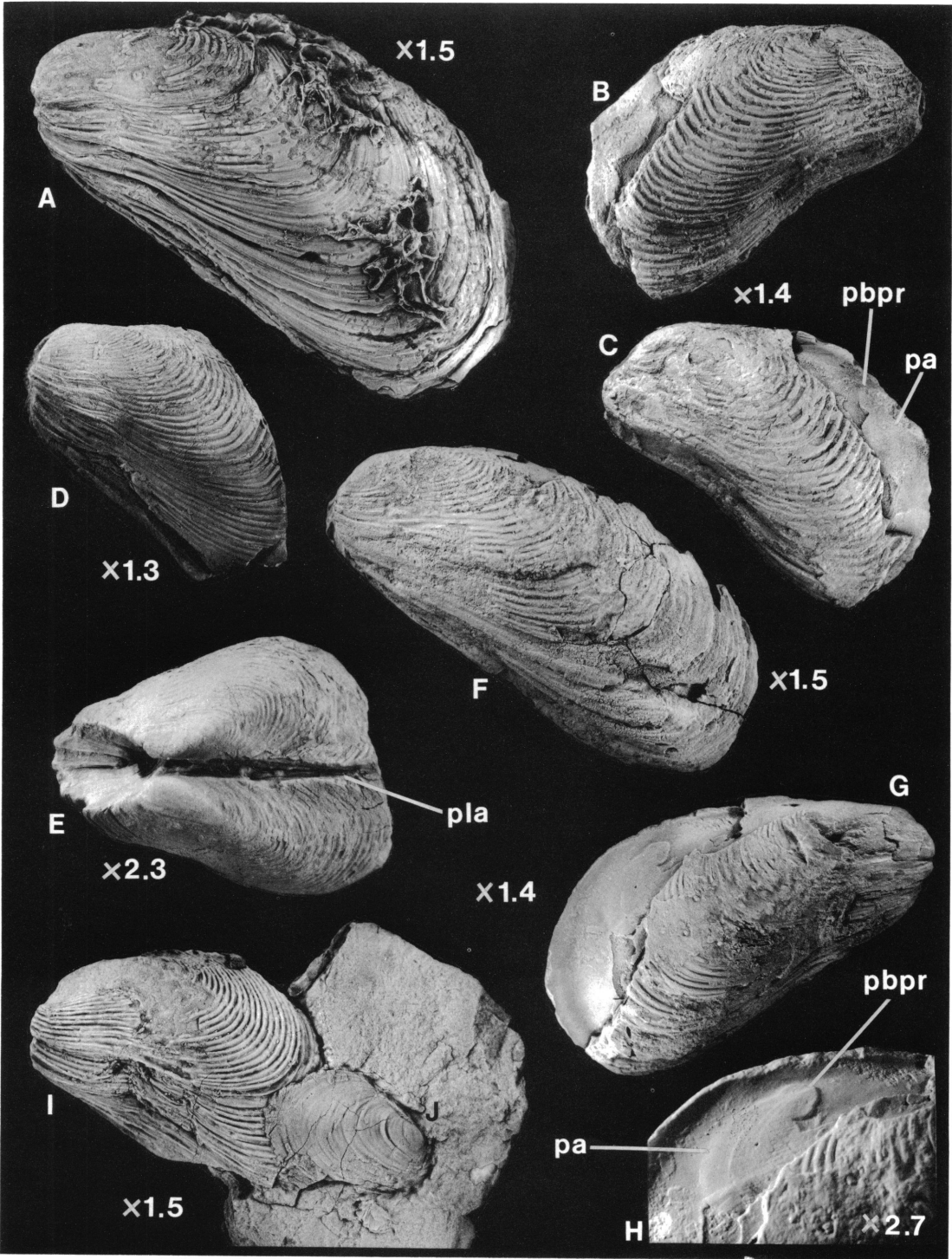


FIG. 46. A–I. *Modiomorpha concentrica* (Conrad). A. Left encrusted valve of articulated specimen (AMNH 36240) from AMNH loc. 3013. B, C. Articulated specimen (AMNH 36189) from AMNH loc. 3014. B. Right valve. C. Left valve. D, E. Articulated specimen (AMNH 36192) from AMNH loc. 3013.



(e.g., see LaRocque and Newell in Moore, 1969, p. N393).

The ligament and shell interior have been mostly unknown in *M. concentrica*. Several prominent earlier authors, as previously noted, even regarded the ligament as internal.

The cardinal dentition and anterior adductor scar in Solsville *M. concentrica* are basically similar to those figured by Hall (1885, pl. 36, figs. 15, 16), although Hall's drawings were largely based on gutta percha impressions.

These features are morphologically also closely akin to those of *Modiomorpha simplex* Beushausen (1885, pl. 1, fig. 9, 9a), *Goniophora chemungensis* (Vanuxem), 1842 (see Hall, 1885, pl. 44, figs. 13, 14), and *Modiomorpha bilsteinensis* Beushausen (1895, pl. 1, figs. 18a, b); although the external form of *M. bilsteinensis* mimics *Nyassa* Hall and Whitfield.

COMPARISONS: Beushausen (1895) described 16 *Modiomorpha*-like species in the European Devonian; he placed 14 in the genus *Modiomorpha*. The two remaining species he assigned to *Modiola*; at least one of these, "*Modiola*" *antiqua* Goldfuss (see pl. 1, figs. 3–6 of Beushausen) is undoubtedly *Modiomorpha* and seems akin to *M. concentrica*. Many of the remaining species are difficult to evaluate and require additional study. However, one example of *Modiomorpha westfalica* Beushausen seems similar to *M. concentrica* with respect to both shell shape and prosopon [i.e., compare Beushausen's text-figure 2, p. 27, with Hall's (1885) plate 36] and may prove to be synonymous.

One figured specimen of the upper Emsian species, *M. anulifera*, given by Priesterbach (1925, pl. 11, fig. 3) seems remarkably similar to *M. concentrica*. His specimens figured earlier (1919, pl. 12, figs. 1–5), however, are distinctly different.

Cleland (1911) described and figured *M. concentrica* from the Middle Devonian Mil-

waukee Formation of Wisconsin. Although he admitted considerable hesitancy in doing so, Pohl (1929) divided Cleland's *M. concentrica* specimens into two species, *M. saccula* and *M. elongata*. The figured shells of *M. saccula* Pohl are unmistakably those of *M. concentrica*, and, considering the substantial infraspecific variation apparent in the latter, there is insufficient basis for recognizing these Wisconsin specimens as a separate species. *M. elongata* from the same beds is not so readily evaluated. Cleland (1911) originally described an internal mold as *Nyassa elongata*, a generic assignment which seems credible enough based upon Cleland's figures. Pohl, however, unjustifiably placed this mold in *Modiomorpha elongata* along with specimens from Cleland's *M. concentrica* material. Although these specimens do show slight differences of shape and prosopon, the differences evidently intergrade with *M. saccula* and seem to have been introduced by a combination of diagenetic distortion and weathering.

#### *Modiomorpha mytiloides* (Conrad), 1841

Figures 6B, 46J, 48

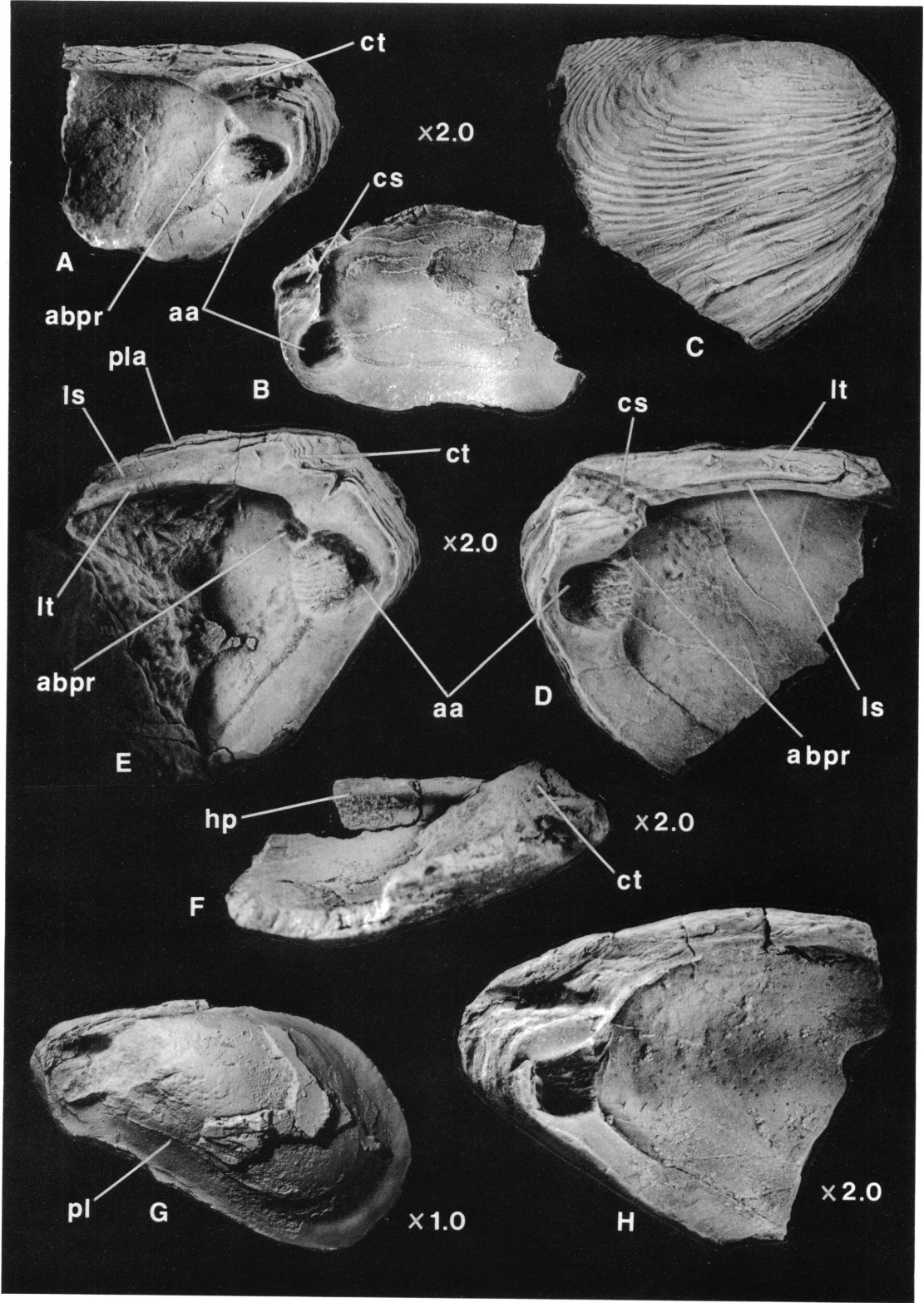
*Cypricardites mytiloides* Conrad, 1841, p. 52. Miller, 1877, p. 189.

*Modiomorpha mytiloides* (Conrad). Hall, 1885, p. 277, pl. 37, fig. 3, pl. 38, figs. 1–16. Nettleroth, 1889, p. 220. Whitfield and Hovey, 1900, p. 290. Clarke and Ruedemann, 1903, p. 450. Cleland, 1903, p. 70; [?] 1911, p. 114, pl. 23, fig. 4. Grabau, 1906, p. 330. Grabau and Shimer, 1909, p. 514, fig. 691b. Prosser and Kindle, 1913, p. 269, pl. 33, figs. 7[?], 8–10. Williams and Breger, 1916, p. 216. [?] Stewart, 1927, p. 53, pl. 5, fig. 5. Pohl, 1929, p. 67. Cooper, 1930, p. 219. [?] Savage, 1931, pp. 228, 232, pl. 29, fig. 3. Shimer and Shrock, 1944, p. 409, pl. 164, fig. 1. McAlester, 1962a, p. 45, pl. 19, figs. 14–16; 1963b, p. 1211, tab. 1, fig. 4. Ellison, 1965, p. 142. Palmer and Brann, 1966, pl. 6, fig. 3, pl. 14, fig. 1. Stumm and Chilman, 1967, p. 130. Wilson, 1975, p. 126.

*Modiomorpha mytiloides* Hall [sic]. Stauffer, 1915,

←  
D. Left valve. E. Dorsal view. F. Left valve of articulated specimen (AMNH 36190) from AMNH loc. 3013. G, H. Articulated specimen (AMNH 36191) from AMNH loc. 3013. G. Right valve. H. Enlargement of composite posterior muscular scar. I. A left valve (AMNH 36238A) from AMNH loc. 3013. J. *Modiomorpha mytiloides* (Conrad). A right valve (AMNH 36238B) from AMNH loc. 3013.

Abbreviations: pa—posterior adductor scar, pbpr—posterior byssal/pedal retractor scar, pla—parivincular ligamental area (nymph).



- p. 239. [not] Willard, 1939, p. 477, etc., pl. 25, fig. 20.
- [not] *Modiolopsis mytiloides* Hall, 1847, p. 157. Ulrich, 1894, 1897, p. 508, pl. 36, fig. 8. [an Ordovician species.]
- Modiomorpha mytiloides* [sic] Conrad. Kindle, 1901, p. 681.
- Modiomorpha mytiloides milwaukeeensis* Pohl, 1929, p. 68, pl. 12, figs. 4, 5.
- Cypricardites alta* Conrad, 1841, p. 52.
- [?] *Cypricardia alata* [sic] Hall, 1843, p. 48, fig. 6, no. 3. [= *M. alta* [in part] in Lesley, 1889, p. 412.]
- Modiomorpha alta* (Conrad). Hall and Whitfield, 1869, p. 75. Miller, 1877, p. 195. Hall, 1883, pl. 37, figs. 1–16, pl. 80, fig. 7; 1885, p. 278, pl. 37, figs. 1, 2, 4–12, 15, 16, pl. 80, fig. 7. Lesley, 1889 [in part], p. 412, lower fig. Grabau, 1899, p. 251, fig. 167. Whitfield and Hovey, 1900, p. 288. Clarke and Ruedemann, 1903, p. 448. Cleland, 1903, p. 70; 1911, p. 115. Grabau and Shimer, 1909, p. 514, fig. 692c. Savage, 1931, pp. 228, 231.
- Modiomorpha alta* Hall [sic]. Kindle, 1901, p. 682, pl. 14, fig. 8.
- Modiomorpha planulata* Hall and Whitfield, 1869, p. 74. [Synonym of Hall, 1885, p. 277; Whitfield and Hovey, 1900, p. 290.]
- Modiomorpha complanata* Hall and Whitfield [in part]. Hall, 1883, p. 12, pl. 38, figs. 1–16. [Synonym, in part, of Hall, 1885, p. 277; Whitfield and Hovey, 1900, p. 288.] Lesley, 1889, p. 414, 1 fig.
- Modiomorpha macilenta* Hall and Whitfield, 1869, p. 76. Miller, 1877, p. 196. Hall, 1883, pl. 37, fig. 17, pl. 39, figs. 17–21; 1885, p. 280, pl. 37, fig. 17, pl. 39, figs. 17–21. Whitfield and Hovey, 1900, p. 288. Clarke and Ruedemann, 1903, p. 450.
- †*Modiomorpha affinis* Hall, 1885, p. 284, pl. 37, figs. 13, 14, pl. 35, fig. 13. Nettleroth, 1889, p. 216. Whitfield and Hovey, 1900, p. 288. Kindle, 1901, p. 681, pl. 14, fig. 9. Savage, 1930, p. 97.
- Modiomorpha tioga* Hall, 1885, p. 291, pl. 40, fig. 18.
- †[?] *Modiomorpha clarkei* Cleland, 1911, p. 115, pl. 24, fig. 5. [= *M. obliqua* Cleland [in part] of Pohl, 1929, p. 67, pl. 12, figs. 1–3.]
- †*Modiomorpha obliqua* Cleland, 1911, p. 114, pl. 24, fig. 4. Pohl 1929, [in part], p. 67, pl. 12, figs. 1–3 [pl. 13, figs. 1–3?].
- †[?] *Modiomorpha pediformis* Pohl, 1929, p. 66, pl. 11, figs. 11, 12. [= *M. mytiloides* (Conrad) of Cleland, 1911, p. 114, pl. 23, fig. 4.]
- †[?] *Modiomorpha subalata* (Conrad). Stumm, 1942, p. 557, pl. 81, fig. 34.
- [See also synonymy of McAlester, 1962a, p. 45.]
- DESCRIPTION: See redescription of McAlester (1962a, p. 45).
- REMARKS ON MORPHOLOGY: *Modiomorpha mytiloides* is here represented by two specimens from AMNH loc. 3013: (1) a small, near complete right valve 18.9 mm. in length and 13.8 mm. in height and (2) a large, incomplete articulated specimen with a preserved length of 55.3 mm. and height of 48.5 mm. (inferred original length and height,  $73 \times 52$  mm.). A third incomplete specimen from AMNH loc. 3014 has an inferred length of 12 mm. and a height of 12 mm. No internal morphology is here exposed; it is poorly known elsewhere.
- The ligament has not been previously described in this species. The larger, articulated specimen shows clear evidence of an external, opisthodontic, parivincular ligament as indicated by the ligamental nymph and flanking suture in each valve (see fig. 48B).
- COMPARISONS: The remarkable shell variation exhibited by this species has generated considerable confusion resulting in the erection of numerous probable junior synonyms. Most are likely little more than variants in a larger morphologic continuum as Hall (1885, p. 279) first observed: "The typical forms here recorded under the specific designations of *M. mytiloides*, *M. alta* and *M. macilenta* are easily distinguishable; but in the study of large collections we find so many intermediate

FIG. 47. *Modiomorpha concentrica* (Conrad). All from AMNH loc. 3013. A. Partial left valve interior (AMNH 36195). B. Partial right valve interior (AMNH 36194). C, D. Partial right valve (AMNH 36236). C. Exterior. D. Interior. E. Partial interior of left valve (AMNH 36238A). F. Ventral view of left hinge fragment (AMNH 36196). G. Left internal mold of articulated specimen (AMNH 36191). H. Partial right valve interior (AMNH 36193), slightly restored above socket.

Abbreviations: aa—anterior adductor scar, abpr—anterior byssal/pedal retractor pit, cs—cardinal socket, ct—cardinal tooth, hp—hinge plate, ls—lateral socket, lt—lateral tooth, pl—pallial line, pla—parivincular ligamental area (nymph).

