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BIVALVIA (PELECYPODA) OF THE BRASSFIELD FORMATION (LOWER SILURIAN) OF KENTUCKY, INDIANA AND OHIO.

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Bivalvia (Pelecypoda) of the Brassfield Formation (Lower Silurian) of Kentucky, Indiana and Ohio

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by

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I hereby recommend that the thesis prepared under my supervision by William B. Harrison, III

entitled Bivalvia (Pelecypoda) of the Brassfield Formation (Lower Silurian) of Kentucky, Indiana and Ohio

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

Approved by:

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ABSTRACT

A restudy of pelecypods of the Brassfield Formation (Lower Silurian) in the Ohio, Indiana and Kentucky area indicates that the basic paleobiogeographic distribution of the pelecypods is restricted to the Ohio outcrops of the formation. The occurrence of this class is further segregated into two faunal associations, one of dominantly epifaunal forms ("Actinopteria brisa assemblage"), the other of infaunal types ("Palaeoneilo fecunda assemblage"). Compared with the abundant and diverse bivalve faunas of the Upper Ordovician, those of the Brassfield are meager; however, local concentrations do occur.

Most of the nomenclature of the fourteen species (representing 13 genera) was revised to reflect current taxonomic concepts. Several of the species were previously unknown from the Brassfield and from rocks younger than Upper Ordovician. These are Deceptrix scofieldi (Ulrich), Nuculites neglectus Hall, Palaeoneilo fecunda (Hall), Praenucula albertina (Ulrich), Lyrodesma sp., and new genus "A" foerstei n. sp. This also represents the first documented occurrence of Lyrodesma in the Silurian. Assignment of Palaeoconcha ohioensis (Clarke and Ruedemann) and Praenucula albertina (Hall) to those genera have extended their generic ranges into the Lower Silurian. Placement of Nucula (Tellinomya) fecunda (Hall, 1862) in Palaeoneilo has created a nomenclatural conflict of

homonomy with *Palaeoneilo fecunda* (Hall, 1870). The name *Palaeoneilo halli* is porposed for *P. fecunda* (Hall, 1870).

Several species of nuculoids are virtually identical to those found in the "Depauperate Zone" of the Maquoketa Formation (Upper Ordovician) of Iowa, Illinois, Wisconsin and Missouri. These, along with the other mollusks, imply a stratigraphically recurrent "Depauperate Zone" community in some horizons of the Brassfield, i.e., a less than salubrious environment for bivalves.

INTRODUCTION

This investigation was designed to deal with the taxonomy, comparative morphology, phylogeny and paleoecology of Early Silurian (Brassfield) bivalves in the Tri-state Area of Ohio, Indiana and Kentucky. The apparent paucity of Early Silurian bivalves, as reported by previous investigators (e.g., Foerste, 1895) and here substantiated, strongly suggests an environmental deficiency (i.e. bivalve hardship) during the Early Silurian in this area, in contrast to the relatively rich bivalve fauna of the Ordovician. Bivalves were still locally abundant in the Early Silurian Brassfield Formation, although their populations were greatly reduced regionally. Unhappily, no pelecypods were found in any Brassfield units outside Ohio (Text-fig. 1). However, in several areas of Ohio (Adams,

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Text-fig. 1--Locality Map of Brassfield sample sites.

Clinton, Green, Montgomery and Clark counties), numerous bivalves were found in several Brassfield horizons (Text-fig. 2). Some of these "populations" (members of the

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Text-fig. 2--Distribution of Bivalve faunal assemblages in the Brassfield Formation of Ohio

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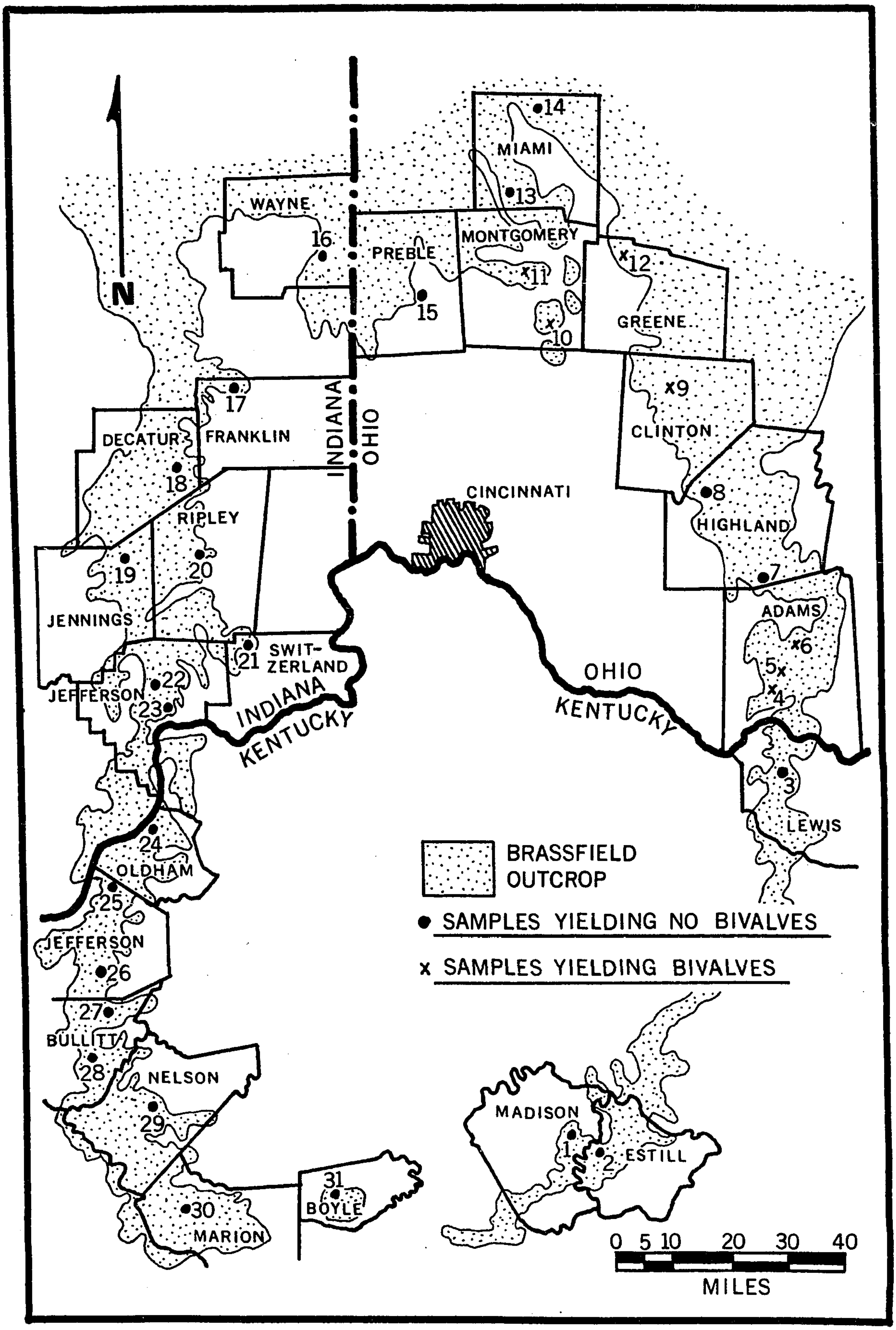
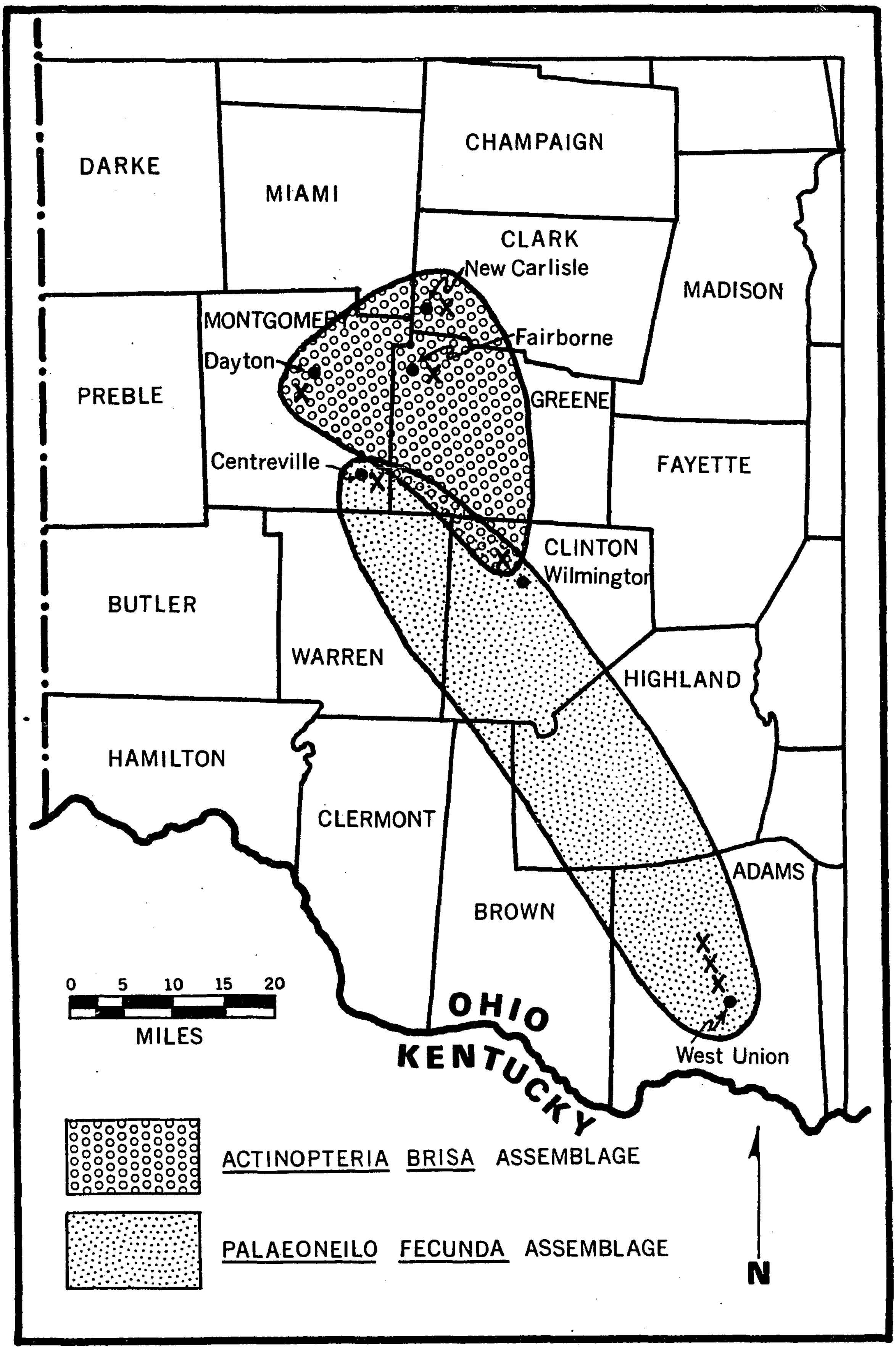
"Paleoneilo fecunda assemblage") appear to have survived, relatively unchanged from Ordovician ancestors; while others (members of the Actinopteria brisa assemblage") are



Text-fig. 1--Locality map of Brassfield sample sites.



Text-fig. 2--Distribution of bivalve faunal assemblages in the Brassfield Formation of Ohio.

distinctly different in taxonomic composition, being much more like Middle and Upper Silurian and Lower Devonian assemblages.

The Brassfield fauna is, as might be expected, intermediate between Ordovician and Silurian bivalve communities. The Ordovician-like assemblage consists of infaunal species, while the Silurian- and Devonian-like species are epifaunal. The conservativeness of infaunal organisms may, in part, explain this dichotomy.