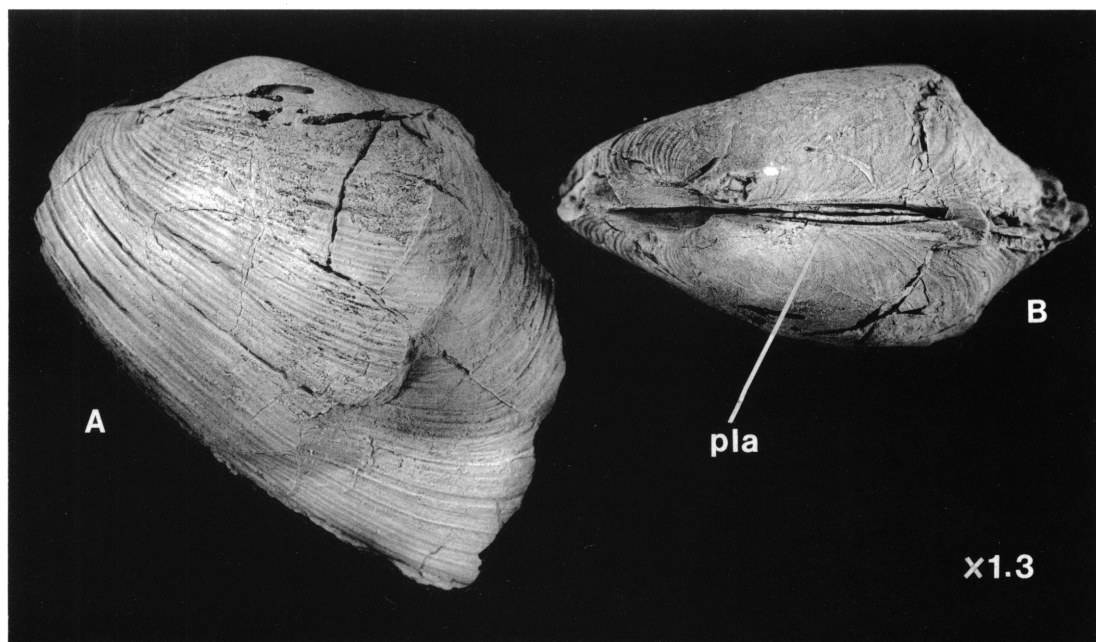


FIG. 48. *Modiomorpha mytiloides* (Conrad). Articulated specimen (AMNH 36218) from AMNH loc. 3013. A. Left valve. B. Dorsal view.

Abbreviation: pla—parivincular ligamental area (showing nymphs and sutures).

forms that it becomes difficult to arrange them under these several designations." Cleland (1911, p. 115), in his later discussion of *M. mytiloides*, further commented on the shell variation within this species: "In fact there is some warrant for assigning almost every specimen of this genus collected in the Milwaukee quarry to a different species. But any attempt to break it up into a number of species results in greater confusion."

An assessment of several probable synonyms of *M. mytiloides* is presented below:

1. *Modiomorpha mytiloides milwaukeensis* Pohl, 1929. Middle Devonian (Milwaukee Formation), Wisconsin. Pohl described the shell of this subspecies as "scarcely distinguishable from *M. mytiloides* (Conrad)." Pohl's figures show two fairly typical *M. mytiloides* shells; the subspecific designation seems unwarranted.
2. *Modiomorpha alta* (Conrad), 1841. Middle Devonian, New York, Ohio-Indiana. Inseparable from *M. mytiloides* in large collections (see Hall's comment above). McAlester (1962a) considered it a junior synonym. Kindle's (1901) figured specimen of *M. alta* is probably also *M. mytiloides*. Walcott (1884)

remarked that some *M. alta* specimens are almost identical to his "*M.*" *altiforme* specimens from the Devonian of Nevada. However, his figure (1884, pl. 5, fig. 9) shows an internal mold misidentified as *Modiomorpha*. The anterior adductor scar is too large, elongated, and lightly impressed, whereas the posterior scar seems too small and too ventrally located. A pholadomyacean?

3. *Modiomorpha planulata* Hall and Whitfield, 1869. Listed by Hall (1885), Whitfield and Hovey (1900) and McAlester (1962a) as a synonym of *M. mytiloides*.
4. *Modiomorpha complanata* Hall and Whitfield. Middle Devonian, Ohio. Hall (1885) noted an earlier labeling error and assigned the sixteen figures of his plate 38 to *M. mytiloides* in the final version. Both the other *M. complanata* specimens (1885, pl. 34, fig. 14, pl. 41, fig. 3) are internal molds, species uncertain (*M. mytiloides*?).
5. *Modiomorpha macilenta* Hall and Whitfield, 1869. Middle Devonian (Hamilton), New York. Inseparable in large collections from *M. mytiloides* (see Hall's comment above). McAlester (1962a) considered it a probable synonym.
6. *Modiomorpha affinis* Hall, 1885. Middle Devonian, New York, Indiana. Hall (1885) placed

part of his earlier (1883, pl. 37, figs. 13, 14) *M. alta* specimens in *M. affinis*. The figures show two typical *M. mytiloides* shells. Hall's remaining illustration (1885, pl. 35, fig. 13) shows an internal mold, species uncertain. Kindle's (1901) figured *M. affinis* is probably *M. mytiloides*.

7. *Modiomorpha tioga* Hall, 1885. Upper Devonian (Chemung), Pennsylvania. Based upon a single right valve (called a left valve by Hall, 1885, pl. 40, fig. 18). Hall compared it with *M. mytiloides*. I support McAlester's (1962a) suggestion that it is a junior synonym.
8. *Modiomorpha clarkei* Cleland, 1911. Middle Devonian (Milwaukee Formation), Wisconsin. Pohl (1929) regarded this form as a synonym of *M. obliqua*, a species I consider synonymous with *M. mytiloides* (see below). Although it closely resembles *M. mytiloides* in the earlier growth stages, it seems too equilateral in the later growth stages. Pohl indicated that these differences were merely the result of vertical diagenetic compression.
9. *Modiomorpha obliqua* Cleland, 1911. Middle Devonian (Milwaukee Fm.), Wisconsin. Cleland's drawings and Pohl's [1929, pl. 12, figs. 1-3; not pl. 13, figs. 1-3 (= *M. clarkei*)] later photographs show shell forms convincingly similar to *M. mytiloides*. There can be little doubt of its synonymy.
10. *Modiomorpha pediformis* Pohl, 1929. Middle Devonian (Milwaukee Fm.), Wisconsin. Cleland (1911) earlier called these *M. mytiloides*. Pohl noted the considerable shell distortion among most specimens. Similarly distorted *M. mytiloides* seem indistinguishable; a possible junior synonym.

In addition to these, *M. mytiloides* shows certain superficial similarities to a few European Lower Devonian species including *M. elevata* (Krantz) and *M. siegenensis* Beushausen as figured by Beushausen (1895, pl. 2, figs. 9-11 and pl. 2, fig. 8) and *M. intermedia* Beushausen as figured by Maillieux (1937, pl. 9, figs. 1-4). Further data, however, are needed.

**AUTECOLOGY:** Although no byssal gape is discernible in any available specimens of *Modiomorpha*, the byssate nature of the genus is confirmed by the well-developed byssal retractor muscular apparatus seen in *M. concentrica*. This apparatus has not been previously described; Hall's (1885) figures of *M. concentrica* show only a vague, rounded posterior adductor scar—the posterior byssal/pedal retractor lobe and the anterior byssal/

pedal retractor pit so clearly evident in the Solsville specimens are lacking in his drawings. Furthermore, the broad byssal sinus, sharp anteroventral prosoponal constriction (byssal notch), and strongly anisomyarian adductor musculature brought about by a secondary reduction of the shell anterior (Yonge, 1953) all point to the presence of a byssus.

McAlester and Doumanni (1966, text-fig. 2) indicated that *Modiomorpha baini* (Sharpe) from the Lower Devonian Horlick Formation of Antarctica was an epibyssate species, attaching itself to hard, elevated surfaces in the manner of modern *Mytilus edulis* as demonstrated by Stanley (1970, 1972). However, morphology suggests a different mode of life for *M. concentrica*: (1) If Stanley's criterion of maximum cross-sectional width is applied, it can be determined that *M. concentrica* with its centrally disposed plane of maximum inflation is probably more suited for a semi-infaunal (endobyssate) existence, commensurate erect, as exemplified by the similarly shaped Recent species, *Modiolus demissus* (see fig. 49A and Stanley, 1972, text-fig. 14b). (2) Unlike *Gosseletia* and *Mytilus* (fig. 18), a pronounced divergence of the hinge line and anteroposterior axis does not exist in *Modiolus demissus* or in *Modiomorpha concentrica*; indeed, the lines are nearly parallel in both species (see also fig. 1). (3) The posterior byssal retractor musculature in both *M. concentrica* and *Modiolus demissus* is attached well behind the byssus itself (whose position in *M. concentrica* is inferred from the byssal notch) producing a resultant force during contraction parallel to the long axis of the valves and pulling the shells down into the sediment (fig. 49). It therefore seems probable that *Modiomorpha* had a mode of life similar to that of *Modiolus demissus*, i.e., an endobyssate filter feeder.

Despite the foregoing arguments to the contrary, one specimen of *M. concentrica* (fig. 46I) shows evidence of having been epibyssate. The byssal notch is disfigured by an unnaturally deep embayment, and the prosoponal lirae are irregularly disrupted as though the shell had been damaged and subsequently mended. Among Recent populations of epibyssate mytilids living in shallow, intertidal waters where oscillating currents are strong, similar damage may occur if water motion

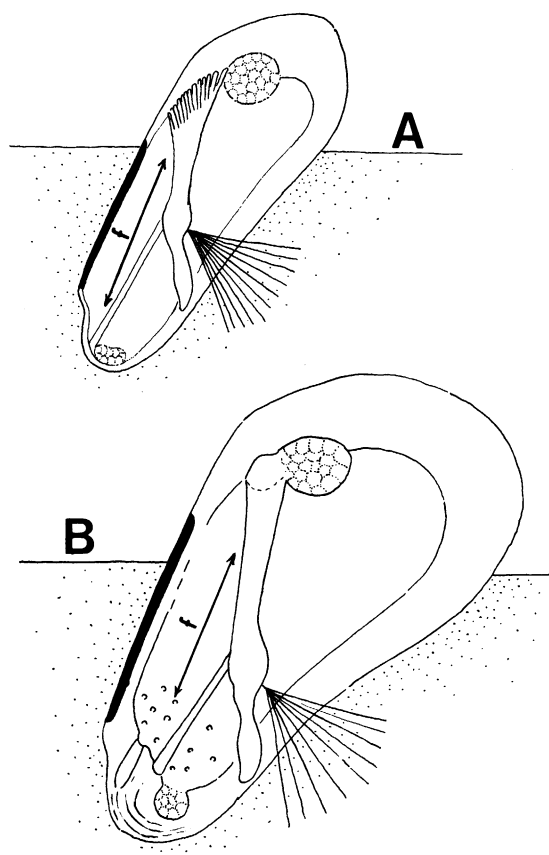


FIG. 49. Comparative adaptations for endobyssate life habits in *Modiolus demissus* (Dillwyn) and *Modiomorpha concentrica* (Conrad). A. *M. demissus*. Contraction of byssal/pedal musculature shown produces a net force (f) nearly parallel to the anteroposterior shell axis. (Based on Stanley, 1972). B. *M. concentrica*. Contraction of the reconstructed byssal/pedal musculature would produce a net force similar to that shown in *M. demissus*.

causes the shells to abruptly pivot or sway to and fro against the byssus. If the shell were endobyssate the surrounding sediments would provide lateral reinforcement, thus minimizing shell movements in fluctuating currents; hence, shell damage near the byssal notch would not be expected. Thus, though *Modiomorpha* seems morphologically best adapted to an endobyssate life, occasional individuals may have been epibyssate particularly if suitable substrates were at a premi-

um or if the shells were exhumed by sedimentary transport.

ORDER UNIONOIDA STOLICZKA, 1871  
SUPERFAMILY ANTHRACOSIACEA  
AMALITSKY, 1892  
FAMILY PALAEOMUTELIDAE WEIR  
IN VOKES, 1967  
GENUS *NYASSA*  
HALL AND WHITFIELD, 1869

TYPE SPECIES: *Nyassa arguta* Hall and Whitfield, 1869, by original designation, from the Middle Devonian (Hamilton) of New York. [= *Sanguinolaria dorsata* Goldfuss, 1840].

GENERIC DIAGNOSIS: [= *Modioconcha* Hall and Whitfield, 1869, *nom. oblit.* (obj.); see LaRocque in Moore, 1969, p. N411.] Shells dorsally thick, equivalve, subelliptical with small, appressed, anteriorly placed umbones and variably developed, subangular carina. Ligament external, opisthodontic. Anterior adductor scar small, well marked; posterior adductor scar faint. Pallial line simple. Weak posterior radial sulcus and posteroventral sinus. Prosopon variably fasciculate consisting of concentric growth lines; radial elements lacking. Hinge plate long, thick, arcuate. Dentition pseudotaxodont, extending over whole arc of the dorsal margin, diminishing middorsally; posterior members of the tooth series becoming greatly elongated, lamellar.

The revised generic diagnosis here proposed importantly differs from past diagnoses (e.g., LaRocque in Moore, 1969) with respect to hinge and prosopon. See additional comments below.

*Nyassa dorsata* (Goldfuss), 1840

Figures 6D, 50

*Sanguinolaria dorsata* Goldfuss, 1840, p. 280, pl. 159, fig. 17. De Verneuil, 1847, p. 697.

*Nyassa dorsata* (Goldfuss). Beushausen, 1895, p. 31, pl. 3, figs. 7–9. Spriestersbach, 1915, p. 39, pl. 11, fig. 4, 4a. Bailey, 1975, p. 209, pl. 15, fig. 6, text-figs. 32–34; 1978a, p. 121, tab. 1.

*Nyassa arguta* Hall and Whitfield, 1869, p. 28. [?] Whitfield, 1890, p. 558, pl. 11, fig. 18. Whitfield and Hovey, 1900, p. 294. LaRocque, 1969, p. N411, fig. D10,4 (in Moore).

*Nyassa arguta* Hall [and Whitfield]. Miller, 1877,

p. 198. Hall, 1883, pl. 53, figs. 9–20; 1885, p. 354, pl. 53, figs. 7–20. Whiteaves, 1898, pp. 399, 417. Clarke and Ruedemann, 1903, p. 467. Grabau and Shimer, 1909, p. 478, fig. 639. Stauffer, 1909, p. 166; 1915, p. 239. Prosser and Kindle, 1913 [in part], p. 262, pl. 31, figs. 7–9 [not fig. 6]. [not] Willard, 1939, p. 477, etc., pl. 26, fig. 31. Stumm, 1942, p. 557, pl. 81, fig. 6. Shimer and Shrock, 1944, p. 399, pl. 155, figs. 13, 14. Stumm and Wright, 1958, p. 93. Bailey, 1975, p. 209; 1978a, p. 121, tab. 1. Wilson, 1975, p. 126.

*Nyassa arguta* [Hall and Whitfield]. Grabau, 1906, pp. 220, 331, fig. 171. Cleland, 1911, p. 111. Cooper, 1930, p. 219, 220, 233; 1933, p. 550.

*Nyassa arguta* Whiteaves [sic]. Shimer and Grabau, 1902, p. 181.

**DESCRIPTION:** Shells medium- to large-size, equivalve, subelliptical. Umbones anteriorly placed, small, appressed line. Anterior, dorsal and posterior margins smoothly curving. Ventral margin with faint posteroventral marginal sinus; above it the shell is faintly sulcate. A subangular umbonal carina extends parallel to the hinge line from the beaks to the posteroventral angle.

Prosopon irregularly undulaform consisting of fine to moderately coarse, subfasciculate concentric growth lines gently embayed above the marginal sinus. No radial elements observed.

Hinge plate wide and thick with irregular, pseudotaxodont tooth series extending obliquely along the entire arc of the lower margin of the hinge plate. Posteriorly, the teeth are especially strong, elongated, lamellar, and lie parallel to the posterodorsal shell margin. Anteriorly, the teeth diminish in length and relief, becoming nearly obsolescent just behind the beak. Directly beneath and anterior to the beak, the teeth increase in relief but not in elongation and remain nearly parallel to the posteriormost teeth.

Ligament external, opisthodontic, probably parivincular and inserting just above and parallel to the posteriormost lamellar tooth.

Remnant shell material show the valves to be extremely thick and heavy in the hinge region becoming rather thin and fragile ventrally. Original shell mineralogy and microstructure unknown.

Other internal morphology not observed.

**REMARKS ON MORPHOLOGY:** An incom-

plete right valve (fig. 50A, B) measures 36.5 mm. in length and 26.9 mm. in height. The original, unbroken length would have been a bit greater, i.e., 40+ mm.

Past misunderstanding of the hinge morphology of *Nyassa* was established by Hall's (1885, pl. 53, figs. 8, 16, 18, 19) incomplete hinge figures. One of these, his figure 18 and enlargement, figure 19 (reproduced here as fig. 50D), seemingly more complete than the others, largely formed the basis for his hinge description of numerous irregular "cardinal" teeth or "callosities" in a random arrangement separated from two or three "lateral" teeth behind. In his enlargement the irregularity of the anterior tooth group is especially apparent. In better known taxa elsewhere I have seen analogous hinge tooth irregularities introduced by the disruptive effects of secondary calcite intergrowths along the hinge. A probably more accurate second specimen of Hall (his fig. 16) anteriorly suggests an orderly tooth series more like that of the Solsville hinge (fig. 50B). Unfortunately, none of Hall's hinge morphology was based upon actual shells, as it is here, but was drawn from gutta percha impressions of partially exposed hinge plates in three internal molds; in each case the hinge plate was medially interrupted by the umbonal cavity mold giving the erroneous impression of two completely disjunct (i.e., cardinal and lateral) dental groupings.

Descriptions of the hinge of *Nyassa* since Hall do not in general contradict him. Beushausen (1895) merely described the dentition as a series of fine lineations along the hinge. Even LaRocque's (in Moore, 1969, p. N411) recent redescription of the hinge as "long, arcuate, with numerous irregular cardinal teeth under the beak and 1 to 4 elongate lamellar teeth" essentially follows Hall's original analysis.