Of the many lineages that were so diverse and abundant in the Ordovician, only the nuculoids maintained that abundance in the Brassfield. Ambonychiids, pterineids, modiomorphids and cyrtodontids are represented by only a few specimens of one or two species each. This represents a significant reduction in the fauna compared to that of the Late Ordovician (see Pojeta, 1971, p. 27). This distribution may, however, partially reflect environmental conditions selectively conducive to nuculoid development. Nuculoids (along with Lyrodesma) comprise the vast majority of bivalves in the Silurian "Lingula community" of Ziegler, et al.(1968), and appear to be an equally dominant bivalve element in some other nearshore environments (Bretsky, 1968).

August F. Foerste is virtually the sole contributor of fundamental information about the paleontology, lithology and stratigraphy of the Brassfield Formation (Foerste 1885, 1888, 1895, 1896, 1901, 1906, 1909, 1919, 1923, 1931 and

1935). His work remained the only authoritative studies of this unit until the 1960's.

More recently, a detailed study of Brassfield lithostratigraphy has been carried out (O'Donnell, 1967). Rexroad (1967) reported on conodont paleontology and biostratigraphy in Indiana and Kentucky outcrops; his work indicated a Late Early Llandoverian age for this part of the Brassfield. Gray and Boucot(1972) described the distribution of palinomorphs throughout the Brassfield in southern Ohio and showed very similar flora in the uppermost Preacherville (Upper Ordovician) Formation and lowermost Brassfield (Belfast member, Lower Silurian) Formation, seemingly indicating a paraconformity at the Ordovician-Silurian boundary. There is, however, a lithologic difference between the two formations: the Preacherville Formation contains more fine-grained (clay) particles than the siltier Brassfield.

Foerste's paleontologic work was perceptive, but it reflected the taxonomic opinions of that time. New thoughts on classification have since been generated (e.g., Cox, 1960 and Newell, 1965), and knowledge of the comparative morphologies of fossil and Recent groups has vastly increased. His bivalve systematics are therefore re-evaluated in light of current knowledge and concepts, and all his type material is reillustrated. Some type material of other authors is also refigured here.

Considerable new information has been obtained about the morphology of some species (particularly nuculoids) collected from acid residues. New details of ligament, dentition and musculature are described. The large bivalve collection thus obtained includes specimes of varying size and morphology so that the ontogeny of several species can be delineated for the first time, and some insight into populations gained.

Sufficient material was obtained in this study for ontogenic analyses of two species of nuculoids (Deceptrix scofieldi [Ulrich] and Palaeoneilo fecunda [Hall]), a lyrodesmatid (Lyrodesma sp.) and a pterineid (Actinopteria brisa [Hall]). The nuculoids were collected from several horizons of ferruginous limestone 35 to 37 feet (11m) above the base of the Brassfield at several sections along State Road 41, 2.5 miles north of West Union, Adams County, Ohio. From these layers, about 30 samples were processed in dilute acetic acid. The residues contained Steinkerns and permineralized shells of mollusks and other invertebrates. The greatest number of individuals (982) and species (7) were recovered from a 6.5-pound block of limestone, sample WU-14. Individuals of this sample are representative of all the shells collected for this study (in these sections); and, since this sample has the most individuals it is used herein for details of ontogeny. The numerical data (tables and graphs) are based on specimens from this sample, while the general conclusions, discussion and plate illustrations are made on the aggregate fauna. There were 437 left and 465 right, disarticulated valves and 80 articulated shells distributed among four nuculoid and one Lyrodesma species from this sample (WU-14).

The bivalve species of the Brassfield may be separated into two distinct faunal groups as mentioned above. The fauna of the "Palaeoneilo fecunda assemblage: is very similar in species content and size distribution to assemblages described by Snyder and Bretsky (1971) from the Ordovician basal Maquoketa Formation in the Midwest. This suggests a stratigraphically recurrent community Raup and Stanley, 1971, p. 229). This phenomenon really represents similar facies in the basal Maquoketa and this part of the Brassfield and the time transgressive migration of that facies from the basal Maquoketa outcrop region (Iowa, Illinois and Missouri) in the Late Ordovician to part of the Brassfield outcrop region (in southern Ohio) in the Early Silurian. Numerous other examples of this phenomenon are known [e.g., Williams (1941) and Caster (1934) dealing with brachiopods and associated fauna, Caster (1938) dealing with limuloid crustaceans, and Kohut (1969) dealing with conodonts are but a few studies relating facies to the distribution of species assemblages].

Although not studied in detail in this investigation, the gastropod, "scaphopod," brachiopod and hyolithid faunas in this zone of the Brassfield are also very similar to the basal Maquoketa as listed in Bretsky and Bermingham (1970) and Ojakangas (1959). The entire molluscan community and some associated species appear to be influenced by this facies phenomenon.

The faunal size frequency and valve sorting in the bivalves were examined to determine whether the fauna (of the "P. fecunda assemblage") had been significantly transported and sorted. Primary sedimentary structures including ripples and cross-laminae in some Brassfield layers indicate some current activity during sediment deposition. The ratio of right to left valves, as well as degree of breakage, however, imply that although some post-mortem transport of the bivalves did occur, it was probably of short duration and low energy level, perhaps only reworking the shells out of their living position (infaunal) into the mobile sediment composing these thin-bedded rippled layers.

An extensive study of the coralline fauna of the Brassfield Formation is currently being conducted by Richard Laub (Ph.D. thesis in preparation at the University of Cincinnati). At the inception of his study there was hope of correlation between the two faunas regarding paleoecology, paleogeography and comparison of the Brassfield organisms with other Ordovician and Silurian taxa. Unfortunately, the occurrences of corals and bivalves in the Brassfield are nearly mutually exclusive. A single species of rugose coral (Zaphrentis sp.) infrequently occurs with the bivalves in both the P. fecunda and A. brisa assemblages. Apparently, those environments proving viable for bivalves was quite inhospitable to most corals.

Specimens borrowed from museums carry the following prefixed abbreviations in this work:

National Museum of Natural History	USNM
American Museum of Natural History	AMNH
University of Cincinnati Geology Museum	UCGM
New York State Museum	NYSM
Ohio State University Museum	OSU
Walker Museum Collection (Field Museum of Natural History)	WM

Specimens collected in this study were given UCGM numbers and deposited in the University of Cincinnati Geology Museum.

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To my wife Linda I extend thanks for typing the manuscript and studying the gastropod, "scaphopod" and hyolithid fauna of the "Palaeoneilo fecunda assemblage" and comparing them with those of the basal Maquoketa Formation.

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SHELL MORPHOLOGY

EXTERNAL FEATURES

Orientation

By convention, bivalve shells are referred to as right and left valves with the zone of articulation by dentition and ligament being dorsal and the opposite margin, ventral. Along the dorsal margin, the internal surface of articulation is the hinge plate (or dental plate). Each valve is lateral to the enclosed viscera. This procedure for orientation is from a biological frame of reference, generally reflecting the distribution of "soft part" anatomy (for example, anterior is determined, among other things, by the position of the mouth), direction of locomotion (most animals move in an anterior direction) and orientation in life (the dorsum is usually the superior direction in life position).

The use of these precise biologic criteria in orientation is restricted to exceedingly few fossil specimens because soft parts (except by reflection in the shell) and life position are seldom certainly demonstrable. Only the use of some evidence of soft parts, such as the placement of muscle scars, can be consistently employed by paleontologists. (The relationship of muscle scars and other internal structures are discussed below under the subheading "Internal Features.")

In many fossil species orientation homologies or analogies may be made with present day forms. Taxa without extant homologues or analogues are often oriented by convention (*e.g.*, Cox, 1969, p. 79). Analysis of shell morphology and anatomy of modern nuculoids (such as by Heath, 1937) and subsequent comparison of these features with fossil forms should yield an interpretation of biologic orientation with considerable confidence. Such an analysis was employed by Driscoll (1964) using accessory muscle scars and is discussed below. Species of the Pterineidae or Cyrtodontidae, for example, have no close living relatives, but may be oriented by comparison with analogous modern forms with similar shape and structure (*e.g.*, Pojeta, 1971, p. 33). Still other extinct taxa (such as the Grammyssiidae) may have few analogous modern forms and are oriented primarily by convention.

Shell Regions

The morphologic features of the Bivalve conch as used in the systematic section of this work are defined and discussed below. Some of the various regions of the shell are also discussed in the section on external features (the beak and umbo, particularly). The term conch or "shell" refers to both valves in an articulated state, essentially as they were when the animal was alive. A valve is half of the shell and is described as either a right or left element. The main part of the shell that presumably encased the greater part of the viscera is called the body. The topography across the surface of the body is usually uniformly curved, although some forms have structures such as umbonal ridges or sulci that produce a local change in the surface topography (as discussed below). A change in shell topography near the anterior or posterior margin marks the boundary of the shell body with an auricle, wing or ear (see discussion following). In some taxa, such as Deceptrix scofieldi (Pl. 1, fig. 1, 2) and Palaeoneilo fecunda (Pl. 4, fig. 1), the body of the shell is virtually the same as the entire volume of the shell. Some forms, however, have regions of the shell that are distinguishable from the shell body due to a difference in shell topography or external surface ornamentation. These distinguishable regions of the shell occur adjacent to the dorsal margin and have had several names applied to them, such as "wing," "ear," "auricle," "alation" or "flange." As Pojeta (1966, p. 138) commented, there has been considerable confusion as to the precise meaning of these terms. He suggested (p. 139) that the use of "alation" or "wing" be restricted to forms that show a projection of the dorsal margin beyond the vertically projected margin of the body. A "wing" is conventionally found posteriorly, while an "ear" or "auricle" would be anterior to the beak. These structures of the shell would be useful for determining orientation in some taxa. "Auricle" has also been used as a general term for any type of anterior or posterior extension or differentiation of the shell in the dorsal region (Cox, 1969, p. 46). "Wings" are usually larger than "ears" and have a triangular or subtriangular outline, while an "ear" is usually lobate or rounded. The term "flange" is often used is describing the dorsal expansions in bivalves (especially unionids) where there is commonly little change in topography and ornament from the shell body (Pl. 9, fig. 13).

In this study, wing, ear, auricle, and flange will be employed. Wing will be used as suggested by Pojeta (1966, p. 139), for a dorsal extension of the shell beyond the general body margin posterior to the beak with the dorsal and posterior margins of this structure usually meeting at an acute angle. A similar structure found anterior to the beak will be called an ear (often with a rounded anterior margin). A wing and ear are both present in Actinopteria brisa (Pl. 8, fig. 4). The more general term auricle is applied to both anterior or posterior dorsal shell extensions.

Shell Shape

The use of shell shape in the description of morphology in pelecypod studies is common. Shell shape should be taken herein to include basic dimensions of the valves, convexity of the valves, any inflation or sinus development, occurrence of auricles ("ear" or "wing"), anterior or posterior elongation or truncation and general valve outline.

Convexity is used when describing the total curvature of the shell surface from beak to ventral margin. Convexity of opposing valves may be similar; in that case, the shell is termed equivalved. If the valves are of different convexities, the shell is termed inequivalved. Many pterineids are inequivalved with an almost flat right valve and a convex left valve. Convexity is rarely used as a taxobasis in the forms found in the Brassfield, and then onlyat the species level. *Palaeoconcha faberi* Miller (Pl. 2, fig. 4) and *P. ohioensis* (Bassler (Pl. 2, fig. 9) may be separated in part by convexity of the shell. Both valves of *P. faberi* are much less convex than the valves of *P. ohioensis*.

Inflation refers to a disproportionate enlargement of a certain region of the shell. The enlargement is, in essence, a local increase in the volume contained inside the shell. Inflation appears to occur most commonly in the region of the umbone and beak and may be used as a taxobasis for separating species. *Cuneamya caswelli* (Foerste) (Pl. 10, fig. 11), for example, shows inflated umbonal regions relative to other species of *Cuneamya*. Inflation of the valve along a line from the beak to the postero-ventral margin, such as seen in Mytilarca foerstei Clark and Ruedemann is called an umbonal ridge (Pl. 7, fig. 5).

Elongation or truncation of anterior or posterior regions of the shell is also considered an aspect of shell shape. Elongation refers to the extension of the shell body anteriorly or posteriorly relative to the beak. This is achieved by allometric growth of the shell on one side of the beak. "Cypricardinia" undulostriata (Hall) (Pl. 10, fig. 8) and Nuculites neglectus (Hall) (Pl. 3, fig. 10) among others, show a posterior elongation of the shell, while Deceptrix scofieldi (Ulrich) (Pl. 1, fig. 1) is anteriorly elongate. Truncation, conversely, is the relative shortening of one end of the shell. A shell may be truncate at one end and elongate at the other, but the truncate margin is generally considered to be a line oblique to the dorsal margin, rather than simply a short, rounded portion of a shell on one side of the beak. (The anterior end of Palaeoneilo fecunda (Hall) (Pl. 4, fig. 1, 10) would not be considered truncated.) All species of Palaeoconcha (Pl. 2, fig. 3,5, 6) are posteriorly truncate, but there is no striking anterior elongation. Deceptrix scofieldi (Ulrich) (Pl. 1, fig. 1) is anteriorly elongate and posteriorly truncate. A valve that exhibits elongation or truncation is referred to as inequilateral because the beak is offset from the midpoint of the shell, while a valve symmetrical antero-posteriorly about the beak is described as equilateral.

Valve proportions are a more quantitative way of expressing some aspects of the shell shape. These proportions are ratios of measurements of valve (or shell) parameters. Valve length to height is a proportion commonly used in this study. Valve length, as used herein, is the maximum shell dimension parallel to the hinge in an anterior-posterior direction. Height is the maximum shell dimension perpendicular to the length. Other ratios used herein include anterior length to posterior length, valve height to shell thickness, anterior length to total length, anterior height to posterior height.

Valve outline, although part of the shape of the shell, is described separately because considerable taxonomic emphasis is often placed on this feature. The valve outline is essentially a plan view of the valve. Descriptive nomenclature of valve outlines may be derived from generic names. Adjectives such as pteriaform, modioliform or grammysioid imply that the valve being described has an outline similar to that of a particular genus (*Pteria*, *Modiolus* or *Grammysia*, respectively).

The valve outline may also be described in geometric terms, such as rectangular, oval, rhomboidal, trigonal.

Beak and Umbo

The beak is often used as a reference point on pelecypod valves. It is a rounded, curved or hooked projection somewhere along the dorsal margin of the valve. A pelecypod grows by differential holoperipheral growth around a very tiny (larval) shell (prodissoconch) which is coextensive with the beak. The beak, strictly speaking, is the tip of the valve and is the oldest part of the valve. A distinct, somewhat inflated region adjacent to the beak is called the umbo. The term beak or beak region is sometimes erroneously applied to that part of the valve which is correctly called the umbo. The size and shape of the umbo and the direction of curvature of beak and slant of the umbo (and sometimes the shell body) are of taxonomic importance at the familial or generic level. The beak and umbo may be rather large and prominent relative to the rest of the valve, as in Cuneamya caswelli (Foerste) (Pl. 10, fig. 10) and Deceptrix scofieldi (Ulrich) (Pl. 1, fig. 1). In other forms, such as Actinopteria brisa (Hall) (Pl. 8, fig. 4) the beak and umbo are relatively small, compared with the rest of the valve. "Mytilarca" foerstei Clark and Ruedemann (Pl. 7, fig. 5) has a relatively pointed beak, while other species, such as Palaeoneilo fecunda (Hall) (Pl. 5, fig. 7, 9) have a blunt beak and umbo region.

A beak curving anteriorly is described as prosogyrous, whereas one curving toward the posterior of the valve is termed opisthogyrous. A beak that does not curve in either direction is referred to as erect or orthogyrous. The slant or inclination of the umbonal region (and often the dorsal part of the shell body) has similar nomenclature, but with a change of suffixes. An anterior inclination is called prosocline, one posterior is opisthocline, and no slanting in either direction is termed orthcline. For example, Palaeoconcha obliqua (Hall) is prosogyrous (Pl. 2, fig. 8) and orthocline (Pl. 2, fig. 7), and Actinopteria brisa Hall is prosogyrous and prosocline (with the whole body slanted anteriorly) (Pl. 7, fig. 12).

The position of the beak is in reference to its distance from one end of the valve; however, if the beak is at the end of the valve it is called terminal. "Mytilarca" foerstei Clark and Ruedemann (Pl. 7, fig. 5) has an anteriorly terminal beak.

Prosopon

"Prosopon" is a term proposed by Gill (1949, p. 572) to replace the term "ornament." Variations in relief on the external shell surface, such as growth varices or radial ridges have been called "ornament." Gill considered the word "ornament" as referring to "nonfunctional, decorative" features. Textural features on the surface of bivalves are generally considered to have a biologic function, albeit the function of some structures may be unknown. Although Gill's criticism of the term "ornament" has considerable merit, the use of "prosopon" as a general category of surface features on organism tests has never gained wide usage. Among the writings of bivalve specialists a number of terms are used in reference to the external surface features of the pelecypod shell. "Surface sculpture" or simply "sculpture" and "ornament" are the most common words, which Gill suggests should be referred to as "prosopon." Prosopon is used herein with reference to these surface markings such as costae, costellae, plicae, growth varices or rugae on the exterior of pelecypod valves.

Whatever the general term for external surface features, the important aspect of then is the particular pattern on each shell. This pattern is distinctive and of considerable taxonomic importance at some levels.

Very fine (closely spaced), low magnitude, comarginal growth varices are found in several species of nuculoids, including Deceptrix scofieldi (Ulrich) (Pl. 1, fig. 17), Palaeoconcha ohioensis (Foerste) (Pl. 2, fig. 17) and Palaeoneilo fecunda (Hall) (Pl. 4 , fig. 1, 2). "Cypricardinia" undulostriata (Hall) (Pl. 10, fig. 2) has comarginal varices similar to each other in size,that occur in clusters between larger rugose varices. These larger varices give the appearance of imbricated lamellae (Pl. 10, fig. 8), but actually are formed by periodic abrupt cessation of shell deposition. Cyrtodonta? ferruginea (Hall and Whitfield) (Pl. 7, fig. 1) has this lamellate surface less prominently developed that "C." undulostriata.

The other type of comarginal prosopon observed among Brassfield clams is the strong corrugation of the shell. Cuneamya caswelli (Foerste) (Pl. 10, fig. 10) bears these broad comarginal ridges. These ridges or corrugations are easily distinguishable from growth varices in that the entire shell is folded in these corrugations, while varices represent only topographic relief on the external surface (no reflection is seen of them interiorly).

Early Paleozoic bivalve representativs of the Ambonychiacea, Praecardiacea and Pteriacea commonly have radial prosoponal elements. In the Brassfield Formation, Actinopteria brisa (Hall) (a pteriacean) is the only bivalve with radial ornament. "Mytilarca" foerstei Clark and Ruedemann (a Brassfield ambonychiid) has only comarginal prosopon. Radial external surface features are variously described depending on the magnitude of the radii. Ribs, riblets, costae and costellae refer to similar structures of different sizes. Although "rib" is sometimes used for any radial type of prosopon, it is herein regarded as synonymous with costa, which was arbitrarily defined by Pojeta (1966, p. 140) as being wider than 1mm. Riblets and costellae would then be defined as radial elements of prosopon with a width of 1mm or less. A. brisa (Hall) has numerous, fine (closely spaced) costellae on the body of the shell that radiate from the beak. New riblets are intercalated ventrally and often become indistinguishable from earlier formed ones. Although new radial structures may also originate by bifurcation of pre-existing ones, this phenomenon does not occur in any Brassfield specimens. Comarginal prosopon of nearly equal magnitude also occurs on A. brisa (Hall), giving the surface of the valves a cancellate pattern (Pl. 8, fig. 5, 6). In some species, the comarginal ornament may be produced into spines at the intersection with the radii (Pl. 8, fig. 11, 14).

Ligament

The site of attachment of ligamental structures in Early Paleozoic bivalves is not commonly known. For example, among Brassfield (Lower silurian) clams the precise position of the ligament (and the morphology of the attachment site) is known in only a few species (3 of 14). This dearth of knowledge is due to less than optimum preservation of most valves. However, in several species of nuculoids recovered from acid residues, an elongate groove is incised into the dorsal margin of the hinge plate posterior to the beak.

In general bivalve terminology, a ligament occurring posterior to the beak is called opisthodetic, while an anterior placement would be termed prosodetic. A ligament on both sides is termed amphidetic. Nuculites neglectus (Hall) (Pl. 3, fig. 17) and Palaeoneilo fecunda (Hall) (Pl. 9, fig. 11) have a well formed opisthodetic ligament groove. The ligament of Deceptrix scofieldi appears to be amphidetic (Pl. 1, fig. 9).

The exact placement of the ligament is unknown for other Brassfield species; however, inference as to the type and position of the ligament may be made through comparison with the known ligament occurrences of species that are apparently closely related on the basis of other morphologic aspects.

INTERNAL FEATURES

Dentition

Although species of genera supposedly containing a wide variety of dentition occur in the Brassfield, the teeth are rarely preserved, and only those specimens acid-etched from the limestones exhibit any recognizable dentition. The Brassfield fauna contains species assigned to the Arcoida (Cyrtodonta?), Pteriacea (Actinopteria), Ambonychiacea ("Mytilarca"), Modiomorphoida (Modiolopsis?), Veneroida ("Cypricardinia"), Pholadomyoida (Cuneamya), Nuculoida (5 genera) and the Trigonioida (Lyrodesma). However, the nuculoids and Lyrodesma collected from acid residues have dental elements preserved. These two groups of shells exhibit taxodont and schizodont dentition types, respectively, as the terms were used by Cox (1969, p. 51-52).

The taxodont teeth of the nuculoids occur on a hinge plate that generally occupies at least half of the dorsal length. The position of the beak marks a separation of the hinge into anterior and posterior dental series. There may be differences in number and morphology of the teeth in the two series. In Deceptrix scofieldi (Ulrich) (Pl. 1, fig. 6, 9, 15) the anterior teeth are larger and fewer than the posterior ones. There are, likewise, fewer anterior teeth in Palaeoneilo fecunda (Hall) (Pl. 5, fig. 7, 8, 9) and Nuculites neglectus (Hall) (Pl. 3, fig. 14, 17), but fewer posterior teeth in Praenucula albertina (Ulrich) (Pl. 9, fig. 1).

Number and shape of the teeth are traditionally significant taxobases. Shape seems to have been used at the species level (*e.g.* Babin, 1966 and Bradshaw, 1970), whereas number and size is employed at a higher level (particularly generic: compare discussions of *Deceptrix* and *Praenucula* herein). The shape of nuculoid teeth is either straight, undulose or chevron-shaped. The straight teeth may be either perpendicular to the venter of the hinge plate or are inclined at an angle to the hinge venter. These teeth may also be perpendicular to the antero-posterior shell axis (i.e. axis of adductor muscle scars) but be inclined to the hinge venter [*e.g.* *Praenucula* *albertina* (Ulrich)] (Pl. 2, fig. 1, see posterior teeth), and *Ctenodonta* *longa* (Ulrich), (Pl. 6, fig. 8, shown by both series). Undulose teeth meet the base of the hinge at varying angles and have several angulations in their length before reaching the dorsal hinge margin.