A significant hinge illustration of *Nyassa* largely overlooked by past authors is that of *N. dorsata* from the Mühlenbergsandstein (Eifelian) shown by Spriestersbach (1915, pl. 11, fig. 4, 4a). His figure 4a (reproduced here as fig. 50C), an enlarged impression of an internal mold of a juvenile (his fig. 4), shows a pseudotaxodont hinge essentially similar to the Solsville specimen. Although the dentition seems middorsally even less obvious in



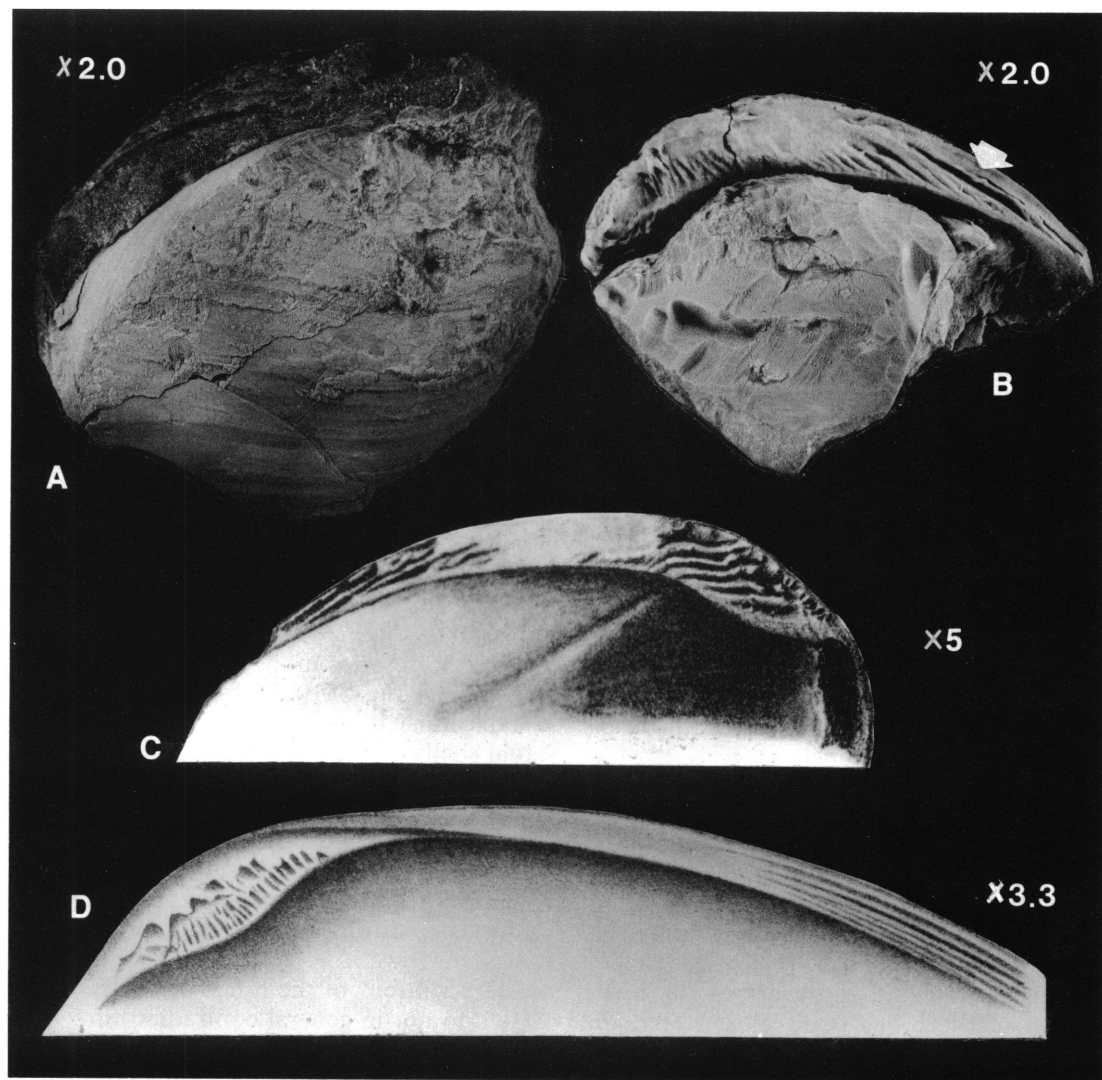


FIG. 50. *Nyassa dorsata* (Goldfuss). A, B. AMNH 36169, "miscellaneous Solsville" (AMNH loc. 3013?). A. Right valve, partially articulated. B. Prepared hinge of same specimen. Arrow indicates (?)nymph. C. Hinge of a left valve from the Mühlenbergsandstein (Ger.) as figured by Spriestersbach (1915, pl. 11, fig. 4a). D. Hinge of "*N. arguta*" Hall and Whitfield as figured by Hall (1885, pl. 53, fig. 19), a gutta percha impression of an internal mold.

the German example, this variance is judged minor in view of the differences in ontogenetic development and mode of preservation.

Internal morphology not shown in the Solsville material has been described by past authors: (1) Hall (1885) and Beushausen (1895) described the pallial line as simple. Beushausen mentioned that it lies close to the shell margin throughout its length. These

observations are verified by Spriestersbach (1915, pl. 11, fig. 4). (2) Hall and Beushausen both described the anterior adductor scar as small and deeply impressed. Beushausen also noted that its outline is weakly reniform and its placement is very near to the anterior margin (cf. Spriestersbach's fig. 4). (3) Hall and Beushausen described the posterior adductor muscle scar as rounded and weakly marked.

(4) The ligament was described by Hall as "narrow, external."

Despite LaRocque's (in Moore, 1969, p. N411) suggestion of "obscure radii" in some species, the evidence seems to support a prosopon in *Nyassa*, *sensu stricto* consisting solely of concentric elements. Beushausen (1895) mentioned only concentric elements. Of the four species described by Hall (1885), only one, *N. subalata* Hall and Whitfield was described as having radial elements. However, as his plate 53, figures 21–26 show, *N. subalata* is probably a grab-bag of various taxa. Some may have cyrtodontid or modiomorphid affinities. At least one, plate 53, figure 24, is probably *N. dorsata*. The one specimen clearly showing prosopon radii (pl. 53, fig. 26) has a well-developed posterior wing and may be a juvenile pterineid.

CLASSIFICATION: LaRocque (in Moore, 1969) placed *Nyassa* in "Family Uncertain" within the Anthracosiacea. However, the hinge in figure 50B strongly suggests affiliations with the Palaeomutelidae. *Nyassa* shows marked similarities to the Permian genus *Palaeomutela* Amalitsky, 1892, which possesses a similar pseudotaxodont dentition extending over the entire arc of the hinge plate (see Weir in Moore, 1969, p. N409) as well as a similar outline (including the posteroventral marginal sinus) and prosopon. However, *Palaeomutela* lacks the well-defined umbonal carina of *Nyassa*.

COMPARISONS: *Nyassa arguta* Hall and Whitfield from the Middle Devonian (Hamilton) of Eastern North America is here considered a junior synonym of *Nyassa dorsata* (Goldfuss) from the Middle Devonian (Eifelian-Givetian) of Germany. The identity of the two was early noted by de Verneuil (1847, p. 697): "*Sanguinolaria dorsata* Goldf. — Cette espèce, du calcaire dévonien de l'Eifel, se retrouve dans le groupe d'Hamilton de l'Etat de New York." Beushausen (1895, pp. 31–32), citing de Verneuil's observations, considered the differences between the two species to be only trivial, suggesting that no distinction greater than the varietal level would be justifiable: "*Nyassa arguta* Hall aus der Hamilton Group unterscheidet sich nur durch einzelne sehr geringfügige Merkmale, die höchstens eine Varietät rechtfertigen könnten. De Verneuil hat die ameri-

kanische Form schon mit *Sanguinolaria dorsata* identificirt."<sup>5</sup> Spriestersbach (1915) understandably disagreed, pointing out the pronounced difference between his *N. dorsata* hinge and the anomalous hinge of *N. arguta* figured by Hall. However, since the Solsville specimen discredits Hall's hinge interpretation but confirms Spriestersbach's, the synonymy of the two species seems assured.

Hall (1885) described and figured four species of *Nyassa*; an evaluative summary of each is offered below:

1. *Nyassa arguta* Hall and Whitfield, 1869. Middle Devonian (Hamilton) of New York. Based on five to eight medium to large specimens (21–52 mm. in length); ovate, posteroventral marginal sinus and umbonal carina usually well defined; prosopon of subfasciculate concentric elements only. = *Nyassa*, *sensu stricto*; junior synonym of *N. dorsata*.
2. *Nyassa subalata* Hall and Whitfield, 1869. Hamilton of New York. Based upon five medium to large specimens (23–41 mm. in length); nonalate-subalate-alate; umbonal carina not defined; modiomorphoid-pterineoid shape. Prosopon concentric with or without radii. One or two strong lateral teeth; strong anterior adductor scar. An artificial grouping of several bivalve taxa (see remarks above). Williams and Breger (1916, p. 155) considered this species to be affiliated with either *Cypricardites* or *Cyrtodonta* (i.e., a cyrtodontid). They described it as like *Cypricardites* but "differing chiefly in having the cardinal teeth more numerous and more irregular." This observation is evidently in error since cardinal teeth are unknown in *N. subalata*. The "cardinals" they refer to are probably those of Hall's hinge enlargement of *N. arguta* shown here in figure 50D. It is a natural mistake since this figure is surrounded by a series of *N. subalata* figures on Hall's plate 53.
3. *Nyassa recta* Hall and Whitfield, 1869. Hamilton of New York. Based upon six medium-sized specimens (20–28 mm. in length); ovate, straight hinge line; umbonal carina absent in some, rectilinear and rounded in others. Ventral marginal sinus not defined. Prosopon concentric. Strong anterior adductor scar; two lateral teeth. A series of shells with an appearance too generalized to be placed in *Nyassa* with any confidence. Some resemble *Nuculites*. Types possibly not even mutually related.

<sup>5</sup> See Bailey's (1975) English translation of Beushausen's original description and remarks.

4. *Nyassa elliptica* Hall and Whitfield, 1869. "Corniferous Limestone" (=Onondaga; see Wilmarth, 1938), New York. Based on one medium-sized specimen (35 mm. in length); ovoid, ventral marginal sinus lacking; umbonal carina undefined; prosopon fine, concentric. Strong anterior adductor scar. Lateral teeth? Outline resembles specimens referred to *Edmondia*; probably not *Nyassa*.

North American species of *Nyassa* described by other authors include:

1. *Nyassa elongata* Cleland, 1911. Middle Devonian (Milwaukee Fm.), Wisconsin. Based on a single internal mold Cleland believed to be similar in outline to *N. arguta*. This conclusion seems supported by his drawings (1911, pl. 22, figs. 10–12) which show the ventral sinus, umbonal carina, pallial line and anterior adductor scar. Pohl (1929), however, justifiably reasigned Cleland's specimen to genus *Modiomorpha*. His photograph (1929, pl. 11, fig. 5) of Cleland's holotype shows a specimen far less nyassaform than in Cleland's original figures; i.e., neither the ventral sinus nor umbonal carina are evident.
2. *Nyassa parva* Walcott, 1884. Devonian of the Eureka District, Nevada. Walcott's description and figures (pl. 15, figs. 14, 14a) provide too little data for generic assignment. Probably not *Nyassa*.

**AUTECOLOGY:** *Nyassa dorsata* is rare in the Solsville. The figured specimen, still partially articulated prior to preparation (hence, probably *in situ*) perhaps originated in the dark, shaly facies of the Solsville as evidenced by the matrix infilling. The precise locality is uncertain, the specimen having been listed by Rollins as "miscellaneous Solsville." Other partial specimens of poorer quality have also been observed in the sandy facies.

With the exception of *Nyassa*, other palaeomutelids are Carboniferous-Permian in age and have been considered as nonmarine; indeed virtually all other anthracosiacians have been judged as freshwater taxa (see Weir in Moore, 1969, p. N404). However, owing to its occurrence in a variety of marine sediments in both Europe and North America, *Nyassa* was undoubtedly a marine indigent. Broad adaptations to a variety of marine habitats are suggested by the occurrence of *Nyassa* in both the sandy and clayey Solsville facies and elsewhere among arenaceous shales and carbonates (see Hall, 1885). Beushausen (1895) even noted its occurrence

in the *Stringocephalus*-Kalk, which, according to Erben and Zagora (1967) is a reef limestone. If, as the morphologic similarities and chronological differences would seem to indicate, later taxa such as *Palaeomutela* are phylogenetic descendents of nyassaform ancestors, then a marine origin for the Palaeomutelidae is implied (see also Bailey, 1979c). A saltwater origin has long been suspected; Weir (in Moore, 1969), for example noted that Wöhrmann had early supposed a marine derivation of *Palaeomutela* from the genus *Palaeoneilo*. However, *Nyassa* seems a far more credible progenitor of the palaeomutelid line.

The shells of *Nyassa dorsata* are analogous to other well-known unionoid bivalves including *Unio* Philipsson, *Anthracosia* King, and *Carbonicola* M'Coy. Based upon its presumed kinship to these taxa and rather similar shell form, somewhat similar life habits are suggested. Although the literature on unionoid bivalves is vast, few details of precise position and depth of burrowing have been reported (Eagar, 1974). However, some attention has been devoted to these problems by Eagar (1948, 1973, 1974), Pryor (1967), and Agrell (1949). Many unionoids burrow at a shallow angle with respect to the substrate surface often leaving much of the dorsal and dorsolateral regions exposed (Eagar, 1974; Pryor, 1967). Some more elongated species such as *Carbonicola bellula* (Bolton) appear to have positioned themselves within the sediments with the long axis of the shell vertically placed and only the posteriormost extremity exposed (Eagar, 1974). Agrell (1949) stressed that among Swedish *Unio* and *Anodonta* the degree of burial varies widely according to species. A reconstruction of the possible life position of *Nyassa* is shown in figure 6.

SUBCLASS HETERODONTA NEUMAYR, 1884  
ORDER VENEROIDA  
ADAMS AND ADAMS, 1856  
SUPERFAMILY LUCINACEA FLEMING, 1828  
FAMILY MACTROMYIDAE COX, 1929  
(=MACTROMYACIDAE COX, 1935)  
GENUS *PARACYCLAS* HALL, 1843

TYPE SPECIES: *Paracyclas elliptica* Hall, 1843 [not *P. elliptica* Phillips, 1841; see DeKoninck, 1898, p. 85; Williams and Bre-

ger, 1916, p. 257; LaRocque, 1950, p. 310] by original monotypy and subsequent designation of Hall (1885) from the "Corniferous Limestone" (=Onondaga), LeRoy, Genesee County, New York. [= *Lucina proavia* Goldfuss, 1840 (see Beushausen, 1895, p. 169; Chavan in Moore, 1969, p. N512) = *Lucina (Paracyclas) elliptica* var. *occidentalis* Hall and Whitfield (not Billings) (see Hall, 1885, p. 440; LaRocque, 1950, pp. 310–311)].

GENERIC USAGE: See diagnosis of Chavan (in Moore, 1969, p. N512) and remarks of LaRocque (1950, pp. 308–309).

INTERNAL MORPHOLOGY: Despite numerous treatments of past authors the internal morphologies of Devonian lucinoids remain poorly understood. In *Paracyclas pallial* and muscular data are sketchy, and the few characterizations of the hinge and ligament of past authors are often either incomplete, vague or contradictory.

Hall (1885, p. xxxviii) gave the following early account of the interior morphology of *Paracyclas*: "Structure of the hinge not fully observed. Ligament supported on each side, internally, by a narrow plate, and leaving in the cast [mold] two diverging grooves, directed forward from the beak. Muscular impression on the post-umbonal slope. Pallial line parallel with and a little within the margin of the shell." Hall's internal or (?) composite mold of *P. elliptica* (reproduced here as fig. 51I, J) shows a simple pallial line, a small, ovoid posterior adductor scar and an anterior adductor scar which is ventrally elongated as in many other lucinaceans. The ventral extension is not separated from the pallial line as it is among the Lucinidae but is evidently attached as in the unguinids (Chavan in Moore, 1969, considered *Paracyclas* to be a mactromyid).

A laterally compressed internal mold (fig. 51M) of *P. marginata* (Maurer), 1886, was used by Beushausen (1895) as the basis for his description and restoration of the hinge of *Paracyclas*, and a representation of *P. proavia* (Goldfuss) was used to illustrate the ligament (see fig. 51K). His (p. 166) interpretations of shell orientation and inner "plates" (ridges) do not agree with Hall [writer's translation]:

The hinge, as far as can be observed, consists in each valve of one or two very small dentic-

ulations under the beak; lateral teeth are missing.

A usually distinct inner ridge runs from the beak in each valve under the hinge line toward the posterior and sometimes toward the anterior. It produces a linear groove on the internal mold. Ligament not visible from the outside; on the inside it is situated in a shorter or longer, hollowed-out cavity just behind the beaks. The supporting ridges for the ligament, often cited, are lacking. In reality these are the above mentioned inner ridges which extend laterally on the inside of the shell, and, as our illustration shows, only approach the ligament at the beak. There is greater reason to consider them as support ridges associated with the muscular impressions. Muscular impressions weak, oval or elongated; pallial line simple.

Later authors have evidently relied solely on Maurer's species for hinge data. Babin (1966), using the figure of Spriestersbach (1919, pl. 3, fig. 1, 1a), described the cardinal teeth as very small, one in the right valve and two in the left, with a short, posterior, internal ligamental groove. Chavan's (in Moore, 1969; his figures are reproduced here as fig. 51N, O) interpretation is somewhat different. In his view the ligamental depression is broad and long, the two cardinal teeth are in the right valve, and there is a possible anterior lateral tooth.

The intrapallial area of the type species is marked by numerous pallial punctae (Hall, 1885), a characteristic appearing in many lucinid subfamilies (see various figs. of Chavan in Moore, 1969, pp. N492–N508). Moreover, the pallial line is evidently discontinuous, consisting of a series of short, radial striae which show up on internal molds as numerous elongate nodes as described by Hall and later confirmed by plate 14, figure 19 of Pohl (1929), though not mentioned in his text. A somewhat similar pallial line is evident in *Lucinella*.

#### *Paracyclas rugosa* (Goldfuss), 1837

Figures 5F, 51A–H

*Lucina rugosa* Goldfuss, 1837, p. 216, pl. 146, fig. 9a, b. De Verneuil, 1847, p. 695. Steininger, 1853, p. 53.

*Paracyclas rugosa* (Goldfuss). Beushausen, 1895, p. 171, pl. 15, figs. 8–11. Renaud, 1930, p. 210, pl. 12, fig. 11; 1942, p. 235. Maillieux, 1932, p. 86, pl. 3, figs. 12, 13. Babin, 1966, p. 285, pl. 12, fig. 7. Bailey, 1975, p. 224, pl. 15, figs. 7–

- 11, text-fig. 35; 1978a, p. 121, tab. 1. [Many other ref. omitted; see Maillieux's (1937, pp. 221–223) exhaustive list.]
- Paracyclas* [sic] *rugosa* (Goldfuss). Maillieux, 1937, p. 221.
- Paracyclas* cf. *rugosa* (Goldfuss). Babin, 1973, p. 58, pl. 6, fig. 3.
- Venulites concentricus* Roemer, 1844, p. 79, pl. 2, fig. 3a–c [synonym of Beushausen, 1895, p. 171, and Maillieux, 1937, p. 221].
- Lucina daleidensis* Steininger, 1853, p. 53 [synonym of Beushausen, 1895, p. 171, and Maillieux, 1937, p. 222].
- Posidonia lateralis* Steininger [not Phillips], 1853, p. 53 [synonym of Maillieux, 1937, p. 222].
- Posidonia lirata* Conrad, 1838, p. 116, pl. [un-numbered], fig. 2.
- Posidonia lyrata* [sic] Conrad. De Verneuil, 1847, p. 695.
- Posidonia* [sic] (= *Paracyclas*) *lirata* Conrad. Hall and Whitfield, 1872, p. 200 [= *Lucina* (*Paracyclas*) *lirata* (Conrad) Hall and Whitfield, 1872, of Hall, 1885, p. 441, and Whiteaves, 1898, p. 399. = *Lucinda* [sic] (*Paracyclas*) *lirata* (Conrad) Hall and Whitfield, 1872, of Ellison, 1965, p. 145.]
- Paracyclas lirata* (Conrad). Miller, 1877, p. 200. Hall, 1883 [in part], pl. 72, figs. 1[?]-19; 1885, p. 441, pl. 72, figs. 2–19, pl. 95, fig. 19. Nettleroth, 1889, p. 211, pl. 2, figs. 4–7. Whiteaves, 1892, p. 306; 1898, p. 399. Beushausen, 1895, p. 172. Grabau, 1899, p. 265, fig. 186. Whitfield and Hovey, 1900, p. 298. Kindle, 1901, p. 673, pl. 15, fig. 10. Shimer and Grabau, 1902, p. 181. Clarke and Ruedemann, 1903, p. 483. Cleland, 1903, p. 73; [?] 1911, p. 118, pl. 25, figs. 6, 7 [= *Paracyclas* sp. Pohl, 1929, p. 72, pl. 14, figs. 22, 23]. Grabau and Shimer, 1909, p. 555, fig. 760b. Stauffer, 1909, p. 166; 1915, pp. 226, 235, 239; 1916, p. 483. Prosser and Kindle, 1913, p. 277, pl. 34, figs. 11–14. Williams and Breger, 1916, p. 257. [not] Butts, 1926, p. 160, pl. 48, fig. 27. Cooper, 1930, pp. 133, 233; 1933, p. 550; 1934, p. 79. Savage, 1930, p. 10, pl. 4, fig. 20; 1931, pl. 31, fig. 3. Willard, 1939, p. 477, etc., pl. 28, figs. 13, 14. Stumm, 1942, p. 557, pl. 81, fig. 31. Shimer and Shrock, 1944, p. 423, pl. 168, fig. 14. LaRocque, 1950, pp. 308–309. Stumm and Wright, 1958, pp. 93, 108. Ellison, 1965, p. 145, pl. 16, figs. 14–17. Zenger, 1965, p. 154, text-fig. 2 [see Zenger's ref. (omitted here) of Upper Devonian occurrences]. Babin, 1966, p. 285. Rollins, Eldredge, and Spiller, 1971, p. 134. Bailey, 1975, p. 225; 1978a, p. 121, tab. 1. Wilson, 1975, p. 143, pl. 272, fig. 8, pl. 115, fig. 8.
- Paracyclas* (*Lucina*) *lirata* Hall [sic]. Lesley, 1889, p. 596, 2 figs.
- Paracyclas lyrata* [sic] (Conrad). Shimer and Grabau, 1902, p. 159.
- Paracyclas lirata* Conrad var. (?) [sic]. Prosser and Kindle, 1913, p. 278, pl. 34, fig. 15.
- Paracyclas* [sic] *lirata* (Conrad). Branson, 1924, p. 116, pl. 25, figs. 9, 12 [see *P. rowleyi* below].
- Paracyclas lirata* [sic] Conrad. Savage, 1930, p. 97.
- †[?] *Lucina occidentalis* Billings, 1859, p. 187, fig. 1b, c. [= *L. elliptica* Conrad [sic] Billings, 1859, p. 187, fig. 1d. = *Paracyclas billingsana* Miller, 1883, p. 311. = *P. elliptica* var. *occidentalis* Billings of Whiteaves, 1892, p. 305, pl. 39, figs. 7–10, [not] Hall and Whitfield, 1872.]
- †[?] *Paracyclas elongata* Nettleroth, 1889, p. 210, pl. 2, fig. 8. Kindle, 1901, p. 674.
- †[?] *Paracyclas elliptica* (Hall). Cleland, 1911 [in part], p. 25, figs. 3[?], 4[?], and esp. 5. [= *P. obesa-umbonata* Pohl, 1929, p. 71, pl. 14, figs. 17, 18.]
- †[?] *Paracyclas tenuis* Hall. Prosser and Kindle, 1913 [in part], p. 278, pl. 34, fig. 17 [not 16].
- [?] *Paracyclas rowleyi* (Branson). McAlester, 1963b, p. 994, pl. 126, figs. 1–29, pl. 127, figs. 1–9. [= *Clinopistha rowleyi* Branson, 1924, p. 111, pl. 25, figs. 7, 8. = *Modiomorpha missouriensis* Branson, 1924, p. 114, pl. 25, figs. 3–6, 10, 11. = *P. elliptica* Hall of Branson, 1924 [in part], p. 115, [not] pl. 36, fig. 1. = *P. lirata* (Conrad) of

FIG. 51. A–H. *Paracyclas rugosa* (Goldfuss). A. A left valve (AMNH 36234) from AMNH loc. 3013. B, C. Articulated specimen (AMNH 36233) from AMNH loc. 3014. B. Left valve. C. Right valve. D, E. Articulated specimen (AMNH 36235) from AMNH loc. 3012. D. Right valve. E. Distorted left valve. F, G. Articulated specimen, upper Coblenz beds, Germany (figures of Beushausen, 1895, pl. 15, fig. 9a, b). F. Right valve. G. Left valve. H. Original illustration of Goldfuss, a left valve (as figured by Beushausen, 1895, pl. 15, fig. 10). I, J. *Paracyclas elliptica* Hall. Internal mold (as figured by Hall, 1885, pl. 72, figs. 27, 28), Onondaga Limestone, Cayuga, Ontario. I. Left lateral view. J. Dorsal view. K. *Paracyclas proavia* (Goldfuss), Devonian, Germany. Dorsal view showing ligamental area (lga) as figured by Beushausen, 1895, fig. 14 (p. 170). L–O. *Paracyclas marginata* (Maurer). L. Restoration of left hinge as figured by Beushausen (1895, fig. 13), enlarged. M. Internal mold, upper Coblenz beds, Niederlahnstein, as figured by Beushausen (1895, fig. 13) and used as basis for L. N, O. Left hinges (enlarged) as figured by Chavan (after Maurer) in Moore, 1969, fig. E15, 5a, b, courtesy, the Geological Society of America and University of Kansas.

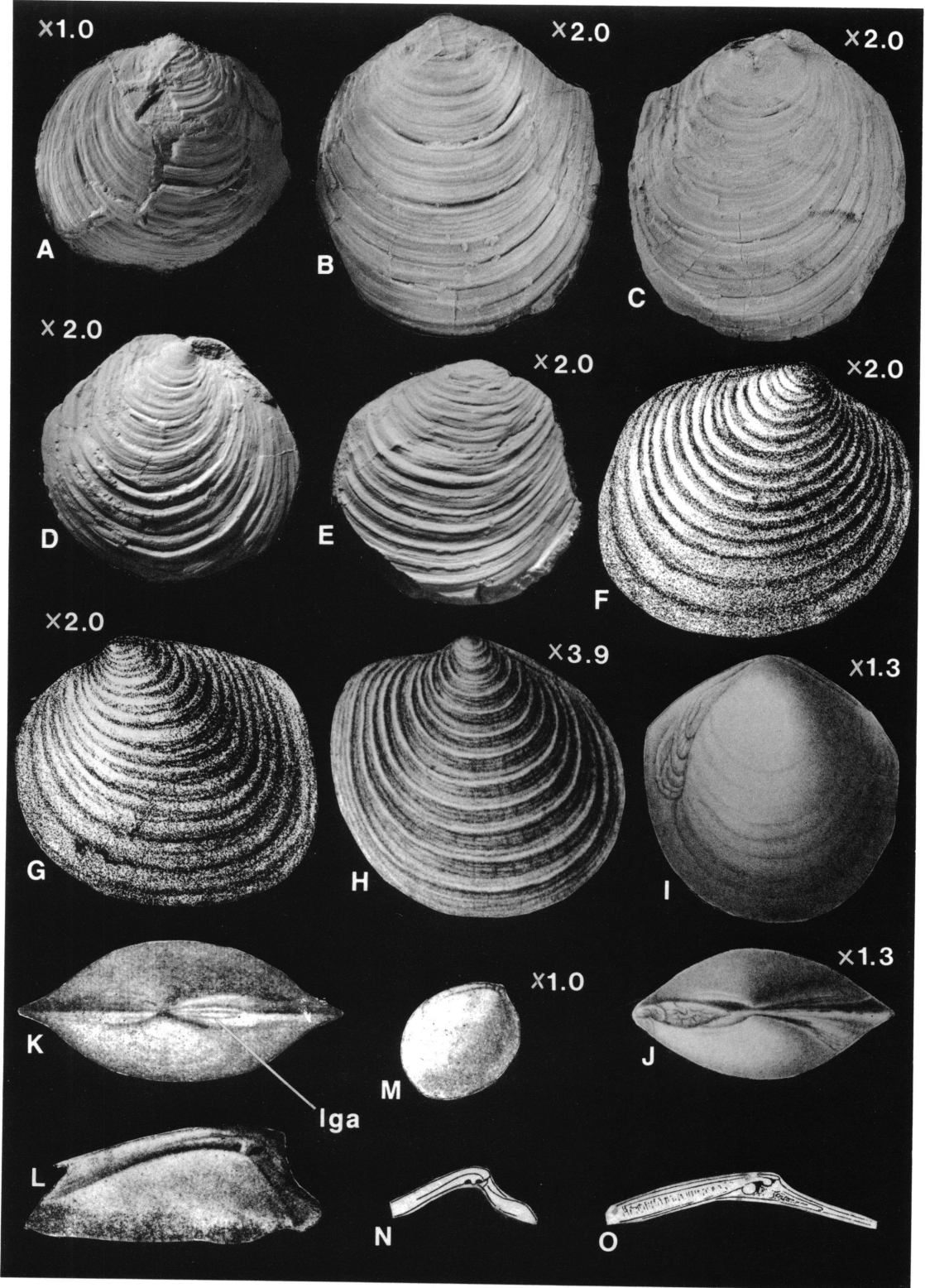




TABLE 11  
Measurements (in Millimeters) of *Paracyclas rugosa* (Goldfuss)

Locality	Length	Height	Width <sup>a</sup>
AMNH 3013	28.7	28.6	—
	23.4	15.4 <sup>b</sup>	6.5 <sup>c</sup>
AMNH 3014	27.8	12.5 <sup>b</sup>	10.3 <sup>c</sup>
	27.9	—	—
	25.8 <sup>b</sup>	12.0 <sup>b</sup>	7.8 <sup>c</sup>
Miscellaneous	22.4	21.2	5.8
Solsville	22.5	25.1	6.4
	29.9	16.6 <sup>b</sup>	12.7 <sup>c</sup>

<sup>a</sup> Total width, both valves articulated.  
<sup>b</sup> Dimension undervalued; specimen vertically compressed.  
<sup>c</sup> Dimension exaggerated; specimen vertically compressed.

Branson, 1924, p. 116, pl. 25, figs. 9–12. [?]=*P. sabini* White, 1876, p. 31. All synonyms of *P. rowleyi*, *sensu* McAlester.]  
\*[[?]] *Lucina proavia* Goldfuss, 1840, p. 226, pl. 146, fig. 6a, b. [= *L. dufrenoyi* d'Archiac and de Verneuill, 1842, p. 375, pl. 37, fig. 2, 2a. = *Paracyclas proavia* (Goldfuss) Beushausen, 1895, p. 169, pl. 15, figs. 1, 2, and later authors.] [= *Paracyclas elliptica* Hall, 1843, p. 171, fig. 67, no. 2; 1883, pl. 72, figs. 23–30; 1885, p. 440, pl. 72, figs. 23–33, pl. 95, fig. 18. = *Lucina* (*Paracyclas*) *elliptica* var. *occidentalis* Hall and Whitfield, 1872, p. 189 (= *P. occidentale* Hall and Whitfield of Williams and Breger, 1916, p. 257, not Billings, 1859).] [? = *P. marginata* (Maurer), 1886, p. 13 (? = *P. tenuis* Hall, 1883, pl. 72, figs. 20–22).] [? = *P. marylandica* Clarke and Swartz, 1913, p. 660, pl. 66, fig. 25.] [? = *P. elliptica incerta* Pohl, 1929, p. 71, pl. 14, figs. 19, 20.] [\*These names, provisionally appended, would have to be placed in synonymy if McAlester's (1963b) conclusions are correct. But see discussion below.]

DESCRIPTION: Shape and prosopon variable. Shells very thin, medium size, equi-valve, orbicular, faintly (?)subalate. Umbones small, subcentral, prosogyrous, rising slightly above the hinge line. Valve convexity slight; articulated specimens often flat, nummular.  
Prosopon marked by obscure concentric striae lying among numerous coarsely prominent concentric lirae or rugae; regular to irregular.  
Ligament and interior morphology not here observed.

Original microstructure and mineralogy unknown.  
REMARKS: Although variable, the nummular shape and deep prosoponal relief of this species are distinctive. Specimens here show very thin remnants of the shell. Since most examples of this species here and elsewhere show obvious compressional distortions, much of the morphologic variation is judged to be diagenetic in origin. Such fragile shells would have had little resistance to post-depositional compaction.  
Hinge, ligament, and internal data are lacking in the Solsville examples and unknown elsewhere. Hall (1885, p. 441) gave evidence for an external ligament; his plate 95, figure 19 shows what he believed to be a "ligament groove" (Beushausen would have interpreted this feature differently; see above) behind the beak in each valve which he described as "distinctly marked and only moderately divergent from the cardinal margin."  
COMPARISONS: The nummular shape and sharp concentric prosoponal lirae mark these Solsville specimens as typical *Paracyclas lirata* (Conrad), a widely distributed but poorly understood species of the Middle to Upper Devonian of eastern and midwestern North America. As noted above I regard this species as a junior (subjective) synonym of *P. rugosa* (Goldfuss) from the Lower to Upper Devonian of Europe. The identity of the two was early recognized by de Verneuill (1847, p. 695): "*Lucina rugosa* Goldf.: (*Posidonia lyrata* Conr.)—Ces deux coquilles, que nous possédons dans notre collection, ne présentent pas de différences spécifiques. L'une est de l'Eifel; M. Goldfuss la signale dans le calcaire, et nous l'avons trouvée dans les schistes qui lui sont immédiatement inférieurs; l'autre appartient au groupe de Hamilton, dans l'Etat de New-York, et au calcaire cornifère, dans celui d'Indiana."  
These similarities were further noted by Beushausen (1895, p. 172): "Ausserordentlich nahe steht, wie schon De Verneuill erkannt hatte, unserer Art *P. lirata* Conrad, die sich nur durch unregelmässigere Sculptur unterscheidet. Exemplare der amerikanischen Art, welche mir vorliegen, stimmen sonst mit *P. rugosa* völlig überein."  
The identity of the two seems further cemented by the placement of *P. lirata* in tentative synonymy with *P. rugosa* by Maillieux



(1937) and by the recent remarks of Babin (1966, p. 285): "Beushausen plaça en synonymie *P. lirata* Conrad d'Amerique du Nord et *P. rugosa*; E. Maillieux émet quelque doute sur cette équivalence; les deux espèces semblent extrêmement voisines d'après la récente figure donnée par D. H. Zenger (1965, f. 2, p. 154) et *P. rugosa* paraît ainsi avoir une très vaste répartition géographique."

These transatlantic similarities are not confined to *P. rugosa-lirata* but are true of several other species of *Paracyclas* as well. An evaluation of European and North American species is presented below [see also writer's English translation of Beushausen's (1895) descriptions and remarks on European species given in Bailey (1975)]:

1. *Paracyclas proavia* (Goldfuss), 1840 [= *Lucina* (*Paracyclas*) *proaria* [sic] Goldf. in Hall and Whitfield, 1872, p. 189]. Middle Devonian (Eifelian-Givetian), Germany. Shell large [two specimens of Beushausen measure (mm.) 49–52 in length and 44–50 in height], inflated. Prosopon concentric, fine, irregular, subfasciculate. Hinge unknown. Integripalliate, adductors elliptical; ligament internal, opisthodic. I agree with past authors (e.g., de Verneuil, 1847; Beushausen, 1895; LaRocque, 1950; Chavan in Moore, 1969) who considered it the senior synonym of *P. elliptica* Hall.
2. *Paracyclas rugosa* (Goldfuss), 1837 [= *Venu-lites concentricus* Steininger, 1853]. Lower-Upper Devonian (Siegenian-Frasnian), Germany, Belgium, and France. Shell medium to small [four specimens of Beushausen (1895) measure (mm.) 12–25 in length and 11–23 in height], compressed. Prosopon concentric, coarse. Hinge and interior unknown. Lectotype, designated by Mauz (1935), is Goldfuss's plate 146, figure 9a, b (figured by Beushausen and reproduced here as fig. 51H).
3. *Paracyclas marginata* (Maurer), 1886. Lower-Middle Devonian (Siegenian-Eifelian), Germany, Belgium, and France. Lectotype, designated by Mauz (1935), is plate 15, figure 3 of Beushausen (1895). Shell medium [four specimens of Beushausen (1895) measure (mm.) 16–20 in length and 15–19 in height], compressed. Prosopon concentric, fine, subfasciculate. Hinge and ligament described. Integripalliate, adductors elliptical. Beushausen (1895) remarked at the close similarity of this species to a specimen of *P. tenuis* Hall in his possession. Maillieux (1937) speculated that the two were identical as did Babin (1966). In my opinion *P. marginata* individuals are probably little more than young or stunted *P. proavia*. This seems supported by Babin's remarks on the additional similarities of *P. marginata* to specimens of *P. elliptica* [= *P. proavia*] as figured by Whiteaves (1892, pl. 39, figs. 7–10) and LaRocque (1950, pl. 12, figs. 1–7). I suspect four species names have been applied to what is, in fact, a single biological species: *P. elliptica* and *P. proavia* are, respectively, the American and European names applied to the adults, whereas *P. tenuis* and *P. marginata* are the respective American and European names for the juveniles.
4. "*Paracyclas*" *antiqua* (Goldfuss), 1840 [= *Lucina lineata* Goldfuss, 1840, according to Roemer (1844) and Beushausen (1895)]. Middle Devonian (Eifelian-Givetian) of Germany. Shell medium to large [two specimens of Beushausen (1895) measure (mm.) 21–44 in length and 20–41 in height]. Shell irregularly rhomboid; oblique posterior sulcus. Prosopon concentric, fine, irregularly fasciculate. Hinge unknown. Adductors elongated, especially the anterior one. Regarded by Whiteaves (1892) and Beushausen (1895) as senior synonym of *Paracyclas ohioensis* (Meek). LaRocque (1950) suggested that *P. antiqua-ohioensis* might not be *Paracyclas* but a member species of genus *Phenacocyclus* LaRocque.
5. *Paracyclas praecursor* Beushausen, 1895. Lower Devonian (Emsian), Germany. Based on a single right valve like *P. antiqua* but lacking the radial sulcus. Hinge and interior unknown. *Phenacocyclas*?
6. *Paracyclas dubia* Beushausen, 1895. Upper Devonian (Famennian), Germany. Apparently known only from internal molds. Nuculiform, integripalliate with elliptical adductors and single radial sulcus. Prosopon fine, concentric. Hinge unknown.
7. *Paracyclas rectangularis* (Sandberger and Sandberger), 1850–1856. Middle Devonian (Givetian), Germany. Based on very few specimens. Inequilateral, nuculiform. Hinge and interior unknown. Beushausen (1895) considered it to be, in part, *Nucula* [i.e., *N. sandbergeri* Beushausen] and, in part, a species of *Paracyclas* closely related to *P. antiqua* [*Phenacocyclas*?].
8. *Paracyclas elliptica* Hall, 1843 [= *P. occidentale* Hall and Whitfield of Williams and Breger, 1916]. Middle Devonian, eastern North America. Shell large [five specimens of Hall (1885) measure (mm.) 30–48 in length and 29–44 in height], inflated. Prosopon concentric, fine, irregularly fasciculate. Hinge unknown. Integripalliate; anterior adductor ventrally elongate. See *P. proavia*. *P. elliptica* var. *occidentalis* Hall and Whitfield from the Mid-