Although these shape terms would seem to be self-explanatory, some comments should be made as to the use of chevron or "chevron-shaped." Strictly speaking, a chevron is an inverted "V" shape, with the point of the "V" directed vertically upward (Text-fig. 3). The shape of the "chevron"

Text-fig. 3--Schematic diagram of the "chevron-shape" tooth structure in nuculoid pelecypods

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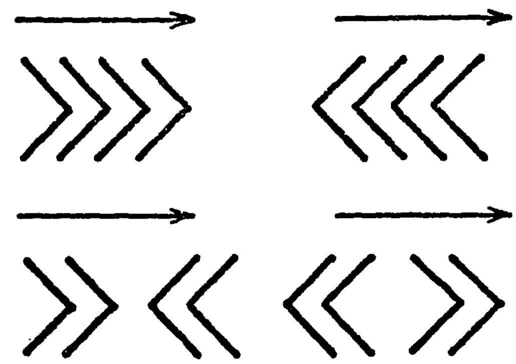
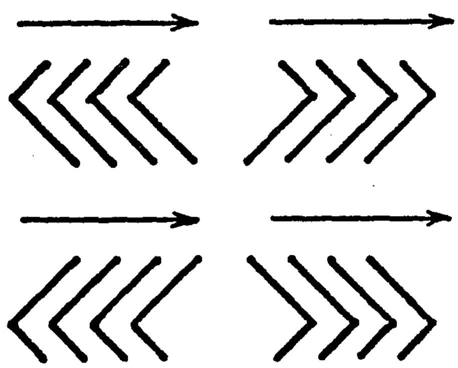
teeth in nuculoids is, however, a "V" with the axis of the

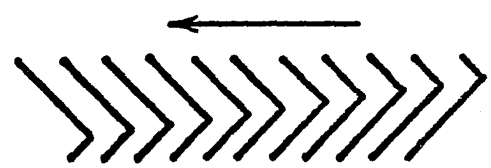
A. Shape of chevron as initially defined



B. Theoretically possible shape variation in nuculoid dentition with symmetrical chevrons. Arrow indicates posterior.



C. Possible shape variation of dentition with assymetrical chevrons. Arrow indicates posterior.



D. Chevron symmetry variation through the length of the dental series. This variation is similar to that which occurs in the posterior series of Palaeoneilo fecunda (Pl. 5 fig. 13). Arrow indicates posterior.

Text-fig. 3--Schematic diagram of the "chevron-shape" tooth structure in nuculoid pelecypods horizontal and the point directed either left or right. This shape (a chevron or a "V" rotated 90°), might more properly be termed an "angle bracket" or referred to as having the same shape as the "greater than" or "less than" symbols used in mathematics (Text-fig. 3, part b). No term other than "chevron" seems to have been used by bivalve workers in the past. Since the use of "angle-bracket shaped" or "greater-than-sign-shaped" seems cumbersome in decribing these teeth and "chevron-shaped" is so deeply entrenched in the literature, its use as a shape description for some nuculoid teeth is retained. Although it must be reiterated that "chevron" does not precisely describe the shape of these nuculoid teeth, it is used herein with this notation.

The posterior teeth of Palaeoneilo fecunda (Hall) (Pl. 5, fig. 11, 13) are chevron-shaped, while the anterior teeth are straight (inclined). In small (juvenile?) individuals of this species both anterior and posterior teeth are straight (inclined) (Pl. 5, fig. 1). In Nuculites neglectus (Hall) (Pl. 3, fig. 11) posterior teeth farthest from the beak are chevron-shaped (similar to P. fecunda, text-fig. 3, part d). The anterior teeth of N. neglectus are undulose and occasionally may bifurcate dorsally (Pl. 3, fig. 17). Posterior teeth of Praenucula albertina (Ulrich) (Pl. 2, fig. 1) and Deceptrix scofieldi (Ulrich) (Pl. 1, fig. 16) are straight (vertical to the antero-posterior axis), whereas their anterior teeth are chevron-shaped. All these nuculoid teeth are classified as taxodont (or ctenodont) type, in that they occur as a series (like a comb) of similar, but not necessarily identical, teeth.

The only other specimens collected in the Brassfield that have dentition preserved are assignable to Lyrodesma. Pojeta (1971, p. 10) implied homology of the teeth in Early Ordovician lyrodesmids and actinodonts such as Cycloconcha. Small juvenile(?) specimens of an unnamed species of Lyrodesma collected from the Brassfield Formation support a somewhat different line of reasoning. A comparison of the dentition of the Brassfield specimens and that of Trigonia shows striking similarities in morphology (Text-fig. 4.) Dental

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Text-fig. 4--Comparison of dentition of Trigonia sp. (Treatise of Invertebrate Paleontology, 472N, 1969) and Lyrodesma sp. (Brassfield, herein) using the Douvillé application of Bernard numbering system for heterodont dentition

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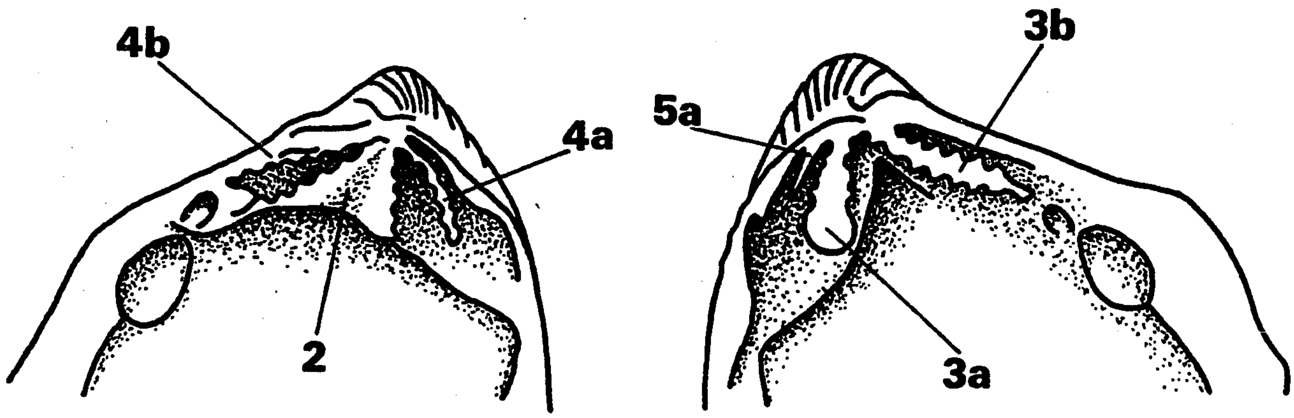
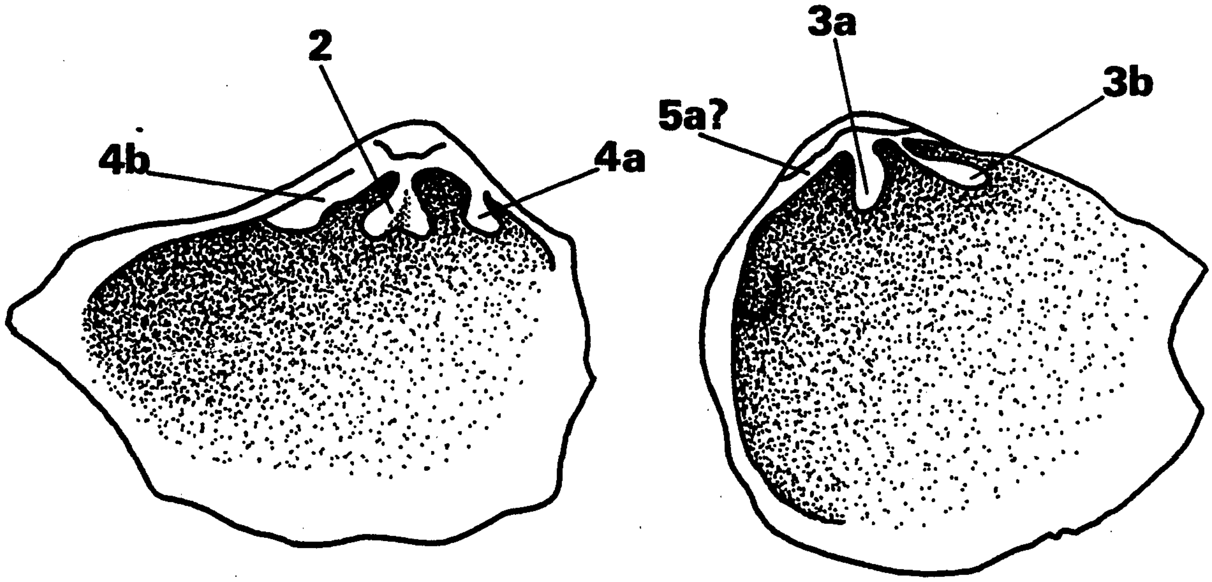
elements of Lyrodesma sp. and Trigonia sp. may be designated using the Douvillé numbering system. This numbering system was originated by Bernard (1895) for describing heterodont dentition but was applied to palaeoheterodonts by Douvillé (1912). The left valve contains a massive central cardinal tooth, the "2" tooth, and two other cardinals on each side, the "4a" and "4b" teeth, which are thinner and smaller than the "2" tooth. There are two teeth in the right valve of approximately equal size, designated "3a" and "3b."



Trigonia sp. Left valve **Trigonia sp. Right valve**
(redrawn from Cox, 1969, p. N 472)



Lyrodesma sp.
WU-1-12 Left valve
(Pl. 9, fig. 10, herein)

Lyrodesma sp.
WU-1-1 Right valve
(Pl. 9, fig. 9, herein)

Text-fig. 4--Comparison of dentition of Trigonia sp. (Treatise of Invertebrate Paleontology, 472N, 1969) and Lyrodesma sp. (Brassfield, herein) using the Douvillé application of Bernard numbering system for heterodont dentition

This arrangement of teeth is apparently true for all growth stages of species of Trigonia, although the smallest specimens seen by the author were far from being juveniles (10 to 15mm in length). On the other hand, this type of dentition (two or three cardinal teeth in each valve) is developed in only small individuals of Lyrodesma (less than 2.0mm in length) from the Brassfield (Pl. 9, fig. 6, 7). Individuals of larger size have additional cardinal teeth, that are seemingly added at the anterior or posterior end of the hinge plate, until five to nine teeth occupy the hinge of each valve (Pl. 9, fig. 8). While the teeth of larger (adult) Lyrodesma have lateral striations, no such striations appear on the teeth of these smaller specimens (juveniles). This feature, however, may not have been preserved. The isolated larger Lyrodesma teeth and the complete and partial hinge plates recovered from the Brassfield do have lateral striations (Pl. 9, fig. 4, 8).

Musculature

The only muscle scars on the interior of valves observed in this study are those of the adductor, pedal-byssal and the pallial systems. Of these, the adductor scars are the largest and most deeply impressed (that is, have the deepest pits in the shell). In nuculoids, there are two adductor muscle scars that are nealy equal in size (isomyarian) in each valve in an anterior and posterior position. In the holotype of Actinopteria brisa (Hall) (Pl. 7, fig. 12) the posterior adductor scar is three to four times larger than the anterior one. This arrangement is termed anisomyarian musculature. If only a single adductor muscle scar were present, the shell would be described as having monomyarian musculature. No bivalves in the Brassfield are known to exhibit monomyarian musculature although "Mytilarca" foerstei may be monomyarian if it is a Mytilarca. Pojeta (written communication) feels that mytilarcids may be monomyarian.

As with dentition, the only groups of bivalves in the Brassfield with preserved muscle scars are the nuculoids and Lyrodesma sp. The adductor scars of the nuculoids are ovoid, and with relation to the shells' dorso-ventral axis, the scars of Deceptrix scofieldi (Ulrich) (Pl. 1, fig. 1) are prolate (elongate parallel to the dorso-ventral axis) while those of Palaeoneilo fecunda (Hall) (Pl. 5, fig. 5) and Nuculites neglectus (Hall) (Pl. 3, fig. 12) are oblate (elongate perpendicular to the dorso-ventral axis). An additional feature associated with the anterior adductor scar of Nuculites neglectus (Ulrich) is a dorso-ventral ridge marking the adductor's inner margin (Pl. 3, fig. 13, 16). This ridge has been interpreted as a buttress for the adductor or associated muscles (e.g. Ulrich, 1894). The adductor scars of Lyrodesma sp. are infrequently preserved but appear to be essentially circular or slightly prolate.

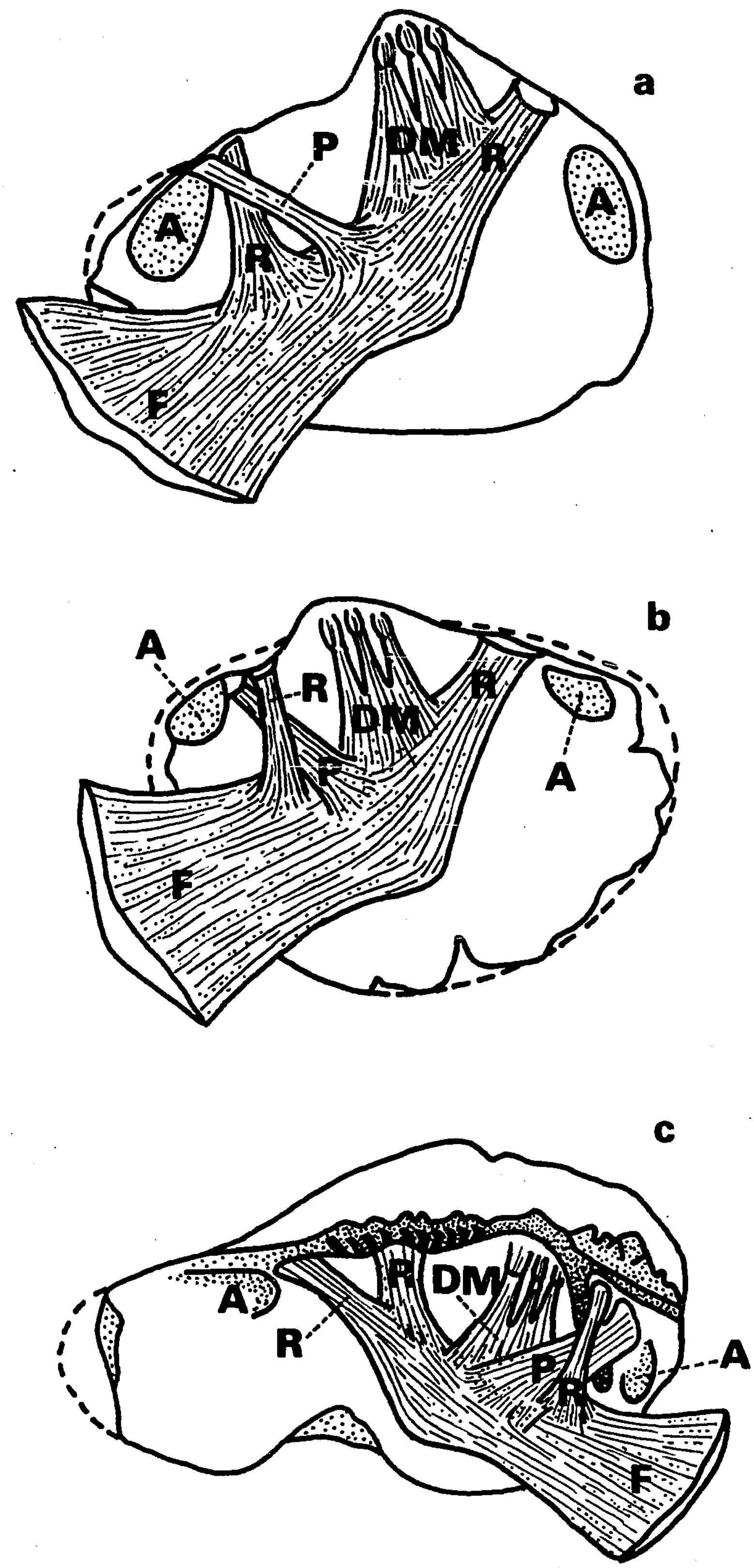
Smaller muscle scars are usually grouped together under the inclusive heading of accessory muscle scars. Most accessory muscle scars, particularly the larger ones, are produced by the pedal and/or byssal muscle system, although some bivalve shells have scars of visceral, branchial muscles and other muscles of unknown or uncertain function. The pedal muscle scars of nuculoids (there are apparently no byssal ones) are often well preserved on the specimens collected from the Brassfield (particularly Steinkerns). In Deceptrix scofieldi (Ulrich) (Pl. 1, fig. 12) and Nuculites nelgectus (Hall) (Pl. 3, fig. 13) the anterior pedal protractor scar (the muscle of which is partially responsible for extruding the foot) is located just dorsal to the adductor scar and partially confluent with it. The anterior protractor scars of Palaeoneilo fecunda (Hall) are dorsal to and disjunct from the adductor scars. The pedal retractor muscle scars are located anteriorly and posteriorly. In D. scofieldi (Pl. 1, fig. 12) and P. fecunda (Pl. 4, fig. 7), the anterior retractor scar is dorsal to and confluent with the protractor scar, while a single posterior retractor scar is disjunct from the adductor scar. In N. neglectus the anterior, as well as two posterior retractor scars are disjunct from the adductor or the protractor scars (Pl. 3, fig. 12, 13, 14). The shape of these accessory scars is taxonomically significant. The anterior retractor and protractor scars are roughly oval in all the nuculoids, but the single posterior retractor scar of D. scofieldi (Pl. 1, fig. 15) is nearly circular, while the posterior retractor of Palaeoconcha ohioensis Bassler (Pl. 2, fig. 12) and P. fecunda (Pl. 4, fig. 11) are narrow and antero-posteriorly elongate. Likewise, both posterior retractor scars of N. neglectus are narrow and elongate (Pl. 3, fig. 12, 14). The positioning of these accessory scars has proven useful for orientation of bivalves of this type.

With Heath's (1937) work as a template, Driscoll (1964) deduced the anterior and posterior of various Paleozoic nuculoids by the position of accessory muscle scars on the shells and Steinkerns (the single accessory muscle separate from an adductor was considered posterior, while the pair of scars fused to an adductor were anterior). A similar approach to orientation of nuculoids is applied to the Brassfield forms studied here. Reconstructions of muscle anatomy for several species of nuculoids in the Brassfield (Text-fig. 5) are made through homology with the morphology of Recent protobranchs as described by Heath (1937).

Text-fig. 5--Reconstructions of shell musculature based on muscle scars for (a) Deceptrix scofieldi (Ulrich) (Pl. 1, fig. 1), (b) Palaeoneilo fecunda (Hall) (Pl. 4, fig. 12), and (c) Nuculites neglectus (Hall) (Pl. 3, fig. 10) from the Brassfield.

In the region of the beak and umbone, there are several pairs of small, circular or elongate (prolate) muscle scars.

Text-fig. 5--Reconstructions of shell musculature based on muscle scars for (a) Deceptrix scofieldi (Ulrich) (Pl. 1, fig. 1), (b) Palaeoneilo fecunda (Hall) (Pl. 4, fig. 12), and (c) Nuculites neglectus (Hall) (Pl. 3, fig. 10) from the Brassfield.



A-Adductor **P-Protractor** **F-Foot**

R-Retractor **DM-Dorso-ventro median**

These seem to be similar in morphology and position to those scars produced by muscles named "dorso-median" and ventro-median" by Heath (1937) in his anatomical studies of Recent protobranchs (nuculoids). These scars occur in D. scofieldi (Pl. 1, fig. 15), N. neglectus (Pl. 3, fig. 10) and P. fecunda, (Pl. 4, fig. 12) from the Brassfield.

The pallial muscle scars are reflected on the shell as a pallial line (continuous or discontinuous series of scars), marking the attachment of the mantle to the shell. Pallial lines are rarely preserved in early Paleozoic pelecypods; however, several specimens in this study have some evidence of a pallial line. Palaeoneilo fecunda (Hall) has a faint pallial line (Pl. 5, fig. 6), as does Modiolopsis[?] rhomboidea Hall (Pl. 9, fig. 2). The holotype of Actinopteria brisa (Hall) has a well preserved pallial line (Pl. 7, fig. 12). When the pallial line is continuous from adductor to adductor, it is described as entire. No specimens with a discontinuous pallial line are known from the Brassfield. A pallial line that is indented (recurved) along its posterior course is described as sinupalliate. This indentation houses part of the retractible siphons and is a clue to the presence of these fused mantle stuctures in fossil bivlaves.

A summary of the occurrence of major morphologic features in the species of Brassfield pelecypods is presented in Table 1. Notation is made as to whether the features

Table 1--Occurrence of major morphologic features in species of Brassfield bivalves

Table 1

Occurrence of major morphologic features in species of Brassfield bivalves

Species	Occurrence of species restricted to Brassfield	Right valve	Left valve	Adductor muscles	Pedal muscles and accessory muscles	Dentition	Prosopon	Ligament area	Pallial line	Anterior or posterior alation (auricle) development
Actinopteria brisa		?	B	X	X	X	B	?	X	B
Cuneamya caswelli	*	B	B	?	?	?	B	?	?	--
"*Cypricardinia*" *undulostriata*		B	B	?	?	?	B	B	?	--
Cyrtodonta[?] *ferruginea*	*	B	?	?	?	?	B	?	?	B
Deceptrix scofieldi		B	B	B	B	B	B	B	?	--
Genus "A" *foerstei* n. sp.	*	?	B	?	?	B	B	B	?	--
Lyrodesma sp.	*	B	B	B	B	B	B	B	?	--
Modiolopsis[?] *rhomboidea*		B	B	X	X	--	?	?	X	--
[?] *Modiolopsis subrhomboidea*		B	?	X	?	--	B	?	?	--
"*Mytilarca*" *foerstei*	*	?	B	?	?	?	B	?	?	--
Nuculites neglectus		B	B	B	B	B	?	B	?	--
Palaeoconcha ohioensis	*	B	B	B	B	B	B	?	?	--
Palaeoneilo fecunda		B	B	B	B	B	B	B	B	--
Praenucula albertina		B	B	B	B	B	?	?	?	--

B The structure or feature is known to occur in Brassfield members of the species.

X Feature occurs in species, but not in specimens from the Brassfield

-- Feature does not occur in the species

? It is unknown whether feature occurs in species; species is too poorly preserved to determine presence or absence are observed in specimens collected from the Brassfield Formation.

CLASSIFICATION

This is not the place to evaluate the merits of the competing names Pelecypoda and Bivalvia which are in current usage for the class of molluscan bivalves. Here the names are used interchangeably. There was no attempt made during this study to intensively evaluate the suprageneric taxa used herein. The genera to which the Brassfield species are assigned are placed in higher taxa primarily in accordance with the system used by R. C. Moore (1969) in the *Treatise of Invertebrate Paleontology, Part N Bivalvia*. An exception to this procedure is in the systematics of *Lyrodesma*, where some alteration in the Treatise taxonomy has been made.

Generic assignments made herein were based on recently published information (including McAlester, 1968; Moore 1969; and Pojeta, 1966 and 1971), with a few modifications that seem reasonable on the basis of observation of type specimens.

Several genera contained species heretofore supposedly not ranging beyond the Ordovician are here used for Brassfield species (*e.g.*, *Palaeoconcha* and *Lyrodesma*). Genera traditionally used for mainly Devonian species are likewise here reported (*e.g.*, *Nuculites*, *Palaeoneilo* and *Actinopteria*. This assignment is based on comparison of

Brassfield material with the type species of these genera. Taxobases as presently understood leave no alternative to assigning Brassfield species to these traditionally non-Silurian genera.

The assignment of two Brassfield species to Modiolopsis (usually Ordovician) must be considered tenuous because of their poor preservation Cyrtodonta[?] ferruginea (Hall and Whitfield) may only tentatively be assigned to Cyrtodonta because none of the Brassfield specimens have internal features preserved. The shell shape of this species is cyrtodontid, but knowledge of dentition placement and morphology is necessary for certain generic assignment.