- dle Devonian near Louisville, Kentucky [not *Lucina occidentalis* Billings, 1859, from the Devonian of Manitoba; although Whiteaves (1892) placed this Canadian species in *P. elliptica*, Billings's figures suggest a closer kinship with *P. rugosa-lirata*] and is probably nothing more than a preservational variant as noted in the original description. Hall (1885) later admitted that there are no differences of varietal importance.
9. *Paracyclas lirata* (Conrad), 1838. Middle-Upper Devonian (Cazenovian-Fingerlakesian), eastern North America. Shell medium [four specimens of Hall (1885) measure (mm.) 15–28 in length and 13–26 in height], compressed. Prosopon concentric, fairly regular, coarse. Hinge and interior unknown. See *P. rugosa*. Hall (1885) incorrectly compared it to *Lucina lineata* Goldfuss, a species which Beushausen (1895) considered a synonym of *P. antiqua* [= *Phenacocyclus*?].
  10. "*Paracyclas*" *ohioensis* (Meek), 1871 [not *P. ohioensis* var. *tenuistriata* Cleland, 1911 (= *Iliona tenuistriata* (Cleland) Pohl, 1929; = *Phenacocyclus pohli* LaRocque, 1950)]. Middle Devonian, upper Midwest of North America. Shells small [Hall's (1885, pl. 72, fig. 1 and pl. 95, fig. 24) measure 13 × 12.5 and 12 × 11 mm., respectively; the latter could be a distorted specimen of *Palaeoneilo constricta*], subrhomboid with oblique posterior sulcus. Prosopon fine, concentric. Hinge and interior unknown. Considered as possibly belonging to *Phenacocyclus* by LaRocque, 1950 (see *P. antiqua*) who designated a small specimen (no. 12113G, collections of Columbia University, New York) as the lectotype of *P. ohioensis*. However, as his plate 13, figure 3, shows, the suggested lectotype has neither the shape, prosopon, nor sulcus of *P. ohioensis*, *sensu* Meek and *sensu* Hall; instead, it has the nummular shape and coarse lirae of a typical *P. rugosa-lirata* and, hence, is unacceptable as the lectotype.
  11. *Paracyclas tenuis* Hall, 1883. Middle Devonian (Hamilton), New York. Shells small [four specimens of Hall (1885) measure (mm.) 7–10 in length and 7–9 in height]. Prosopon concentric, fine, ventrally subfasciculate. Hinge and interior unknown. Hall's plate 72, figures 20–22, are probably juveniles of *P. proavia-elliptica* (see above); his plate 95, figure 25, is, perhaps, a brachiopod (*Orbiculoidea*?).
  12. "*Paracyclas*" *chemungensis* Hall, 1885. Upper Devonian (Chemung), Pennsylvania. Based on a single large specimen (30 × 29 mm.). Hinge and interior unknown. Possibly not *Paracyclas* [compare with *Edmondia philipi* Hall and Whitfield as figured in Hall (1885, pl. 95, figs. 1–4)].
  13. *Paracyclas ignota* Hall, 1883. Upper Devonian (Chemung), Pennsylvania. Based on a single large specimen (41 × 38 mm.). Hinge and interior unknown. Prosopon concentric, fine, subfasciculate. Probably *P. proavia-elliptica*.
  14. "*Paracyclas*" *rotunda* (Hall), 1883. Upper Devonian (Chemung), New York. Based on two large specimens (one specimen of Hall measures 48 × 43 mm.). Hinge and interior unknown. McAlester (1962a) placed this species in *Eoschizodus*? *chemungensis*.
  15. "*Paracyclas*" *erecta* Hall, 1885. Upper Devonian (Chemung), Pennsylvania. Evidently based on a single medium specimen (25 × 20 mm.). Truncate. Two (?) ligamental grooves. Hall (1885) compared it to both *Paracyclas* and *Schizodus*. Affinities indeterminate.
  16. "*Paracyclas*?" *pauper* Hall, 1883. Upper Devonian (Chemung), New York. Shells medium [three specimens of Hall (1885) measure (mm.) 15–22 in length and 14–20 in height], subnuculiform, resembling *Eoschizodus* but less angular. Hinge and interior unknown. Affinities indeterminate.
  17. *Paracyclas elongata* Nettleroth, 1889. Middle Devonian (Sellersburg), northern Kentucky and southern Indiana. Nettleroth's (pl. 2, fig. 8) single figure appears to be a diagenetically deformed *P. rugosa-lirata*. He admitted that the similarities to *P. lirata* are strong and suspected that it intergrades with *P. elongata*.
  18. *Paracyclas marylandica* Clarke and Swartz, 1913. Upper Devonian (Jennings Formation), Maryland. A probable synonym of *P. proavia-elliptica*. The original illustration (pl. 66, fig. 25) is convincingly similar, and the authors conceded that it may be regarded as merely a "mutation" of *P. elliptica*. Evidently based on a single specimen.
  19. *Paracyclas paradoxica* Pohl, 1929. Middle Devonian (Milwaukee Fm.), Wisconsin. Evidently based on a single, circular internal mold of medium size (27 mm. diameter). (?) Anterior adductor markedly extended ventrally; integripalliate. Hinge unknown.
  20. *Paracyclas obesa-umbonata* Pohl, 1929 [= *P. elliptica* Hall, in part, of Cleland, 1911]. Middle Devonian (Lake Church Fm.), Wisconsin. Shell small to medium (Pohl indicated an average specimen diameter of 23 mm.), inflated. Prosopon concentric, fine, but dominated by coarse, regular lirae. Hinge unknown. (?) Anterior adductor ventrally elongated. Combines *P. proavia-elliptica* and *P. rugosa-lirata* characters but favors the latter.

21. *Paracyclas elliptica incerta* Pohl, 1929. In limestone, glacially transported. Based on a single, large, composite mold (50 mm. diameter) with the size, form and prosopon of *P. proavia-elliptica*. Pallial line simple, consisting of intermittent radial striae as in *P. elliptica*, *sensu stricto*.
22. *Paracyclas rowleyi* (Branson), 1924 of McAlester (1963b). Upper Devonian (Snyder Creek Shale) of Missouri. Prosopon, size, and inflation intermediate between *P. proavia-elliptica* and *P. rugosa-lirata* (see discussion below). Hinge, ligament and interior unknown.

DISCUSSION: As noted above, *P. proavia-elliptica* is placed in questionable synonymy with *P. rugosa-lirata*. Owing to their marked differences my reticence in this step is considerable. Reasons for doing so are not mine but are based on McAlester's (1963b) study of the Upper Devonian Snyder Creek Shale (Missouri), one of the most prolific occurrences of *Paracyclas* known. Here he found evidence that prosopon, size, and inflation are ecophenotypic characters. He suggested *P. elliptica* and *P. lirata* are ecophenotypes of a single biological species, the larger *P. elliptica* occurring in the purer limestones and the smaller, more strongly sculptured *P. lirata* in the shales; hence, in his view, *P. lirata* are perhaps merely stunted *P. elliptica*. In support of this view he noted that his Snyder Creek species, *P. rowleyi*, is intermediate between these two species not only in morphology but also in lithologic occurrence. Elsewhere I can find additional support for McAlester's contention: (1) according to Beushausen (1895) *P. proavia* occurs in Europe among calcareous sediments and *P. rugosa* among arenaceous or argillaceous sediments; (2) specimens which Whiteaves (1892, p. 306) reported as "almost exactly intermediate in their characters between *P. elliptica* Hall and *P. lirata* Conrad" were found in an argillaceous limestone of Snake Island (Lake Winnipegosis, Manitoba). However, I can likewise find evidence contrary to McAlester's argument: (1) *P. obesa-umbonata* Pohl, which shows the smaller size and coarse lirae of *P. rugosa-lirata*, occurs in the limestones of the Middle Devonian Lake Church Formation of Wisconsin. (2) Savage (1930) noted the mutual occurrence in a Louisville, Kentucky,

quarry of both *P. elliptica* and *P. lirata* in the Silver Creek Limestone, Sellersburg Formation (lithologically a thin-bedded, argillaceous to dolomitic limestone), and again in 1931 where his figures (i.e., pl. 31, figs. 3, 11) verify his earlier identifications. (3) *P. marginata-tenuis* (probable dwarfs or young of *P. proavia-elliptica*) are found in argillaceous or arenaceous deposits of both Europe and North America. In conclusion, although McAlester's suggestion is compelling it cannot at present be confirmed. Hence, I prefer to regard *P. proavia-elliptica* and *P. rugosa-lirata* as specifically distinct pending further study.

AUTECOLOGY: Although *P. rugosa* occurs in both arenaceous and argillaceous facies of the Solsville, its greater abundance in the latter coupled with the extreme thinness of the shells probably reflect a preference for quiet, sheltered marine habitats. European occurrences suggest that the species flourished in a variety of clastic environments. Beushausen (1895) noted a progressive size increase in the species up section from its earliest German occurrence in the lower "Coblenz beds" (=lower Emsian) to its latest occurrence in the upper Frasnian. Erben (1964), Erben and Zagora (1967), and Sutton (1968) have shown that the Rheinisch Devonian sediments have a concomitant vertical shift in lithology: whereas the Emsian consists of arenaceous, shallow, nearshore sediments with a diversity of byssally attached bivalves, the overlying Eifelian, Givetian, and Frasnian become progressively more argillaceous and depleted in byssally attached taxa. This sedimentary sequence has been interpreted by these authors as a marine transgression associated with subsidence and erosion of the "Old Red Continent" (=Laurussia *sensu* Bambach, Scotese, and Ziegler, 1980) following the cessation of the Caledonian uplifts (see also Bailey, 1978a, p. 123). Thus it may be assumed that while *P. rugosa* thrived in sandy nearshore habitats, it prospered to a greater extent in the deeper, quieter pelitic substrates.

Examples of *P. rugosa* here (not illustrated) and elsewhere (e.g., see Hall, 1885, pl. 72, fig. 9) frequently show substantial dorsal crushing and resulting lateral bulging of the shells. This could only occur if the sedimentary compactional forces were acting parallel to

the plane of commissure, i.e., if the shells were placed upright in the sediment instead of reclining on one valve (this conclusion has been confirmed by field observation of *in situ* specimens). This shell orientation is similar to the usual life position of many lucinaceans (e.g., see Stanley, 1970, fig. 18a), i.e., shells erect, beaks upright, and suggests that the mode of life in *Paracyclas* may have been similar. It may be further supposed that this genus, like many other lucinaceans, was a nonbyssate filter feeder possessing only a posterior (exhalant) siphon, the inhalant function being served by a mucus-lined tube in the sediment formed anteriorly by the vermiform foot (see fig. 5).

Stanley (1970, fig. 46) has shown that lucinaceans may burrow to depths up to 25 cm. depending on shell size and habitat. He has further shown that they are, in general, sluggish burrowers although the smoother, less ornamented species seem to burrow with greater facility than highly ornamented forms. Hence, the concentric rugae in the sculpture of *P. rugosa* suggest especially sluggish burrowing habits. However, they would have increased the frictional resistance of the shell in the substrate thereby increasing positional stability in thixotropic muds. It is also possible, however, that they may have acted as a rasp in the penetration of firmer, more resistant substrates.

#### LITERATURE CITED

- Adams, H., and A. Adams  
1853-1858. The genera of Recent Mollusca, vol. 1 (1853-1854), 484 pp.; vol. 2 (1854-1858), 661 pp.; vol. 3 (1858), 136 pls.
- Agrell, I.  
1949. The shell morphology of some Swedish unionids as affected by ecological conditions. *Arkiv för Zoologi*, vol. 41A, pp. 1-30.
- Allen, J. A.  
1954. A comparative study of the British species of *Nucula* and *Nuculana*. *Jour. Marine Biol. Assoc. U.K.*, vol. 33, pp. 457-472, pl. 1 and figs. 1-8.
- Allen, J. R. L.  
1965. Late Quaternary Niger Delta, and adjacent areas: sedimentary environments and lithofacies. *Bull. American Assoc. Petrol. Geol.*, vol. 49, no. 5, pp. 547-600, 29 figs., 6 pls.
- Allen, J. R. L., and P. F. Friend  
1968. Deposition of the Catskill facies, Appalachian region, with notes on some other Old Red Sandstone basins, in Klein, G. deV. (ed.), Late Paleozoic and Mesozoic continental sedimentation, northeastern North America, a symposium. *Geol. Soc. America Spec. Paper* 106, pp. 2-74.
- Amalitsky, W.  
1892. Ueber die Anthracosien der Permformation Russlands. *Palaeontographica*, vol. 39, pp. 125-213, pls. 19-23.
- Angelin, N. P., and G. Lindström  
1880. *Fragmenta silurica e dono Caroli Henrici Wegelin. Opus studio Nicolai Petri Angelini inchoatum jussu et impensis Academiae regiae scientiarum suecicae edendum curavit G. Lindström. Holmiae, Samson & Wallin*, 60 pp., 20 pls.
- Archiac, A., Viscount d' (A. Desmier de Saint-Simon), and E. de Verneuil.  
1842. On the fossils of the older deposits in the Rhenish Provinces [etc.]. *Trans. Geol. Soc. London Series 2*, vol. 6, pp. 303-410, 13 pls.
- Atherton, E.  
1971. Tectonic development of the eastern interior region of the United States, in Background materials for symposium on the future petroleum potential of NPC region 9 (Illinois Basin, Cincinnati Arch., and northern part of Mississippi Embayment). *Illinois St. Geol. Surv., Ill. Petrol.* 96, pp. 29-43, figs. 1-4.
- Babin, C.  
1966. Mollusques, bivalves et céphalopodes du Paléozoïque Armoricaïn. *Brest. Imprimerie Commerciale et Administrative*. 471 pp., 18 pls.
1973. Bivalvia of the Kartal Formation of Devonian age, Istanbul. In Kaya, O. (ed.), *Paleozoic of Istanbul*. *Ege Univ. Fen. Fak. Kitaplar Serisi*, no. 40, pp. 37-71, 8 pls.
- Bailey, J. B.  
1975. Systematics, functional morphology and ecology of Middle Devonian bivalves from the Solsville Member (Marcellus Formation), Chenango Valley, New

- York. 290 pp., 15 pls., 36 figs., 13 tabs. (Unpubl. Ph.D. dissertation, Univ. Illinois.)
- 1978a. Provincialism and migration in Lower and Middle Devonian pelecypods. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, vol. 23, pp. 119–130.
- 1978b. Disjunct distributions in time and space: an occurrence of the European Triassic bivalve, *Palaeonucula strigilata* (Goldfuss), in the Mississippian of Arkansas. Abstracts with programs, North Central Sec. Geol. Soc. America 12th Ann. Meet., vol. 10, no. 6, p. 246.
- 1979a. North American Devonian Caryidiidae (Bivalvia). Abstr. with Progr., North Central Sec. Geol. Soc. America 13th Ann. Meet., vol. 11, no. 5, p. 225.
- 1979b. Michigan Basin endemism and the evolution of *Nuculopsis* Girty (Bivalvia). Abstr. with Progr., North Central Sec. Geol. Soc. America 13th Ann. Meet., vol. 11, no. 5, p. 225.
- 1979c. Marine origins of Permo-Carboniferous fresh water bivalves (Palaeomutelidae). Ninth Intl. Cong. Carboniferous Stratig. and Geol., Abstracts of Papers, p. 8.
- [MS.] North American Devonian Caryidiidae (Bivalvia): systematics, phylogeny and implications in early diversification of the class. 3 pls.
- Bailey, J. B., and P. A. Sandberg
1979. Preserved mineralogy and ultrastructure in two new Pennsylvanian bivalves. Ninth Intl. Cong. Carboniferous Stratig. and Geol., Abstr. of Papers, pp. 8–9. [Repr., 1980, Oklahoma Geol. Notes, vol. 40, no. 1, pp. 31.]
- [In press] Preserved mineralogy and ultrastructure in two new Pennsylvanian bivalves. *Compte Rendu, Ninth Intl. Cong. Carboniferous Stratig. and Geol.*, 3 pls.
- Bambach, R. K.
1971. Adaptations in *Grammysia obliqua*. *Lethaia*, vol. 4, no. 2, pp. 169–183, 11 figs.
- Bambach, R. K., C. R. Scotese, and A. M. Ziegler
1980. Before Pangea: the geographies of the Paleozoic world. *American Scientist*, vol. 68, no. 1 (Jan–Feb), pp. 26–38, 15 figs.
- Barrell, J.
1913. The Upper Devonian delta of the Appalachian geosyncline. *American Jour. Sci.*, 4th ser., vol. 36, pp. 429–472.
1914. The Upper Devonian delta of the Appalachian geosyncline. *Ibid.*, 4th ser., vol. 37, pp. 87–109, 225–253.
- Barrois, C.
1882. Recherches sur les terrains anciens des Asturies et de la Galice. [Lille]. *Mém. Soc. Géol. du Nord*, vol. 2, mém. 1.
1891. Mémoire sur la faune du grès armoricain. *Ann. Soc. Géol. du Nord*, vol. 19, pp. 134–237, 5 pls.
- Beurlen, K.
1944. Beiträge zur Stammesgeschichte der Muscheln. *Bayer. Akad. Wiss., Sitzungsber.*, no. 1–2, pp. 133–145.
- Beushausen, L.
1884. Beiträge zur Kenntniss des Oberharzer Spiriferensandsteins und seiner Fauna. *Geol. Spezialk. Preuss. Thüring. Staat., Abhandl.*, vol. 6, no. 1, 133 pp., atlas 6 pls.
1889. Ueber einige Lamellibranchiaten des rheinischen Unterdevon. *Jahrb. Preuss. Geol. Landesanst.* (1888), vol. 9, pp. 212–236.
1895. Die Lamellibranchiaten des rheinischen Devon mit Ausschluss der Aviculiden. *Kgl. Preuss. Geol. Landesanst., Abhandl.*, new ser., vol. 17, 514 pp., atlas 38 pls.
- Billings, E.
1858. Report for the year 1857 [Black River fauna; descriptions of the Devonian and Ordovician fossils]. *Geol. Surv. Canada, Repts. Prog.* 1857, pp. 147–192, illus.
1859. On some of the Silurian and Devonian fossils collected by Professor Henry Y. Hind on the Assiniboine and Saskatchewan exploring expedition, in Hind, H. Y., Northwest Territory; reports of progress, together with a preliminary general report on the Assiniboine and Saskatchewan exploring expedition, pp. 186–187.
1874. On some new genera and species of Paleozoic Mollusca. *Canadian Naturalist*, new ser., vol. 7, pp. 301–302.
- Bowen, Z. P., D. C. Rhoads, and A. L. McAlester
1974. Marine benthic communities in the Upper Devonian of New York. *Lethaia*, vol. 7, no. 2, pp. 93–120, 22 figs.
- Bradshaw, J. D., and M. A. Bradshaw
1971. Functional morphology of some paleotaxodont bivalve hinges as a guide to orientation. *Palaeontology*, vol. 14, pt. 2, pp. 242–249, 6 figs.
- Bradshaw, M.
1974. Morphology and mode of life of the bivalves *Nuculoidea vespa* n. sp. and *Nuculoidea umbra* n. sp. from the Devonian of New Zealand. *New Zealand Jour. Geol. and Geophys.*, vol. 17, no. 2, pp. 447–464, 16 figs.