Taxobases vary from "superfamily" to "superfamily." For example, nuculoids are distinguished primarily by dentition and shell shape, while ambonychiid and pterineid genera are separated by shell shape and prosopon. Other groups such as modiolopsids, cyrtodontids and cardiids are distinguished by various combinations of dentition, prosopon and shell shape. Thoughts on classification of various taxa (especially nuculoids) have changed substantially during the last century primarily because of an increase in knowledge about comparative morphologies. Taxonomic philosophy of James Hall, E. O. Ulrich and August F. Foerste seems conservative today. For example, Ulrich (1894) informally subdivided Ctenodonta Salter into six groups, apparently based on consistent differences in morphology of the encompassed species. Although intimating that these groups should probably be separate genera, he hesitated to propose these new taxa. Based on Ulrich's observations and considerable new data, most of his (1894) "groups" of Ctenodonta have now been incorporated into one or more genera (e.g. species in his "Ctenodonta recurva group" are now placed in Palaeoconcha Miller or Similodonta Soot-Ryen).

STRATIGRAPHY

The Brassfield Formation was formally named the Brassfield Limestone by Foerste (1906, p. 18) for rocks exposed in a series of sections along the now abandoned Louisville and Atlantic railroad berm between Brassfield and Panola, Madison County, Kentucky. This sequence of rocks was, however, recognized as distinct at a considerably earlier time. Owen (1857, fide O'Donnell, 1967, p. 16) used the name "Clinton" for some oölitic iron beds capping the Cincinnatian strata in Kentucky, while Orton (1890, p. 145) applied that name to a similar unit in Ohio.

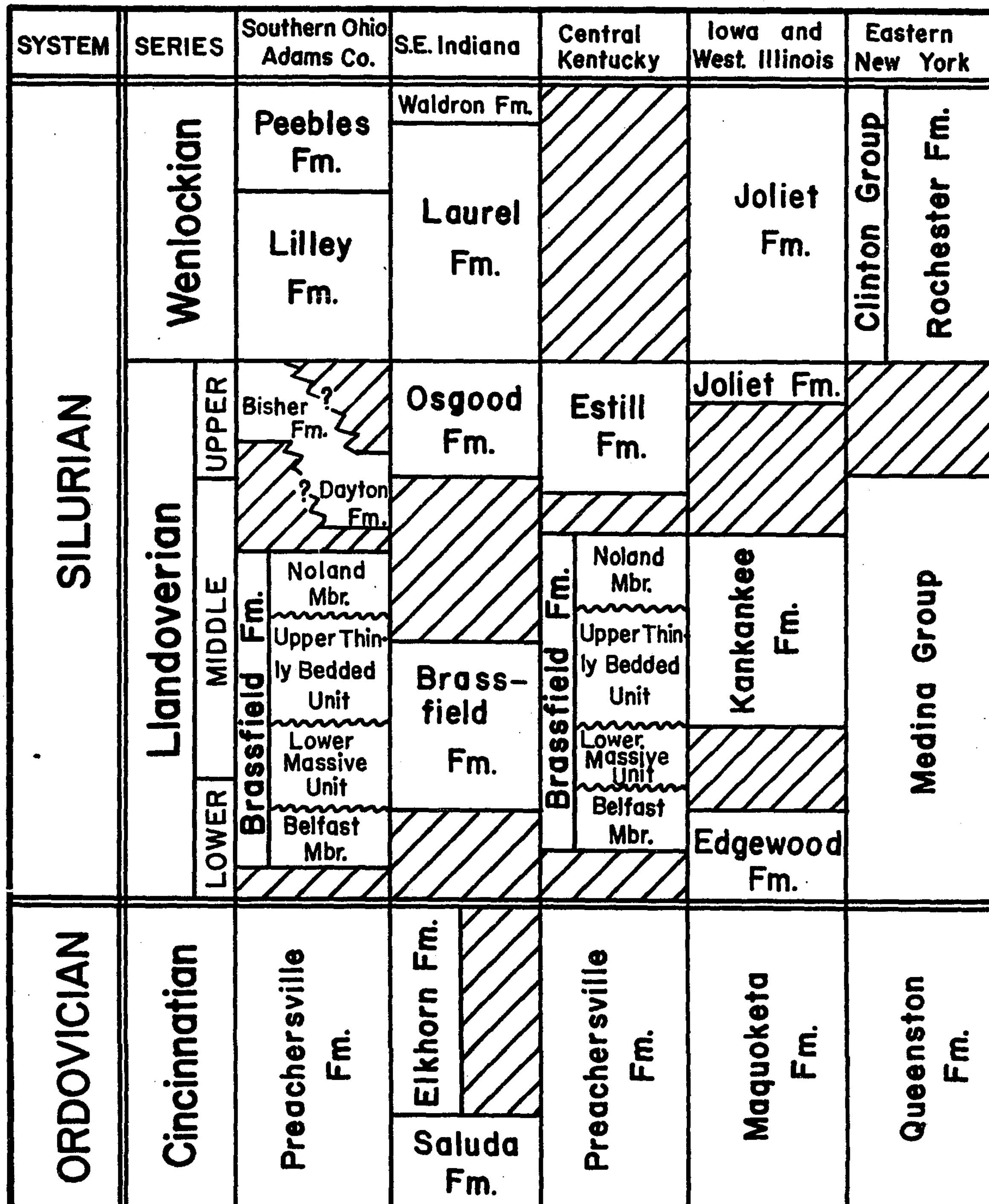
Foerste (1885, 1895, 1896, etc.) was the first person to intensively investigate the Brassfield Formation. He analyzed stratigraphy and did detailed paleontologyof the "Clinton" limestone, first in Ohio (1885, 1895), then in Indiana, Kentucky and Tennessee (1896, 1901). Foerste's series of studies were, and are still the most comprehensive ones dealing with the Brassfield. As early as 1896 (p. 189), Foerste realized that the "Clinton," particularly in Ohio, was not time equivalent with the New York Clinton, although it may have represented a similar facies. He proposed the name Montgomery Formation for the "Clinton" in Ohio, but found the name to be preocupied and returned to the use of Clinton (1904, p. 340). The stratigraphic position of the Brassfield Formation relative to other Upper Ordovician and Silurian formations is shown in Text-fig. 6.

Text-fig. 6--Generalized regional stratigraphic distribution of Upper Ordovician and Lower Silurian formations of the continental interior of the United States (modified from Berry and Boucot, 1970).

The term Brassfield Limestone was subsequently used by him and other authors (*e.g.*, Rexroad, *et al.* 1965) essentially as originally proposed until O'Donnell (1967, p. 31) emended it to include several overlying units placed by Rexroad, *et al.*, (1965) in the Noland Formation.

The Brassfield Formation, as currently conceived (O'Donnell, 1967), consists of four general lithologic units, two of which are recognized as members. From the base upward, they are:

1) The Belfast Member, originally recognized by Foerste (1895), is an approximately 6-foot thickness of calcareous or dolomitic thinly-bedded shales and siltstones, resting on the top of the Preachersville Formation of the Cincinnatian Group. This Belfast member includes a shaley unit called the Centerville Formation by Foerste (1931, p. 184).



Text-fig. 6--Generalized regional stratigraphic distribution of Upper Ordovician and Lower Silurian formations of the continental interior of the United States (modified from Berry and Boucot, 1970).

2) The "lower massive unit" consists of limestone or dolomite beds 4 to 15 inches thick, occurring above the Belfast member. This unit in some sections (especially in southeastern Indiana) appears as a single bed, virtually continuous upward, composed of medium to coarsely crystalline carbonate having few fossils other than disarticulated echinoderm plates.

3) Above the massive unit is a thinly bedded unit consisting of alternating beds of shale and limestone or dolomite, rarely greater than 6 inches thick each (see Text-fig. 7). This unit contains the most fossiliferous strata, including the "bead bed" (a layer rich in large crinoid columnals) and the ferruginous zones from which many pelecypods were acid-etched for this study. Several chert-bearing zones also occur in this unit on the eastern side of the Cincinnati Arch. The "bead bed" was conventionally used as a marker for the top of the Brassfield by Foerste (1896, 1906, etc.), but may occur in other horizons (O'Donnell, 1967, p. 35).

4) The Noland Member was designated as a formation by Rexroad, et al. (1965) to include two pairs of alternating shale and carbonate beds described as overlying the Brassfield in Central Kentucky by Foerste (1906). The Plum Creek Shale, Oldham Dolomite, Lulbegrud Shale and Waco Dolomite are now considered tongues and lentils within the Noland Member (O'Donnell, 1967, p. 31). These beds are

difficult to trace for any great distance, and O'Donnell remarked that the Noland is difficult to recognize north of Bath County, Kentucky. The upper shales and limestone of the upper thin-bedded unit in the eastern and northern outcrop regions may be traceable to the Noland farther south (O'Donnell, 1967, p. 38). However, Rexroad et al. (1965, p. 21) suggested that the basal carbonate bed of the Waco may correlate with the Dayton Limestone in sections farther north.

Text-fig. 7--One of the outcrops in the West Union, Ohio area on State Road 41

The inclusion or exclusion of the Noland in the Brassfield is immaterial to this study, since no pelecypods were found in any of the Noland units. Rexroad et al. (1965) first considered Foerste's "Brassfield Limestone" to be a formation.

The above description is a composite stratigraphic subdivision of the Brassfield. In most sections, some of the component stratigraphic units are missing or unrecognizable. For example, in most Indiana outcrops of the Brassfield, only a massively bedded carbonate unit is observed. While in other sections, more than four units are recognizable. In Adams County, Ohio, an additional thinly bedded (lower) and massively bedded unit (upper) can be recognized between the "lower massive unit" and the "upper thinly bedded unit."

Text-fig. 7--One of the outcrops in the West Union, Ohio area on State Road 41. Massive layer at top of section marks the top of the Brassfield. Entire section is in the upper thin-bedded unit. The bottom 26 feet of the formation are not exposed here. The man's right hand is at the level of sample WU-14.

The locations of the sections studied are given in the appendix to this work.

The Brassfield is generally considered to lie unconformably upon rocks of the Cincinnatian Series in the Ohio valley region. In general, the contact of the base of the Brassfield with Cincinnatian (usually the Elkhorn, Preachersville, or Saluda) Formations of the Richmond Group, marks a change in lithology. The unconformable contact is distinct when the massively bedded crystalline carbonate phase of the Brassfield overlies the shales and thin limestones of the Elkhorn Formation(Preachersville Formation in eastern Kentucky and adjacent Ohio). However, some sections show superficially similar lithologies in the Richmond beds and the superjacent Brassfield. Near Madison, Indiana (at Hanging Rock) the coaresly crystalline, massive Brassfield overlies the massively bedded crystalline dolomites of the Saluda Formation. Distinguishing the Brassfield in these sections is difficult. However, the Brassfield is more coarsely cyrstalline and of a dark bronze color. The contact surface is irregular, suggesting some erosion of the Saluda prior to Brassfield deposition. The environments of deposition of these two formations are likely to be similar because of the similar lithologies.

On the east side of the Cincinnati Arch, especially in Adams County, the Brassfield overlies shales of the Preachersville Formation (Text-figs. 8, 9a, b). The basal

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Text-fig. 8--Basal contact of the Brassfield Formation (Lower Silurian) with the underlying Preachersville Formation (Upper Ordovician) near Bentonville and West Union, Adams County, Ohio

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Text-fig. 9a--Gradational contact between Elkhorn Formation (Ordovician) and Brassfield (Lower Silurian) in creek 2.4 miles north of West Union, Ohio

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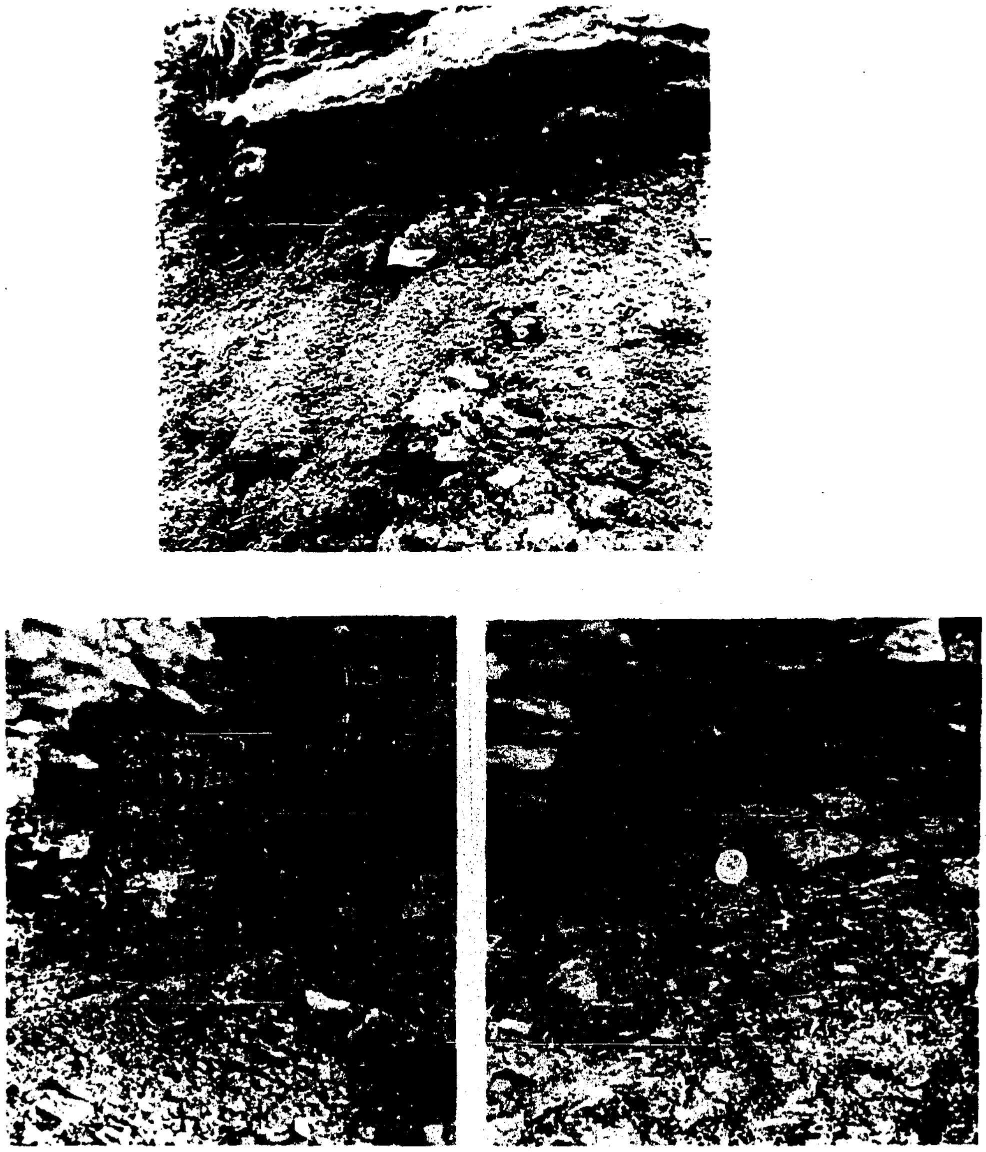
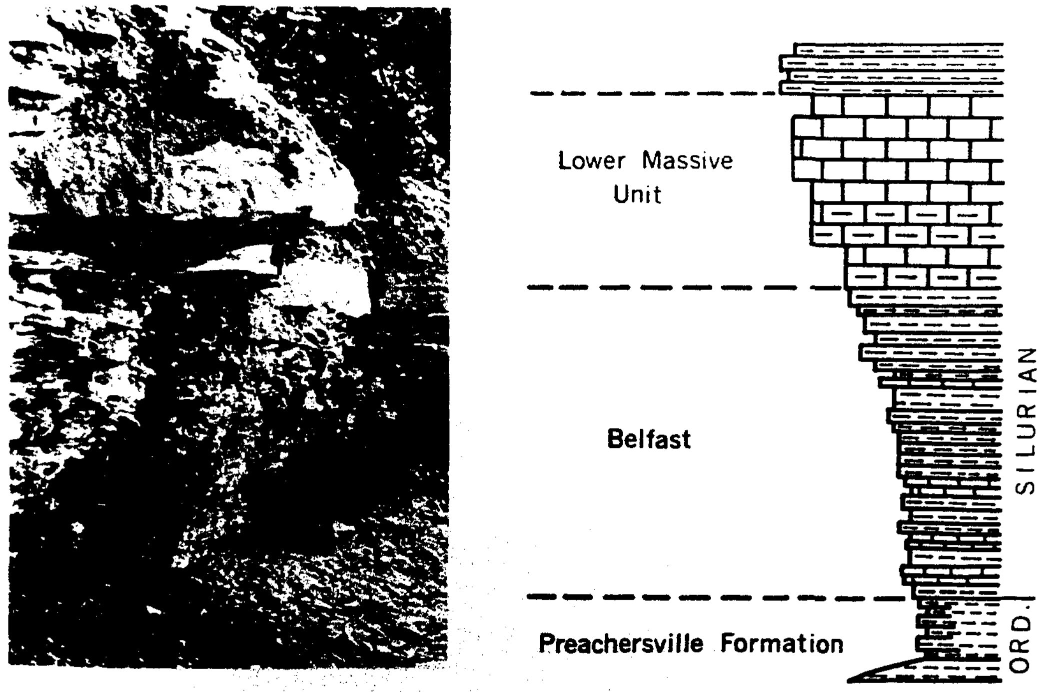
Text-fig. 9b--Sharper contact between Brassfield and Preachersville Formations.

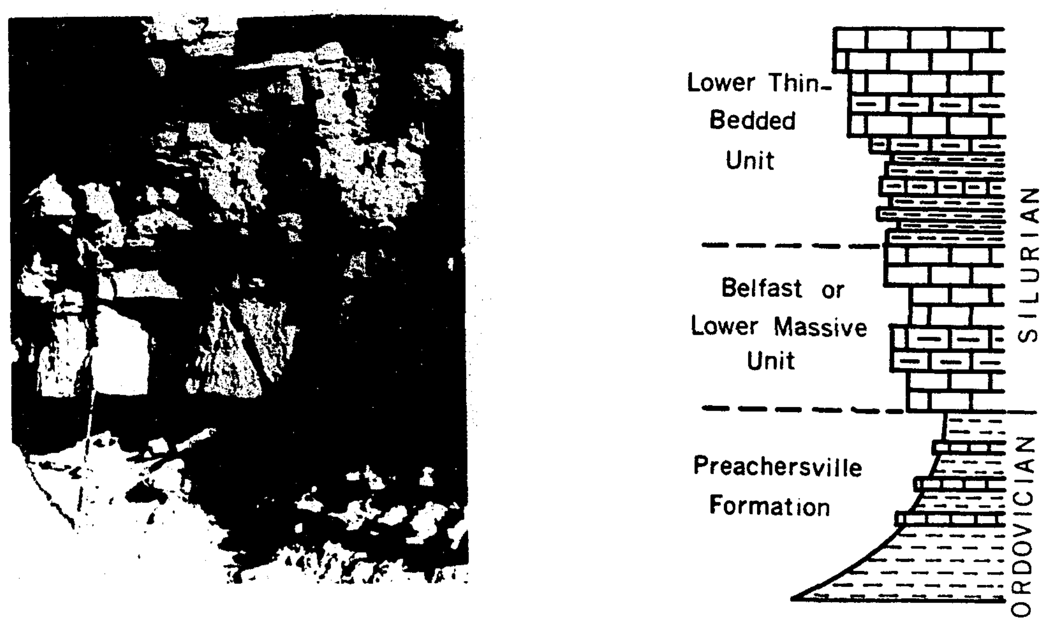
Brassfield in the area is the Belfast Member, a sequence of thinly bedded shales and siltstones. The contact between the underlying Ordovician and Brassfield in this area is the least distinct in the Ohio valley region. In a section about one-fourth mile south of Bentonville, Ohio, on State Road 136, a relatively thick sequence of red, green and greenish-gray shales and siltstones of the Preachersville Formation are capped by Brassfield. Near the top of the Preachersville, thin lentils of dolomitic limestone occur. These stringers are lithologically very similar to the overlying lower massive beds of the Brassfield. About two feet below the main carbonate beds of the Brassfield are several 2- to 3-inch thick layers of calcareous shale and siltstone with some shale parting (Text-fig. 8). The



Text-fig. 8--Basal contact of the Brassfield Formation (Lower Silurian) with the underlying Preachersville Formation (Upper Ordovician) near Bentonville and West Union, Adams County, Ohio



Text-fig. 9a--Gradational contact between Preachersville Formation (Ordovician) and Brassfield (Lower Silurian) in creek 2.4 miles north of West Union, Ohio



Text-fig. 9b--Sharper contact between Brassfield and Preachersville. Lentiles of carbonate are visible in Preachersville. Road cut on State Road 41 Ohio Brush Creek, Adams County, Ohio increasing amount of carbonate and the stringers of limestone seem to have been a prelude to the mainly calcareous Brassfield sedimentation to follow. The base of the Belfast should be drawn about 2 feet below the first massive carbonate bed, and the gradation between Belfast and Preachersville seems subtle enough that only a rather short interruption in sedimentation across the contact occurred. The only organisms known from these two units are palinomorphs. This flora is very similar in both formations (see discussion below of Gray and Boucot, 1972).

Farther north in Adams County, in several road cuts along State Road 41, the Belfast is again superjacent to the Preachersville shales. In these sections (Text-figs. 8, 9a) there are no limestone lentils in the upper Preachersville, but the overlying Belfast is also less calcareous. About 6 feet below the base of the first massive carbonate bed (of the Brassfield) is a subtle change in bedding, coloration, and lithology. At this point, there is a bedding plane that is nearly horizontal and coated with a film of dark (organic?) material. Below this plane are thinly laminated clayey Preachersville shales, and above are slightly thicker bedded, somewhat more calcareous shales and siltstones of the Belfast, but become more limey approaching the massively-bedded Brassfield above. This type of contact of the Brassfield Formation with the various Upper Ordovician formations (Text-fig. 9) is rather atypical for most of the

Brassfield. For the mostpart, the Brassfield distinctly unconformably overlies the Ordovician, with obvious differences in lithology. The "typical" Brassfield is a dense, coaresly crystalline dolomite or limestone bronze or "salmon" pink in color. However, the underlying Ordovician rocks are commonly bluish or greenish gray shales or limestone (although some reddish shales are known in part of the Preachersville Formation).

Bivalves were conspicuously absent from most rocks of the "typical" Brassfield lithology. Only a few horizons of the massive, crystalline lithology at Fairborne, Ohio (samples FB-1,2) yielded any bivalves (Actinopteria brisa assemblage). It appears that this environment must have been hostile to bivalve colonization. The shales, siltstones and more finely crystalline limestones of several sections in Adams County, Ohio were apparently formed in environments more conducive to bivalve existence. Bivalves are common in several crystalline limestone layers in the upper thin-bedded unit and in some ferruginous carbonate beds immediately overlying these limestone layers. Concentrations of many taxa other than bivalves (other mollusks, brachiopods and bryozoans) in these layers probably represent lag or current concentration of biogenic particles.