1978. Position of soft parts in fossil Palaeotaxodont bivalves as suggested by features of the shell interior. *Alcheringa*, vol. 2, pp. 203–215, 14 figs.
- Branson, E. B.  
1922. The Devonian of Missouri. *Missouri Bur. Geol. and Mines*, vol. 16, 2nd ser., 279 pp., 71 pls. [1924].
- Bretsky, P. W.  
1968. Evolution of Paleozoic marine invertebrate communities. *Science*, vol. 159, pp. 1231–1233, 1 fig.  
1969. Central Appalachian Late Ordovician communities. *Geol. Soc. America Bull.*, vol. 80, pp. 193–212, 11 figs., 2 pls.  
1970. Late Ordovician benthic marine communities in north-central New York. *New York State Mus. and Sci. Service Bull.* 414, 34 pp.  
1973. Evolutionary patterns in the Paleozoic Bivalvia: documentation and some theoretical considerations. *Geol. Soc. America Bull.*, vol. 84, pp. 2079–2096, 5 figs.
- Bruun, A. F.  
1957. Deep sea and abyssal depths, in Hedgpeth, J. W. (ed.), *Treatise on marine ecology and paleoecology*, vol. 1, ecology. *Geol. Soc. America Mem.* no. 67, pp. 641–672, 9 figs., 3 pls.
- Butts, C.  
1915. Geology and mineral resources of Jefferson County, Kentucky. *Kentucky Geol. Surv.*, 1914–1915, 270 pp., 65 pls.  
1926. Geology of Alabama: the Paleozoic rocks. *Geol. Surv. Alabama Spec. Rept.* no. 14, pp. 41–230, 74 pls.  
1941. Geology of the Appalachian Valley in Virginia; pt. 2, fossil plates and explanations. *Virginia Geol. Surv. Bull.* 52, pt. 2, 271 pp., 72 pls.
- Carter, J. G., and M. J. S. Tevesz  
1978a. The shell structure of *Ptychodesma* (Cyrtodontidae; Bivalvia) and its bearing on the evolution of the Pteriomorpha. *Phil. Trans., Roy. Soc. London B.* 284, pp. 367–374, 5 figs.  
1978b. Shell microstructure of a Middle Devonian (Hamilton Group) bivalve fauna from central New York. *Jour. Paleont.*, vol. 52, no. 4, pp. 859–880, 21 figs.
- Caster, K. E.  
1930. Higher fossil faunas of the upper Allegheny. *Bull. American Paleont.* no. 58, pp. 37–71, 8 pls.
- Chadwick, G. H.  
1933. Hamilton red beds in eastern New York. *Science*, vol. 77, pp. 86–87.
1944. Geology of the Catskill and Kaaterskill quadrangles, pt. II. *New York State Mus. Bull.* 336. 251 pp.
- Chavan, A.  
1954. *Les Pleurophorus et genres voisins*. *Cahiers Géol. Seyssel*, no. 22, p. 200.  
1966. Sur l'évolution de la charnière des Hé-térodontes (Mollusques Pélécypodes). *Soc. Géol. France Compte Rendu*, pt. 10, pp. 408–409.
- Clarke, J. M.  
1900. The Devonian molluscan fauna of the state of Pará, in Clarke, J. M., *The Paleozoic faunas of Pará, Brazil*, author's English ed. (*Archivos do Museu Nacional do Rio de Janeiro*, vol. 10, 1899), pp. 25–100, 8 pls.  
1904. Naples fauna in western New York, pt. 2. *New York State Mus. Mem.* 6, pp. 199–454, 20 pls.  
1907a. Some new Devonian fossils. *New York State Mus. Bull.* 107, *Geol.* 12, *New York State Educ. Dept. Geol. Papers*, pp. 193–291.  
1907b. Evidences of a Coblenzian invasion in the Devonian of eastern America. *Festschrift Adolf v. Koenen gewidmet von seinen Schuelern zum siebzigsten Geburtstage am 21 Maerz 1907*. Stuttgart, E. Schweizerbartsche Verlagsbuchhandl., pp. 359–368.  
1908. Early Devonian history of New York and eastern North America, pt. 1. *New York State Mus. Mem.* 9, pt. 1, 366 pp., 48 pls.  
1909. Early Devonian history of New York and eastern North America, pt. 2, *Ibid.*, 9, pt. 2, 250 pp., 34 pls.
- Clarke, J. M., and R. Ruedemann  
1903. Catalogue of type specimens of Paleozoic fossils in the New York State Museum. *New York State Mus. Bull.*, vol. 65, 847 pp.
- Clarke, J. M., and C. K. Swartz  
1913. Systematic paleontology of the Upper Devonian deposits of Maryland. *Maryland Geol. Surv.*, Middle and Upper Devonian, pp. 539–699, 29 pls.
- Cleland, H. F.  
1903. A study of the fauna of the Hamilton formation of the Cayuga Lake section in central New York. *U.S. Geol. Surv. Bull.* 206, 112 pp.  
1911. The fossils and stratigraphy of the middle Devonian of Wisconsin. *Wisconsin Geol. and Nat. Hist. Surv. Bull.* no. 21, *Sci. Ser.* no. 6, chapt. 7, *Pelecypoda*, pp. 97–120, pls. 20–27.

1916. *Geology, physical and historical*. New York, American Book Co., 718 pp., 588 figs.
- Collinson, C.  
1967. Devonian of the north-central region, United States. *Internatl. Symp. Devonian System*, Calgary, vol. 1, pp. 933–971, 13 figs. *Alberta Soc. Petrol. Geol.*
- Conrad, T. A.  
1837. First annual report on the geological survey of the third district of the state of New York. *New York Geol. Surv. Ann. Rept.* 1, pp. 155–186.  
1838. Report on the paleontological department of the survey [of New York]. *New York Geol. Surv. Ann. Rept.* 2, pp. 107–119.  
1841. Fifth annual report on the paleontology of the state of New York. *Commun. transmitting rept.* *Geol. Survey [New York]*, pp. 25–57.  
1842. Observations on the Silurian and Devonian systems of the United States with descriptions of new organic remains. *Acad. Nat. Sci. Philadelphia Jour.*, vol. 8, pt. 2, pp. 228–280, 6 pls.
- Cooper, C. L.  
1935. Ammonium chloride sublimate apparatus. *Jour. Paleont.*, vol. 9, pp. 357–359.
- Cooper, G. A.  
1930. Stratigraphy of the Hamilton Group of New York. Pts. 1 and 2, *American Jour. Sci.*, vol. 19, pp. 116–134, 214–235, 6 figs.  
1933. Stratigraphy of the Hamilton Group of eastern New York. *Ibid.*, 5th ser., vol. 26, no. 156, pp. 537–551, 3 figs.  
1934. Stratigraphy of the Hamilton Group of eastern New York, part II. *Ibid.*, 5th ser., vol. 27, no. 157, pp. 1–12.  
1957. Paleocology of the Middle Devonian of eastern and central United States. *Geol. Soc. America Mem.* 67, pp. 249–278, 1 pl., 2 figs.
- Cooper, G. A., and P. E. Cloud  
1938. New Devonian fossils from Calhoun County, Illinois. *Jour. Paleont.*, vol. 12, no. 5, pp. 444–460, pls. 54, 55.
- Cooper, G. A., et al.  
1942. Correlation of the Devonian sedimentary formation of North America. *Geol. Soc. America Bull.*, vol. 53, pp. 1729–1749, 1 pl., 1 fig.
- Cossmann, M.  
1907. Paléontologie, in Thiéry, P. and M. Cossmann, *Note sur le Callovien de la Haute-Marne et spécialement sur un gisement situé dans la commune de Briccon*. *Soc. Agriculture, Let., Sci. et Arts du Dépt. de la Haute-Saône Bull.* 1907, pt. 2, pp. 69–147, pls. 1–3.
- Cox, L. R.  
1929. A synopsis of the Lamellibranchia and Gastropoda of the Portland beds of England. Part 1. Lamellibranchia. *Dorset Nat. Hist. and Arch. Soc. Proc.*, vol. 50, pp. 131–202, pls. 1–6.  
1935. Jurassic Gastropoda and Lamellibranchia, in the Mesozoic palaeontology of British Somaliland, pp. 148–197, pls. 14–21.  
1959. The geological history of the Protobranchia and the dual origin of taxodont Lamellibranchia. *Malacol. Soc. of London, Proc.*, vol. 33, pt. 5, pp. 200–209, 5 figs.  
1960. Thoughts on the classification of the Bivalvia. *Malacol. Soc. London, Proc.*, vol. 34, pt. 2, pp. 60–88, 2 figs.
- Dahmer, G.  
1936. Die Fauna der Obersten Siegener Schichten von der Unkelmühle bei Eitorf a. d. Sieg. *Preuss. Geol. Landes., Abhandl.*, new ser., no. 168, 36 pp., 6 pls.  
1940. Die Fauna der Unterkoblenzschichten vom Landstein im östlichen Taunus. *Senckenbergiana*, vol. 22, no. 3/4, pp. 260–274.  
1942. Die Fauna des Unter-Koblenz von Ziegenberg (Unter-Devon, östlicher Taunus). *Senckenbergiana*, vol. 25, no. 4/6, pp. 263–291, 34 figs.  
1943. Die Mollusken des Wetteldorfener Richtschnittes. *Senckenbergiana*, vol. 26, no. 5, pp. 325–396, 9 pls.
- Dales, R. P.  
1957. Interrelation of organisms. A. Commensalism, in Hedgpeth, J. (ed.), *Treatise on marine ecology and paleoecology*. *Geol. Soc. America Mem.* 67, vol. 1, pp. 391–412, 9 figs., 1 pl.
- Dall, W. H.  
1889. On the hinge of pelecypods and its development with an attempt toward a better subdivision of the group. *American Jour. Sci.*, vol. 38, no. 3, pp. 445–462.
- Davis, F. M.  
1925. Quantitative studies on the fauna of the sea bottom, no. 2. *Southern North Sea*. *Great Britain Fish. Invest.*, ser. 11, vol. 8, pp. 1–50.
- Dechaseaux, C.  
1952. Classe des Lamellibranches, in Pive-



- teau, J. (ed.), *Traité de paléontologie*, vol. 2, pp. 220–364, 215 figs. Paris, Masson et Cie.
- DeFrance, M. J. L.  
1825. *In* Cuvier, F. (ed.), *Dictionnaire des Sciences Naturelles*, etc., vol. 35, pp. 215–219. Paris, Le Normant.
- Doumani, G. A., et al.  
1965. Lower Devonian fauna of the Horlick Formation, Ohio Range, Antarctica. *American Geophys. Union Antarctic Res. Ser.*, vol. 6, pp. 241–281, pls. 1–18.
- Douvillé, H.  
1912. Un essai de classification phylogénique des lamellibranches. *Acad. Sci. Paris, Comptes Rendus*, vol. 154, pp. 1677–1682.
- Dienst, P.  
1913. Die Fauna der Unterkoblenzschichten (Michelbacher Schichten) des oberen Bernbachtales bei Densberg im Kellerwald. *Jahrb. Preuss. Geol. Landesanst. f. 1913*, vol. 34, no. 1, pp. 539–615, pls. 16–18. [1914]
- Drevermann, F.  
1907. Palaeozoische Notizen. *Ber. Senckenb. Naturforsch. Ges. Frankfurt am Main*, pp. 125–136, 1 pl.
- Drew, G. A.  
1901. The life history of *Nucula delphinodonta* (Mighels). *Quar. Jour. Micr. Sci.*, vol. 44, pp. 313–391.
- Driscoll, E. G.  
1964. Accessory muscle scars, an aid to protobranch orientation. *Jour. Paleont.*, vol. 38, pp. 61–66, pl. 16.  
1966. Morphology and evolution of certain Paleozoic Nuculanidae from the mid-continental United States. *Sborník Národního Muzea V Praze, Acta Musei Nationalis Pragae*, vol. 22B, no. 1, pp. 1–26, 4 pls.
- Duluk, C.  
1965. Fossil fauna of the Silica Formation, *in* *Fossils of the mid-continent of North America*. Reprinted from *Earth Sci.*, 1965, pp. 37–42, 2 pls.
- Eagar, R. M.  
1948. Variation in shape of shell with respect to ecological station. A review dealing with Recent Unionidae and certain species of the Anthracosiidae in Upper Carboniferous times. *Roy. Soc. Edinburgh, Proc.*, sec. B, vol. 63, pp. 130–148, figs. 1–9.  
1973. Variation in shape of shell in relation to palaeoecological station in some non-marine Bivalvia of the Coal Measures of south-east Kentucky and Great Britain. *Compte Rendu, Septième Congr. Intl. Strat. Geol. Carbonifère*, 1971, vol. 7, no. 2, pp. 387–416, illus.
1974. Shape of shell of *Carbonicola* in relation to burrowing. *Lethaia*, vol. 7, pp. 219–238, 12 figs.
- Eardley, A. J.  
1962. *Structural geology of North America*. New York and Evanston, Ill., Harper and Row, 2nd ed., 743 pp., illus.
- Eberzin, A. G.  
1960. Osnovy paleontologii, spravochnik dlya paleontologov i geologov SSSR [t.3], Mollyuski; pantsirnye, dvustvorchatye, lopatonogie. Pp. 18–197, 44 pls. *Akad. Nauk. SSSR, Moscow*.
- Ehlers, G. M., E. C. Stumm, and R. V. Kesling  
1951. Devonian rocks of southeastern Michigan and northwestern Ohio. *Guidebook, Geol. Soc. America field trip, Detroit meeting*, 40 pp., 5 pls., 3 figs.
- Ellis, D. V.  
1960. Marine infaunal benthos in Arctic North America. *Arctic Inst. North America Tech. Paper 5*, 53 pp., 17 figs.
- Ellison, R. L.  
1965. Stratigraphy and paleontology of the Mahantango Formation in south-central Pennsylvania. *Pennsylvania Geol. Surv. Bull. G48*, 4th ser., 298 pp., 19 pls.
- Erben, H. K.  
1964. Facies development in the marine Devonian of the Old World. *Proc. Ussher Soc.*, vol. 1, pt. 3, no. 61, pp. 92–118.  
1967. Devonian of Germany, *in* Oswald, D. H. (ed.), *Internatl. Symp. Devonian System*, Calgary, vol. 1, pp. 53–68, 6 figs. *Alberta Soc. Petrol. Geol.*
- Férussac, A. de  
1821–1822. Tableaux systématiques des animaux mollusques classés en familles naturelles, dans lesquels on a établi la concordance de tous les systèmes; suivis d'un prodrome général pour tous les mollusques terrestres ou fluviatiles, vivants ou fossiles. Paris, A. Bertrand. [Issued in parts.]
- Fischer, P.  
1880–1887. *Manuel de conchyliologie et de paléontologie conchyliologique ou histoire naturelle des mollusques vivants et fossiles*. Paris, F. Savy, 1369 pp., 23 pls.
- Follmann, O.

1885. Ueber devonische Aviculaceen. Verhandl. Naturhist. Vereines der Preuss. Rheinlande, Westfalens, u. Reg.-Bezirks Osnabrück, vol. 42, pp. 181–216, 7 pls.
- Frech, F.  
1891. Die devonische Aviculiden Deutschlands; ein Beitrag zur Systematik und Stammesgeschichte der Zweischaler. Abhandl. Geol. Spezialkarte von Preuss. u. d. Thüringischen Staat., vol. 9, no. 3, 261 pp., 18 pls.
- Friedman, G. M., and K. G. Johnson  
1966. The Devonian Catskill Delta complex of New York, type example of a "tectonic delta complex," in Shirley, M. L. (ed.), Deltas in their geologic framework. Houston Geol. Soc., pp. 171–188.
- Friedman, G. M., and J. E. Sanders  
1978. Principles of sedimentology. New York, John Wiley & Sons, 792 pp., illus.
- Fuchs, A.  
1912. Ueber einige neue oder weniger bekannte Molluskoiden und Mollusken aus deutschem Devon. Jahrb. Preuss. Geol. Landesanst., vol. 33, pt. 2, no. 1, pp. 49–76, pls. 4–8.  
1915. Der Hunsrückschiefer und die Unterkoblenzschichten am Mittelrhein (Loreleigegend). I. Teil. Beitrag zur Kenntnis der Hunsrückschiefer und Unterkoblenzfauna der Loreleigegend. Kgl. Preuss. Geol. Landesanst., Abhandl., new ser., no. 79, 79 pp., 18 pls.  
1919. Beitrag zur kenntnis der devonfauna der Verse- und Hobracker Schichten des sauerländischen faciesgebietes. Jahrb. Preuss. Geol. Landesanst. 1918, vol. 29, pt. 1, no. 1, pp. 58–95, pls. 5–9.
- Gignoux, M.  
1950. Stratigraphic geology. Engl. transl. from the 4th Fr. ed. by Woodford, G. G., 1954. San Francisco and London, W. H. Freeman and Co., 682 pp., illus.
- Girty, G. H.  
1911. On some new genera and species of Pennsylvanian fossils from the Wewoka Formation of Oklahoma. New York Acad. Sci. Annals, vol. 21, pp. 119–156, 1912 [preprints distrib. 1911].
- Goldfuss, G. A.  
1833–1840. Petrefacta Germaniae. Pt. 2, pp. 1–68, pl. 72–96 (1833); lief. 5, pp. 69–140, pl. 97–121 (1836); lief. 6, pp. 141–224, pl. 122–146 (1837); lief. 7, pp. 225–312, pl. 147–165 (1840), Arnz (Düsseldorf).
- Grabau, A. W.  
1899. Geology and palaeontology of Eighteen Mile Creek and the lake shore section of Erie County, New York, pt. 2, palaeontology. Bull. Buffalo Soc. Nat. Sci., vol. 6, pt. 2, pp. 97–390, 263 figs.  
1906. Guide to the geology and paleontology of the Schoharie Valley of eastern New York. New York State Mus. Bull. 92, Paleont. 13, 386 pp., 24 pls.
- Grabau, A. W., and H. W. Shimer  
1909–1910. North American index fossils; invertebrates. New York, A. G. Seiler & Co., vol. 1, 853 pp.; vol. 2, 909 pp., illus.
- Grant, R. E.  
1966. Spine arrangement and life habits of the productoid brachiopod *Waagenoconcha*. Jour. Paleont., vol. 40, pp. 1063–1069, 2 pls., 2 figs.  
1968. Structural adaptation in two Permian brachiopod genera, Salt Range, west Pakistan. *Ibid.*, vol. 42, pp. 1–32, 9 pls., 21 figs.
- Gray, J. E.  
1847. A list of the genera of recent Mollusca, their synonyms and types. Zool. Soc. London, Proc., vol. 15, pp. 129–219.
- Haffer J.  
1959. Der Schlossbau früh-heterodonter Lamellibranchiaten aus dem rheinischen Devon. Palaeontographica, pt. A, vol. 112, pp. 133–192, pls. 11–14.
- Hall, J.  
1843. Geology of New York. pt. IV. Survey of the Fourth Geological District. Albany, Nat. Hist. of New York, 683 pp., 192 figs., 74 illus., 19 pls., map.  
1852. Paleontology, vol. 2, containing descriptions of the organic remains of the lower middle division of the New York system (equivalent in part to the middle Silurian rocks of Europe). Albany, Nat. Hist. of New York, 362 pp., 85 pls.  
1859. Descriptions and figures of the organic remains of the Lower Helderberg Group and Oriskany Sandstone. New York Geol. Surv., Paleont., vol. 3, 532 pp., 120 pls. (text, 1860, pls. 1861).  
1861. Report of the Superintendent of the Geological Survey [Wisconsin], exhibiting the progress of the work, Jan. 1, 1861 [including descriptions of new species of fossils from the investigations of the survey], 52 pp.
1883. Lamellibranchiata, plates and explanations. Nat. History of New York, Paleont., vol. 5, pt. 1, 20 pp., 79 pls.  
1884. Lamellibranchiata I, descriptions and figures of the Monomyaria of the upper Helderberg, Hamilton and Chemung

- groups. New York State Geol. Surv., Paleont. (Nat. Hist. of New York), vol. 5, pt. 1, pp. 1-268, 33 pls.
1885. Lamellibranchiata II, descriptions and figures of the Dimyaria of the upper Helderberg, Hamilton, Portage and Chemung groups. *Ibid.* (Nat. Hist. of New York), vol. 5, pt. 1, pp. 269-561, 63 pls.
- Hall, J., and R. P. Whitfield  
1869-1870. Preliminary notice of the lamellibranchiate shells of the upper Helderberg, Hamilton, and Chemung groups, with others from the Waverly sandstones, pt. 2. Albany. New York State Mus., 96 pp. [pp. 1-80 issued Dec 1869; pp. 81-96 issued Jan 1870.]
1872. Descriptions of new fossils from the vicinity of Louisville, Kentucky, and the Falls of the Ohio. New York State Mus., Ann. Rept. 24, pp. 181-200a.
1875. Fossils from the Hudson River Group (Cincinnati formations). Geol. Surv. Ohio Rept., vol. 2, pt. 2, pp. 67-161, pls. 1-13.
- Heath, H.  
1937. The anatomy of some protobranch Mollusks. Mém. Mus. Roy. Hist. Nat. Belgique, ser. 2, vol. 10, 26 pp., 9 pls.
- Holzapfel, E.  
1882. Die Goniatitenkalk von Adorf in Waldeck. Palaeontographica, vol. 28, pp. 229-259.
1895. Das obere Mitteldevon (Schichten mit *Stringocephalus burtini* und *Maeneceras terebratum*) im rheinischen Gebirge. Kgl. Preuss. Geol. Landesanst., Abhandl., new ser., no. 16, 459 pp., 19 pls.
- Isberg, O.  
1934. Studien über Lamellibranchiaten des Leptaenakalkes in Dalarna; Beitrag zu einer Orientierung über die Muschelfauna im Ordoviciun und Silur. Lund, Håkan Ohlssons Buchdruckerei. 492 pp., 32 pls.
- Kayser, E.  
1878. Die Fauna der ältesten Devon-Ablagerungen des Harzes. Abhandl. Specialk. v. Preuss. u. Thüring. Staaten, vol. 2, no. 4, 295 pp., 36 pls.
1901. Ein Molluskenfauna vom Grey Hook auf Spitzbergen. Bihang Till K. Svenska Vet. Akad. Handlingar, vol. 27, Afd. 4, no. 2, 24 pp., 2 pls.
- Keferstein, W.  
1857. Ueber einige deutsche devonische Conchiferen aus der Verwandtschaft der Trigoniceen und Carditaceen. Deutsch. Geol. Gesell., Zeitschr., vol. 9, pp. 148-162, pl. 4.
- Kegel, W.  
1913. Der Taunusquarzit von Katzenelnbogen. Kgl. Preuss. Geol. Landesanst., Abhandl., new ser., no. 76, 163 pp., 6 pls.
- Kier, P. M., R. E. Grant, and E. L. Yochelson  
1965. Whitening fossils, in Kummel, B. and D. Raup (eds.), Handbook of paleontological techniques. San Francisco and London, W. H. Freeman & Co., pp. 453-456.
- Kindle, E. M.  
1896. The relation of the fauna of the Ithaca Group to the fauna of the Portage and Chemung. Bull. American Paleont., no. 6, 56 pp., 1 pl., map.
1899. The Devonian and Lower Carboniferous faunas of southern Indiana and central Kentucky. Bull. American Paleont., no. 12, 111 pp.
1901. The Devonian fossils and stratigraphy of Indiana. Indiana Dept. Geol. and Nat. Res. Ann. Rept. 25 [1900], pp. 529-775, 31 pls.
1909. The Devonian fauna of the Ouray Limestone. U.S. Geol. Surv. Bull. 391, 60 pp., 10 pls.
1912. The Onondaga fauna of the Allegheny region. *Ibid.*, 508, 144 pp., 13 pls.
1914. The Silurian and Devonian section of western Manitoba. Summ. Rept. Geol. Surv. [Canada] Dept. Mines, 1912, Sess. Paper no. 26, pp. 247-261.
- Knod, R.  
1908. Devonische Faunen Boliviens, in Steinmann, G., Beiträge zur Geologie und Paläontologie von Südamerika. Neu. Jahrb. Mineral., Geol. u. Paläont. 25 (beilageband), pp. 493-600, pls. 21-31.
- Koninck, L. G. de  
1883. Faune du calcaire Carbonifère de la Belgique, 4th partie, Gastéropodes (Suite et fin). Mus. Roy. d'Hist. Nat. de Belgique, Ann., vol. 8, p. 28.
1898. Descriptions of the Paleozoic fossils of New South Wales, Australia. Geol. Surv. New South Wales Mem., Paleont., no. 6, 298 pp., 24 pls.
- Korobkov, I. A.  
1954. Spravochnik i metodicheskoe Rukovodstvo po tretichnym mollyuskam Plastinchatozhabernye. Gosud. Nauchno-tech. Issledov. Nefti. Gorno-toplivnoi lit-ry, Leningradskoi Otdelenie, 444 pp., 96 pls.

- Lamarck, J. B. de  
 1799. Prodrôme d'une nouvelle classification des coquilles comprenant une rédaction appropriée des caractères génériques, et l'établissement d'un grand nombre de genres nouveau, par le citoyen Lamarck. Mém. Soc. d'Hist. Nat. de Paris, vol. 1, pp. 63–91.  
 1809. Philosophie zoologique, ou exposition des considérations relatives à l'histoire naturelle des animaux, la diversité de leur organisation et des facultés qu'ils en obtiennent, aux causes physiques qui main tiennent en eux la vie, et donnent lieu aux mouvements qu'ils exécutent; enfin, à celles qui produisent les unes les sentiments, et les autres l'intelligence de ceux qui en sont doués. Paris, 2 vols., pp. 1–422, 1–473.
- LaRocque, A.  
 1950. Pre-Devonian pelecypods of Michigan. Contrib. Mus. Paleont., Univ. of Michigan, Ann Arbor, vol. 7, no. 10, pp. 271–366, 19 pls.
- LaRocque, A., and M. F. Marple  
 1955. Ohio fossils. State of Ohio Dept. Nat. Res. Div. Geol. Surv. Bull. 54, 152 pp., 413 figs.
- Leriche, M.  
 1912a. Lamellibranches, gastropodes, ptéropodes (Conularida), ostracodes et mérostomes de la faune Siluro-Dévonienne de Liévin (Pas-de-Calais). Mém. Soc. Géol. du Nord, vol. 6, mém. no. 2, pp. 37–64, pls. 5–9.  
 1912b. La faune du Gedinnien inférieur de l'Ardenne. Mém. Mus. Roy. d'Hist. Nat. de Belgique, vol. 6, no. 3 (mém. 23), 58 pp., 3 pls.
- Lesley, J. P.  
 1889–1890. A dictionary of the fossils of Pennsylvania and neighboring states. Pennsylvania Geol. Surv. Rept. P4, vol. 1 [A–M, pp. 1–438], vol. 2 (N–R, pp. 439–914), 1889; vol. 3 [S–Z, pp. 915–1283], 1890, illus.
- Levinton, J. S., and R. K. Bambach  
 1975. A comparative study of Silurian and recent deposit-feeding bivalve communities. Paleobiology, vol. 1, pp. 97–124, 13 figs.
- Lim, C. F.  
 1966. A comparative study of the ciliary feeding mechanisms of *Anadara* species from different habitats. Biol. Bull., vol. 130, pp. 106–117.
- Linné, C.  
 1758. Systema naturae regnum animale. London, Brit. Mus. Nat. Hist. (facsimile).
- McAlester, A. L.  
 1962a. Upper Devonian pelecypods of the New York Chemung stage. Peabody Mus. Nat. Hist. Bull. 16, 88 pp., 32 pls.  
 1962b. Mode of preservation in early Paleozoic pelecypods and its morphologic and ecologic significance. Jour. Paleont., vol. 36, no. 1, pp. 69–73, pl. 16, 1 text-fig.  
 1963a. Pelecypods as stratigraphic guides in the Appalachian Upper Devonian. Geol. Soc. America, Bull., vol. 74, no. 10, pp. 1209–1224, 10 figs.  
 1963b. Pelecypods from the Snyder Creek Shale (Upper Devonian) of Missouri. Jour. Paleont., vol. 37, no. 5, pp. 981–1000, pls. 121–127.  
 1964. Preliminary suggestion for a classification of nuculoid bivalves. *Ibid.*, vol. 38, no. 2, pp. 397–400.  
 1965. Bivalves, in Doumani, G. A., et al., Lower Devonian fauna of the Horlick Formation, Ohio Range, Antarctica. American Geophys. Union Antarctic Res. Ser., vol. 6, pp. 261–267, pls. 9–14.  
 1968. Type species of Paleozoic nuculoid genera. Geol. Soc. America Mem. 105, 143 pp., 36 pls.
- McAlester, A. L., and G. A. Doumani  
 1966. Bivalve ecology in the Devonian of Antarctica. Jour. Paleont., vol. 40, no. 1, pp. 752–755, 2 text-figs.
- McCave, I.  
 1969. Correlation using a sedimentological model of part of the Hamilton Group (Middle Devonian), New York State. American Jour. Sci., vol. 267, pp. 567–591, 11 figs.
- M'Coy, F.  
 1844. A synopsis of the characters of the Carboniferous limestone fossils of Ireland. Privately printed, 1844; re-issued, Williams and Norgate (London), 1862, 274 pp., 29 pls.  
 1851. On some new Silurian Mollusca. Ann. and Mag. Nat. Hist., ser. 2, vol. 7, pp. 45–63.
- MacKinnon, D. I.  
 1982. *Tuarangia paparua* n. gen. and n. sp., a late middle Cambrian pelecypod from New Zealand. Jour. Paleont., vol. 56, no. 3, pp. 589–598, 2 pls.
- Maillieux, E.  
 1920. Notes sur quelques groupes de Mollusques acéphales des terrains paléozo-

- zoïques. Soc. Belg. Géol., Paleont., et d'Hydrol., Bull., vol. 29, pp. 140-150, 3 figs.
1932. La faune de l'assise de Winenne (Emisien moyen) sur les bordures méridionale et orientale du bassin de Dinant. Mém. Mus. Roy. d'Hist. Nat. Belgique, no. 52, 102 pp. 5 pls.
1933. Terrains, roches et fossiles de la Belgique, 2nd ed. Brussels. Mus. Roy. d'Hist. Nat. Belgique, 217 pp., illus., 3 maps.
1935. Contribution à la connaissance de quelques Brachiopodes et Pélécypodes dévoniens. Mém. Mus. Roy. d'Hist. Nat. Belgique, no. 70, 42 pp., 4 pls.
1937. Les Lamellibranches du Dévonien inférieur de l'Ardenne. Mém. Mus. Roy. d'Hist. Nat. Belgique, no. 81, 274 pp., 14 pls.
- Maurer, F.
1886. Die Fauna des rechtsrheinischen Unterdevon. Darmstadt.
1902. Der Quarzit von Neuweilnau. Ber. Senckenb. Naturforsch. Ges. in Frankfurt am Main, 1901 II Teil. Wiss. Abhandl., pp. 27-76, pls. 3-6.
- Mauz, J.
1933. Zur Fauna der Unterkoblenz-Stufe. Senckenbergiana, vol. 15, no. 3/4, pp. 274-294, 26 figs.
1935. Vergleichende Untersuchung über die Unterkoblenz-Stufe bei Oberstadtfeld und Koblenz. Abhandl. Senckenb. Naturforsch. Ges. 429, 94 pp., 3 pls.
- Mazzullo, S. J.
1973. Deltaic depositional environments in the Hamilton Group (Middle Devonian), southeastern New York State. Jour. Sed. Petrol., vol. 43, no. 4, pp. 1061-1071, figs. 1-6.
- Meek, F. B.
1875. Descriptions of invertebrate fossils from the Carboniferous System, in Rept. Geol. Surv. Ohio, vol. 2, Geol. and Paleont., pt. 2, Paleont., 535 pp., 59 pls., pp. 269-347.
- Merrill, G. P.
1905. Catalogue of the type and figured specimens of fossils, minerals, rocks, and ores in the department of geology, U.S. Natl. Mus. Part I, Fossil Invertebrates, 704 pp.
- Miller, S. A.
1877. The American Paleozoic fossils; a catalogue of the genera and species, etc. Cincinnati (Ohio). Pub. by the author, 334 pp. [2nd ed., 1883].
- Moore, R. C. (ED.)
1969. Treatise on invertebrate paleontology, pt. N, Mollusca 6, Bivalvia, vols. 1, 2 by Cox, L. R., et al., 952 pp., illus.
- Morris, P. A.
1973. A field guide to shells of the Atlantic and Gulf coasts and West Indies. Boston, Houghton Mifflin Co., 3rd ed., 330 pp., 76 pls.
- Nettleroth, H.
1889. Kentucky fossil shells, a monograph of the fossil shells of the Silurian and Devonian rocks of Kentucky. Kentucky Geol. Surv. [Frankfort], 245 pp., 36 pls.
- Neumayr, M.
1884. Zur Morphologie des Bivalvenschlosses. S. B. Akad. Wissensch. Wien, vol. 88, pp. 385-415, pls. 1, 2.
- Newell, N. D.
- 1937 (1938). Late Paleozoic pelecypods: Pectenacea. Kansas St. Geol. Surv. Publ., vol. 10, no. 1, 123 pp., 20 pls.
1942. Late Paleozoic pelecypods: Mytilacea. Kansas St. Geol. Surv. Publ., vol. 10, no. 2, 115 pp., 20 pls.
1954. Status of invertebrate paleontology, 1953, V. Mollusca. Harvard Mus. Comp. Zool. Bull., vol. 112, pp. 161-172.
1965. Classification of the Bivalvia. Amer. Mus. Novitates no. 2206, 25 pp.
- Newell, N. D., and D. W. Boyd
1975. Parallel evolution in early trigonacean bivalves. Bull. Amer. Mus. Nat. Hist., vol. 154, art. 2, pp. 53-162, 98 figs.
- Nicol, D.
1955. An analysis of the arctic marine pelecypod fauna. Nautilus, vol. 68, no. 4, pp. 115-122.
- Öckelmann, W. K.
1958. Marine lamellibranchiata. In The zoology of east Greenland. Meddel. om Grønland, vol. 122, no. 4, 256 pp., 3 pls., 29 figs.
- Ohern, D. W., and T. P. Maynard
1913. Pelecypoda, in systematic paleontology of the Lower Devonian deposits of Maryland. Maryland Geol. Surv., Lower Devonian, pp. 450-465, pls. 75-78.
- Oldroyd, I. S.
1924. Marine shells of the west coast of North America. Stanford Univ. Publ., Univ. Ser., Geol. Sci., vol. 1, no. 1.
- Oliver, W. A.
1973. Devonian coral endemism in eastern North America and its bearing on paleogeography, in Hughes, N. (ed.), Or-

- ganisms and continents through time. Sp. Papers in Palaeont., no. 12, Palaeont. Assoc. [London], pp. 318–319, 1 fig.
1976. Presidential address: biogeography of Devonian rugose corals. Jour. Paleont., vol. 50, no. 3, pp. 365–373, 5 figs.
- Oliver, W. A., et al.
1969. Correlation of Devonian rock units in the Appalachian Basin. U.S. Geol. Surv. Oil & Gas Invest. Chart, OC-64.
- Orbigny, A. d'
1844. Paléontologie française. Description des Mollusques et Rayonnés fossiles, Terrains Crétacés, vol. 3, Paris, Lamellibranches [1843–1847], pp. 161–185.
- Palmer, K., and D. Brann
1966. Illustrations of fossils of the Ithaca area. Paleont. Res. Inst., 20 pls.
- Pelseneer, P.
1891. Contribution à l'étude des lamellibranches. Arch. Biol., vol. 11, pp. 147–312, pls. 6–23.
- Philip, G. M.
1962. The paleontology and stratigraphy of the Siluro-Devonian sediments of the Tyers area, Gippsland, Victoria. Victoria [Australia] Roy. Soc. Proc., new ser., vol. 75, pp. 123–246, pls. 11–36.
- Phillips, J.
1841. Figures and descriptions of the Palaeozoic fossils of Cornwall, Devon, and West Somerset; observed in the course of the Ordnance geological survey of that district. Great Britain Geol. Surv., Mem. Geol. Survey of England and Wales, 231 pp., 40 pls.
- Pitt, W. H.
1873. On a new species of *Grammysia* from the Chemung Group. Buffalo Soc. Nat. Sci. Bull., vol. 1, pp. 199–200 [1874?].
- Pohl, E. R.
1929. The Devonian of Wisconsin, part 1, Lamellibranchiata. Bull. Milwaukee Publ. Mus., vol. 11, no. 1, 100 pp., 14 pls.
1930. The Middle Devonian Traverse Group of rocks in Michigan, a summary of existing knowledge. Proc. U.S. Natl. Mus., vol. 76, art. 14, no. 2811, 34 pp.
- Pojeta, J.
1966. North American Ambonychiidae (Pelecypoda). Palaeontographica Americana, vol. 5, no. 36, pp. 131–241, pls. 19–47.
1971. Review of Ordovician pelecypods. U.S. Geol. Surv. Prof. Paper 695, 46 pp., 20 pls.
1978. The origin and early taxonomic diversification of pelecypods. Phil. Trans. R. Soc. London B, vol. 284, pp. 225–246, 15 pls.
- Prosser, C. S., and E. M. Kindle
1913. Pelecypoda, in Systematic paleontology of the Middle Devonian deposits of Maryland. Maryland Geol. Surv., Middle and Upper Devonian, pp. 214–279, 14 pls.
- Pryor, W.
1967. Biogenic directional features on several Recent point bars. Sedimentary Geol., vol. 1, pp. 235–245.
- Quenstedt, W.
1930. Die Anpassung an die grabende Lebensweise in der Geschichte der Solenomyiden und Nuculaceen. Geol. u. Palaeont. Abhandl., vol. 22 (new ser., vol. 18), no. 1, 119 pp., 3 pls.
- Raup, D. M., and S. M. Stanley
1971. Principles of paleontology. San Francisco and London, W. H. Freeman & Co., 388 pp., illus.
- Renaud, A.
1930. Etude de la faune des calcaires de Boissieux. Bull. Soc. Géol. Min. Bret. 9 (1928), pp. 142–292, 4 pls.
1942. Le Dévonien du Synclinorium médian Brest-Laval. Mém. Soc. Géol. Min. Bret. no. 7, 633 pp., 14 pls.
- Roemer, C. F.
1844. Das Rheinische Uebergangsgebirge. Eine paläontologisch-geognostische Darstellung. Hannover, 96 pp., 6 pls.
- Roemer, F. A.
1854. Beiträge zur geologischen Kenntniss des nordwestlichen Harzgebirges. Th. Fischer (Cassel). 5 pts. [1850–1856], 237 pp., illus.
- Rollins, H. B., N. Eldredge, and J. Spiller
1971. Gastropoda and Monoplacophora of the Solsville Member (Middle Devonian), Marcellus Formation in the Chenango Valley, New York State. Bull. Amer. Mus. Nat. Hist., vol. 144, art. 2, pp. 129–170, 21 figs.
- Runnegar, B.
1974. Evolutionary history of the bivalve subclass Anomalodesmata. Jour. Paleont., vol. 48, no. 5, pp. 904–939, 5 pls., 10 figs.
- Runnegar, B., and N. D. Newell
1974. *Edmondia* and the Edmondiaacea (Palaeozoic Bivalvia). American Mus. Novitates, no. 2533, 19 pp., 11 figs.
- Sandberger, F.

1891. Bemerkungen über *Ditichia*, eine neue Nuculaceen-Gattung aus dem Unterdevon. Neues Jahrb. f. Mineral., Geol., u. Palaeont., Jahrg. 1891, vol. 2, pp. 104–105.
- Sandberger, G., and F. Sandberger  
1850–1856. Die Versteinerungen des rheinischen Schichten-Systems in Nassau. [Wiesbaden.] 564 pp., 39 pls.
- Sanders, H. L.  
1956. Oceanography of Long Island Sound, 1952–1954. X. The biology of marine bottom communities. Yale Univ. Bingham Oceanogr. Coll. Bull., vol. 15, pp. 345–413.  
1958. Benthic studies in Buzzards Bay. I. Animal-sediment relationships. Limnol. and Oceanogr., vol. 3, no. 3, pp. 245–258.
- Saul, J. M., A. J. Boucot, and R. M. Finks  
1963. Fauna of the Accraian Series (Devonian of Ghana) including a revision of the gastropod *Plectonotus*. Jour. Paleont., vol. 37, no. 5, pp. 1042–1053, pls. 135–138.
- Saul, L. R.  
1976. Reinterpretation of the hinge structures of two Devonian Bivalvia: *Congeriomorpha* and *Tusayana*. Jour. Paleont., vol. 50, no. 1, pp. 153–157, 4 figs.
- Savage, T. E.  
1930. The Devonian rocks of Kentucky. Kentucky Geol. Surv. Ser. 6, vol. 33, 161 pp., 52 figs.  
1931. Devonian fauna of Kentucky, in Jillson, W. R. (ed.), The paleontology of Kentucky. Kentucky Geol. Surv. Ser. 6, vol. 36, pp. 217–247, pls. 27–32.
- Schenck, H. G.  
1934. Classification of nuculid pelecypods. Mus. Roy. d'Hist. Nat. Belgique, Bull., vol. 10, no. 28, 78 pp., 5 pls.  
1939. Revised nomenclature for some nuculid pelecypods. Jour. Paleont., vol. 13, pp. 21–41, pls. 5–8.
- Shimer, H. W., and A. W. Grabau  
1902. The Hamilton Group of Thedford, Ontario. Bull. Geol. Soc. America, vol. 13, pp. 149–186.
- Shimer, H. W., and R. R. Shrock  
1944. Index fossils of North America. Cambridge, Mass., M.I.T. Press, 837 pp., 303 pls.
- Siebenthal, C. E.  
1900. Silver Creek Hydraulic Limestone of southeastern Indiana. Indiana Dept. Geol. and Nat. Hist. Res. 25th Ann. Rept. (1900), pp. 331–389.
- Simpson, G. G., A. Roe, and R. C. Lewontin  
1960. Quantitative zoology. New York, Harcourt, Brace, and World, 440 pp.
- Slocum, A. W.  
1906. A list of Devonian fossils collected in western New York with notes on their stratigraphic distribution. Publ. Field Columbian Mus., Geol. Ser., vol. 22, pp. 257–265.
- Solle, G.  
1936. Revision der Fauna des Koblenzquarzits an Rhein und Mosel. Senckenbergiana, vol. 18, pp. 154–215, 16 figs.
- Southworth, C.  
1967. A guide to the fossil bearing areas of Arkona, Thedford and vicinity. Petrolia, Ontario, Lambton County Hist. Soc., Petrolia Advertiser-Topic, 21 pp., 4 pls., map.
- Sowerby, J.  
1812–1846. The mineral conchology of Great Britain; or coloured figures and descriptions of those remains of testaceous animals or shells, which have been preserved at various times and depths in the earth. London, B. Meredith, 7 vols.
- Sparck, R.  
1937. The benthonic animal communities of the coastal waters. Copenhagen and Reykjavik, Zool. Iceland, vol. 1, pt. 6, pp. 1–45.
- Spriestersbach, J.  
1915. Neue oder wenig bekannte Versteinerungen aus dem rheinischen Devon, besonders aus dem Lenneschiefer. Kgl. Preuss. Geol. Landesanst., Abhandl., new ser., vol. 80, 80 pp., 23 pls.  
1919. Die Stellung von *Montanaria* Spriestersbach und *Crassatellopsis* Beushausen. Jahrb. Preuss. Geol. Landesanst. (1918), vol. 39, no. 1, pp. 32–40, 3 pls.  
1925. Die Oberkoblenzschichten des Bergischen Landes und Sauerlandes. Jahrb. Preuss. Geol. Landesanst. Berlin, (1924), vol. 45, pp. 367–450, pls. 10–17.
- Spriestersbach, J., and A. Fuchs  
1909. Die Fauna der Remscheider Schichten. Kgl. Preuss. Geol. Landesanst., Abhandl., new ser., vol. 58, 81 pp., 11 pls.
- Stanley, S. M.  
1970. Relation of shell form to life habits of the Bivalvia (Mollusca). Geol. Soc. America Mem. 125, 296 pp., 40 pls., 48 figs.  
1972. Functional morphology and evolution of byssally attached bivalve mollusks. Jour. Paleont., vol. 46, no. 2, pp. 165–212, 34 figs.



- Stasek, C. R.  
1963. Orientation and form in the bivalved Mollusca. *Jour. Morphol.*, vol. 112, no. 3, pp. 195-214, 12 figs.
- Stauffer, C. R.  
1909. The Middle Devonian of Ohio. *Geol. Surv. Ohio*, 4th ser., Bull. 10, 204 pp., illus.  
1915. The Devonian of southwestern Ontario. *Canadian Dept. Mines Geol. Surv. Mem.* 34, 341 pp., illus.  
1916. The relationships of the Olentangy Shale and associated deposits of northern Ohio. *Jour. Geol.*, vol. 24, no. 5, pp. 476-487, 6 figs.
- Steininger, J.  
1853. *Geognostische Beschreibung der Eifel*. [Trier]. 114 pp., 10 pls.
- Stempell, W.  
1898. Beiträge zur Kenntniss der Nuculiden. *Zool. Jahrb., Jena, Suppl.*, vol. 4 (Fauna Chilensis), pp. 339-430, pls. 22-25.
- Stewart, G. A.  
1927. Fauna of the Silica Shale of Lucas County. *Ohio Geol. Surv. Bull.*, ser. 4, no. 32, 76 pp., 5 pls.  
1933. A new pelecypod from the Silica Shale, Devonian of Ohio. *Jour. Paleont.*, vol. 7, no. 2, pp. 178-180, pl. 24, figs. 15-17.
- Stoyanow, A.  
1948. Molluscan faunule from the Devonian Island Mesa beds, Arizona. *Jour. Paleont.*, vol. 22, no. 6, pp. 783-791, pls. 120-121.
- Stumm, E. C.  
1942. Fauna and stratigraphic relations of the Prout Limestone and Plum Brook Shale of northern Ohio. *Jour. Paleont.*, vol. 16, no. 5, pp. 549-563, 5 pls.
- Stumm, E. C., and R. B. Chilman  
1967. Check list of fossil invertebrates described from the Middle Devonian Silica Formation of northwestern Ohio and southeastern Michigan. *Contrib. Mus. Paleont. Univ. Michigan*, vol. 21, no. 7, pp. 123-137.
- Stumm, E. C., and J. D. Wright  
1958. Check list of the fossil invertebrates described from the Middle Devonian rocks of the Thedford-Arkona region of southwestern Ontario. *Contrib. Mus. Paleont. Univ. Michigan*, vol. 14, no. 7, pp. 81-132.
- Stoliczka, F.  
1871. Cretaceous fauna of southern India, vol. 3, the Pelecypoda, with a review of all known genera of this class, fossil and Recent. *Geol. Surv. India, Palaeontographica Indica*, ser. 6, vol. 3, 537 pp., 50 pls.
- Stucker, G. F., M. J. Galusha, and M. C. McKenna  
1965. Removing matrix from fossils by miniature sandblasting, *in* Kummel, B. and D. Raup (eds.), *Handbook of paleontological techniques*. San Francisco and London, W. H. Freeman & Co., pp. 273-275.
- Sutton, D. G., and A. H. Sutton  
1937. Middle Devonian of southern Indiana. *Jour. Geol.*, vol. 45, pp. 320-331, 1 fig.
- Sutton, J.  
1968. Development of the continental framework of the Atlantic. *Proc. Geologists' Assoc.*, vol. 79, pt. 3, no. 1, pp. 275-304, 7 figs.
- Sutton, R. G., Z. P. Bowen, and A. L. McAlester  
1970. Marine shelf environments of the Upper Devonian Sonyea Group of New York. *Geol. Soc. America Bull.*, vol. 81, no. 10, pp. 2975-2992, 11 figs.
- Summerson, C. H., and D. H. Swann  
1970. Patterns of Devonian sand on the North American craton and their interpretation. *Geol. Soc. America Bull.* 81, no. 2, pp. 469-490, 5 figs.
- Taylor, J. D., W. J. Kennedy, and A. Hall  
1973. The shell structure and mineralogy of the Bivalvia. II. Lucinacea-Clavagellacea, conclusions. *Bull. British Mus. (Nat. Hist.) Zool.*, vol. 22, no. 9, 294 pp., 15 pls.
- Tebble, N.  
1966. British bivalve seashells. A handbook for identification. *Trustees British Mus. (Nat. Hist.)*, 212 pp., 110 figs.
- Teichert, C.  
1948. A simple device for coating fossils with ammonium chloride. *Jour. Paleont.*, vol. 22, pp. 102-104, 1 fig.
- Thayer, C. W.  
1974. Marine paleoecology of the Upper Devonian of New York. *Lethaia*, vol. 7, no. 2, pp. 121-156, 24 figs.
- Trueman, E. R.  
1964. Adaptive morphology in paleoecological interpretation, *in* Imbrie, J., and N. D. Newell (eds.), *Approaches to paleoecology*. New York, John Wiley & Sons, pp. 45-74, 10 figs.
- Trueman, E. R., A. R. Brand, and P. Davis  
1966. The effect of substrata and shell shape on the burrowing of some common bivalves. *Malacol. Soc. London, Proc.*, vol. 37, pp. 97-109, 8 figs.
- Ulrich, E. O.

1894. The Lower Silurian Lamellibranchiata of Minnesota, in Vol. 3, Final Rept., Minnesota Geol. and Nat. Hist. Surv., pp. 475-628, pls. 35-42 [pub. under separate cover before entire vol. 3].
1897. The Lower Silurian Lamellibranchiata of Minnesota. Minnesota Geol. and Nat. Hist. Surv., Final Rept., vol. 3, pt. 2, Paleont., pp. 475-628, pls. 35-42 [reprint of Ulrich, 1894].
- Valentine, J. W.  
1973. Evolutionary paleoecology of the marine biosphere. New Jersey, Prentice-Hall, 511 pp., illus.
- Vanuxem, L.  
1842. Geology of New York, pt. III. Comprising the survey of the third geological district. Albany, Nat. Hist. New York, 306 pp., 80 figs.
- Verneuil, E. de  
1847. Note sur le parallélisme des roches de dépôts paléozoïques de l'Amérique Septentrionale avec ceux de l'Europe, suivie d'un tableau des espèces fossiles communes aux deux continents, avec l'indication des étages où elles se rencontrent, et terminée par un examen critique de chacune de ces espèces. Soc. Géol. France, Bull., ser. 2, vol. 4, pp. 646-710.
- Vištor, W.  
1919. Der Koblenzquarzit, seine Fauna, Stellung und linksrheinische Verbreitung. Jahrb. Kgl. Preuss. Geol. Landesanst., vol. 37, pt. 2, no. 3 (1916), pp. 317-476, pls. 16-18.
- Vokes, H. E.  
1949. The hinge and marginal pectenations of *Nuculoidea opima* (Hall), type of *Nuculoidea* Williams and Breger. Washington Acad. Sci., Jour., vol. 39, no. 11, pp. 361-363, fig. 1.  
1957. Miocene fossils of Maryland. Maryland Dept. Geol., Mines and Water Res. Bull. 20, 85 pp., illus.  
1967. Genera of the Bivalvia: a systematic and bibliographic catalogue. Bull. American Paleont., no. 232, pp. 112-394.
- Walcott, C. D.  
1884. Paleontology of the Eureka district (Nevada). U.S. Geol. Surv. Mon. 8, 298 pp., 24 pls.
- Whiteaves, J. F.  
1884. Palaeozoic fossils, vol. III, pt. 1. Geol. and Nat. Hist. Surv. of Canada. Montreal, Dawson Bros., 242 pp., 21 pls.  
1889. On some fossils from the Hamilton formation of Ontario with a list of species at present known from that formation and province. Contrib. Canadian Paleont., vol. 1, pt. 2, pp. 91-125, pls. 12-16.
1891. The fossils of the Devonian rocks of the Mackenzie River Basin. *Ibid.*, vol. 1, pt. 3, no. 5, pp. 197-253, pls. 27-32.
1892. The fossils of the Devonian rocks of the islands, shores or immediate vicinity of Lakes Manitoba and Winnipegosis. *Ibid.*, vol. 1, pt. 4, no. 6, pp. 255-359, pls. 33-47.
1898. On some additional or imperfectly understood fossils from the Hamilton formation of Ontario with a revised list of the species therefrom. *Ibid.*, vol. 1, pt. 5, no. 7, pp. 361-418, pls. 48-50.
- Whitfield, R. P.  
1882. Pt. 3, Paleontology, in Geology of Wisconsin, survey of 1873-1879. Geol. Wisc., vol. 4, pp. 163-366, 27 pls.  
1883. List of Wisconsin fossils, in Geology of Wisconsin, survey of 1873-1879, pt. II, chap. 4, pp. 362-375.  
1890. Contributions to invertebrate paleontology: species from the limestones above the "bone bed", in the vicinity of Columbus, Ohio, and not known to occur below that horizon. Ann. New York Acad. Sci., vol. 5, pp. 505-622.
- Whitfield, R. P., and E. O. Hovey  
1898-1901. Catalogue of the types and figured specimens in the paleontological collection of the geological department, American Museum of Natural History. Bull. Amer. Mus. Nat. Hist., vol. 11, 500 pp.
- Willard, B.  
1939. The Devonian of Pennsylvania. Pennsylvania Geol. Surv., 4th ser., Bull. G19, 481 pp., 32 pls.
- Williams, H. S.  
1886. Devonian Lamellibranchiata and species making. American Jour. Sci., 3rd ser., vol. 32, pp. 192-198.  
1908. On the revision of the mollusk genus *Pterinea* Goldfuss. Proc. U.S. Natl. Mus., vol. 34, pp. 83-90.  
1917. *Nuculites* from the Silurian formations of Washington County, Maine. Proc. U.S. Natl. Mus., vol. 54, pp. 27-58, pls. 11-12.
- Williams, H. S., and C. L. Breger  
1916. The fauna of the Chapman Sandstone of Maine, including descriptions of some related species from the Moose River

- Sandstone. U.S. Geol. Surv. Prof. Paper 89, 347 pp., 27 pls.
- Wilmarth, M. G.  
1938. Lexicon of geologic names of the United States. U.S. Geol. Surv. Bull. 896, 2 vols., 2396 pp.
- Wilson, S.  
1975. Pelecypods of the Silica, in Kesling, R. V., and R. B. Chilman, Strata and megafossils of the Middle Devonian Silica Formation. Univ. of Michigan (Ann Arbor), Mus. of Paleont. Papers on Paleont., no. 8, pp. 124–150, with several scattered plates.
- Wolf, M.  
1930. Alter und Entstehung des Wald-Erbacher Roteisensteins (Grube Braut im Hunsrück) mit einer stratigraphischen Untersuchung der Umgebung. Abhandl. Preuss. Geol. Landesanst., new ser., 123, 105 pp., 4 pls.
- Woodrow, D., and F. Fletcher  
1968. Late Devonian palaeogeography in southeastern New York and northeastern Pennsylvania. Internatl. Symp. Devonian System, Calgary, 1967, vol. 2, pp. 1327–1334, 7 figs., Alberta Soc. Petrol. Geol.
- Yang, Tsun-Yi  
1939. The molluscs of the Traverse Group (Middle Devonian) of Michigan. 185 pp., illus. (Unpubl. Ph.D. dissertation, Yale Univ.)
- Yonge, C. M.  
1939. The protobranchiate Mollusca; a functional interpretation of their structure and evolution. Philos. Trans., Roy. Soc. London, vol. 230, ser. B., no. 566, pp. 79–147, pl. 15, 39 figs.  
1953. The monomyarian condition in the Lamellibranchia. Trans., Roy. Soc. Edinburgh, vol. 62, pt. 2, pp. 443–478, 13 figs.
- Zenger, D. H.  
1965. Occurrence of the pelecypod *Paracyclas* in the Upper Devonian of New York State. Jour. Paleont., vol. 39, no. 1, pp. 153–155, 1 fig.