The apparent paraconformity between the Brassfield and Preachersville in part of Adams County, Ohio was the subject of a study by Gray and Boucot (1972). Palynological evidence was used to determine environments of deposition and water depth of sediment deposition of the Preachersville and Belfast beds on each side of this contact. Data based on spore tetrads and acritarchs indicate that palinomorphs assemblages are nearly identical across the Elkhorn-Belfast contact and change only higher in the Brassfeild away from the paraconformity. Water depths indicated by these data are very shallow and nearshore, essentially intertidal. Gray and Boucot were not willing to rule out nearshore, non-marine environments either (1972, p. 1311). The paleogeographic picture thus inferred from Gray and Boucot's study is that of nearshore,shallow water sedimentation (probably marine) at the top of the Elkhorn and in the lower portion of the Belfast, with water depth increasing higher into the Belfast and lower massive Brassfield. Depth zonation for the Elkhorn and Belfast was determined solely on the basis of palinomorphs, while higher Brassfield beds (lower massive unit and upper thinly-bedded unit) contained megafossils (including brachiopods) which allowed depth zonation with criteria proposed by Ziegler (1965) and Ziegler, Cocks and Bambach (1968) for Lower Silurian marine communities. Although no megafossils were found in the lower Belfast in this study or by previous workers (*e.g.* Gray and Boucot, 1972), it is considered to be equivalent to the "*Lingula* benthic life zone," while the upper Belfast and part of the lower massive unit they thought to be representative of the "*Eocoelia* life zone" (Gray and Boucot 1972, p. 1311). The upper part of the massive beds and some of the thinly-bedded unit would correspond to the "*Pentamerus* life zone," while the rest of the section (to the top) is comparable to the "*Stricklandia* zone" (Gray and Boucot, 1972, p. 1302). In the Brassfield, the "*Eocoelia* life zone" is represented by the "*Cryptothyrella* community"; the "*Pentamerus* life zone" is represented by the"*Platymerella* community"; and the "*Stricklandia* life zone" is represented by the "*Microcardinalia* community" (Ziegler and Boucot, 1970, and Gray and Boucot, 1972). The validity of this extension of Ziegler's ideas to the lithologically quite distinctive Brassfield, where only some of his community bio-indicators occur should be considered tentative until more data about the faunas in the Brassfield are available. However, there appear to be taxa in the Brassfield that are ecologically similar to those of Ziegler's. Several brachiopods, including species of *Cryptothyrella* have been considered analogous to "*Eocoelia*" in Ziegler's "*Eocoelia* zone." And some species of *Platymerella* in the Brassfield are thought to compare ecologically with *Pentamerus* ("*Pentamerus* zone") according to Ziegler and Boucot, 1970).

Although there may have been a gap in sedimentation between the Preachersville and Belfast beds in Adams County, the sediments and microflora support the conclusion that the environment was relatively similar on each side of the contact and that non-deposition for an unknown but relatively short period of time (based on the microflora) is all that separates Ordovician (Elkhorn) from Silurian (Belfast) sediments in this area.

It seems apparent from the foregoing discussion that some type of stratigraphic hiatus (unconformity) is present at the base of the Brassfield throughout most of the Ohio valley region, but that a single general statement about that hiatus is untenable.

The age of the Brassfield is usually considered Late Early Llandoverian (Early Silurian). This conclusion is based on several lines of evidence:

1) Position of Brassfield in the stratigraphic column (between Richmondian Upper Ordovician strata and Niagaran Middle Silurian strata)

2) Occurrence of the brachiopods Platymerella and Cryptothyrella (Ziegler and Boucot, 1970)

3) Occurrence of the conodont Icriodina irregularis (Rexroad, 1967).

All of these indicate a Lower Silurian position for the Brassfield Formation. Numerous Icriodina irregularis Branson and Branson were recovered from acid residues of the samples from the "Palaeoneilo fecunda province" in the Upper thinly-bedded unit. This unit also contained several species of the conodont genus Paltodus which are characteristic of the Brassfield Formation (Rexroad, 1967).

ECOLOGY AND PALEOECOLOGY

It is not possible to give a very meaningful treatment of the bivalve paleoecology of the Brassfield Formation because that would necessitate an ecological evaluation of all species of organisms known from the Brassfield and their interactions. Detailed analysis of the purely physical data would also be necessary. This study deals only with the bivalve fauna, and the bivalves comprise only a very small percentage of all Brassfield species. Moreover, the complete fauna is far from being adequately described.

The total number of species in the Brassfield (including the Noland Formation) is well in excess of the 206 species listed by Foerste (1931, p. 175-176, 186-187). Current work by Laub (personal communication) on the Brassfield corals alone will considerably augment this list. Only 14 species of pelecypods are recognized herein. Since bivalves comprise a small portion of the fauna, little attempt is made herein to analyze any aspects of the Brassfield synecology (community ecological relationships).

Bivalves usually occur in Brassfield strata where other phyla and classes of organisms abound. In horizons of greatest pelecypod abundance, gastropods, trilobites, brachiopods, bryozoa and crinoid stems often occur. There is, however, a conspicuous lack of corals associated with this fauna. Interpretation of life habits, growth, fecundity and mortality of the bivalves of these faunas is presented for the more numerous species. By analogy or homology, all species were compared with modern forms in order to hypothesize probable functional morphology.

Brassfield Bivalve Faunal Associations and their Distributions

Bivalves are commonly divided into infaunal and epifaunal types (*e.g.* Pojeta, 1971, p. 30) depending on their habitus relative to the sediment water interface. Infaunal bivalves live submerged in the substrate, while epifaunal forms live on or above the substrate surface. Some forms, living only partially imbedded in the sediment, are referred to as semi-infaunal (Stanley, 1970).

Bretsky (1970, p. 50) uses habitus and feeding processes to categorize bivalve ecologic types. His subdivisions of epifaunal suspension, infaunal suspension and infaunal deposit feeders are biologically realistic. It should be borne in mind, however, that they do not represent distinct separate environments which support each type. Many modern environments often support more than one type. For example, *Mercenaria mercenaria* (an infaunal suspension feeder) and *Crassostrea virginica* (an epifaunal suspension feeder) are found in the same modern environment, the intertidal salt marsh (personal observation, Beaufort, North Carolina, 1971).

All of Bretsky's habitus and feeding types are represented among the Brassfield bivalves, which, based upon their geographic distribution, compose two distinct faunal assemblages (Text-fig. 2). One assemblage contains infaunal deposit and suspension feeders ("Palaeoneilo fecunda assemblage"); the other, epifaunal suspension feeders (Actinopteria brisa assemblage"). These assemblages are names for the species which is most abundant and omnipresent. Associated in the Actinopteria brisa assemblage are:

Actinopteria brisa (Hall)

"Cypricardinia" undulostriata (Hall)

"Mytilarca" foerstei Clarke and Ruedemann

Modiolopsis[?] rhomboidea Hall

[?]Modiolopsis subrhomboidea Simpson

Cuneamya caswelli (Foerste)

Associated in the Palaeoneilo fecunda assemblage are:

Palaeoneilo fecunda (Hall)

Deceptrix scofieldi (Ulrich)

Praenucula albertina (Ulrich)

Palaeoconcha ohioensis (Bassler)

Genus "A" foerstei n. sp.

Nuculites neglectus (Hall)

Lyrodesma sp.

Cyrtodonta[?] ferruginea (Hall and Whitfield)

The above listed Brassfield infaunal deposit and suspension feeders do not seem to be segregated from each other as they apparently are from epifaunal feeding types. For example, Lyrodesma sp. and Cyrtodonta[?] ferruginea (Hall and Whitfield) are infaunal suspension feeders (Pojeta, 1971, text-fig. 9) and occur in the same assemblage as the infaunal deposit feeding nuculoids.

Although members of each of the two above-described assemblages share a common habitus and feeding types, it is not assumed that this coincidence alone conclusively demonstrates that these fossil assemblages represent communities or "faunal provinces." They do probably represent life associations of the species involved, but until supportive data has been gathered from species of other associated taxa, no community inferences may be drawn.

The species listed as members of these two communities were the only species found in this study, and they occurred only in Ohio. Although the Brassfield Formation was extensively sampled in Indiana and Kentucky (Text-fig. 1), no bivalves were found in those states during the present investigation nor by Foerste during his many years of studying the Brassfield (1885-1931).

One plausible explanation of this limited areal distribution of the Brassfield bivalves is that they simply may not have lived in the environments represented by Kentucky and Indiana sediments. The lithology of Brassfield sediments of Ohio, Kentucky and Indiana may be divided into three major types, distributed in a pattern nearly coextensive with outcrop areas in the three states (O'Donnell, 1967). The Brassfield Formation in Ohio consists primarily of interbedded shales and fine- to medium-grained crystalline (sparry) limestones. Some sections in the southern part of the state (especially Adams County, localities 4 and 5, Text-fig. 1, 7) contain more shale than limestone. In Indiana, the Brassfield lithology is almost wholly massively bedded, coarsely crystalline dolomite (occasionally some limestone). This is the bronze or pink dolomite commonly thought of as "typical" Brassfield lithology. There is very little shale exposed at most outcrops in this region. The Brassfield Formation in Kentucky is generally thin bedded, medium to finely crystalline dolomite (occasionally being more massive) with some interbedded shale. A much lesser porportion of the total section is shale than in most of the Ohio outcrops.

Thus, the environments recorded by the Brassfield lithology in Ohio (interbedded shales and limestones) may well have been more conducive to pelecypod survival and growth than were those in Kentucky and Indiana. There is a greater proportion of shaley and fine-grained sediments in the Ohio section, particularly in Adams and Highland counties, which provided a substrate suitable for proliferation of infaunal deposit and suspension feeding bivalves.

Another explanation for this distribution, and indeed for the distribution of all fossil assemblages, involves preservation. The great majority of the bivalves in this study represent a special selective type of preservation. Limonite permineralization (which may have initially formed as pyrite), phosphoritic molds and Steinkerns are the usual mode of preservation of bivalves in the Ohio Brassfield beds.

This mode of preservation bespeaks a reducing setting which may have been restricted to the Brassfield Sea to the east of the present Cincinnati Arch in the Ohio area, where bottom circulation may have been impeded.

Bivalve Life Habits

Life habit information about bivalves is usually grouped into two major categories. As discussed above, bivalves may be categorized by feeding type (detritus or sediment gathering deposit feeders and suspended particle filtering suspension feeders) and by mode of life (infaunal, epifaunal or semi-infaunal). Mode of life (that is, the orientation and position of bivalves relative to the substratum) may also be thus be inferred. Mode of life and feeding type are necessarily related: virtually all of the epifaunal types are suspension feeders; infaunal species may be suspension or deposit feeders. The feeding type of Brassfield bivalves can be inferred by analogy and homology with Recent forms by analyzing the functional morphology of the shell (Kauffman, 1969, and Stanley, 1972).

Members of the *Palaeoneilo fecunda* assemblage, nuculoids are also represented in Recent sediments. Two superfamilies of Nuculoids are represented in Brassfield sediments: the Nuculacea and Nuculanacea. The two groups have a distinct morphological differences: nuculanids are posteriorly elongate, while nuculids are anteriorly elongate. Recent members of both groups are shallow water, deposit feeders; but the posterior elongation of nuculanaceans indicates a better development of siphonal structures, which allows genera of this group to live more deeply buried in the sediment. The Brassfield nuculacean genera *Deceptrix*, *Praenucula* and *Palaeoconcha* can therefore be interpreted as shallow infaunal deposit feeders; *Nuculites* and *Palaeoneilo*, elongate Brassfield nuculanaceans, were by comparison with Recent nuculanaceans, probably more deeply burrowing deposit feeders.

Snyder and Bretsky (1971, p. 243 and text-fig. 12) presented a reconstruction of the mode of life of *Nuculites neglectus* and *Palaeoneilo fecunda* based primarily on extent of posterior shell elongation. They suggested that *P. fecunda* lived approximately 1cm below the sediment/water interface, while *N. neglectus* lived at about twice that depth based upon its longer posterior region. They presented no data for nuculacean bivlaves. Because of the shallower burrowing habit for nuculaceans, however, it is inferred that they lived with their shell margins less than 1cm below the sediment surface.

Comparison of these fossil forms with living members of their respective superfamilies not only supports the morphologic interpretations of life habits but also can give insight into theorientation of the shells. Yonge (1939) provided such insight into the nuculoids. He described the life position of *Nucula* (a nuculacean) and *Yoldia* (a nuculanacean). *Nucula* lives just below the sediment/water interface with its anterior end uppermost; Yoldia lives slightly deeper, with its antero-posterior axis nearly vertical and its posterior end uppermost (Stanley, 1970). Malletia, a genus in the same superfamily as Yoldia, lives deeper in the sediment, yet in a more nearly horizontal life position. Using the uniformitarian approach, the life position of Deceptrix, Praenucula and Palaeoconcha can be inferred as infaunal, near sediment surface with the anterior edge of the shell uppermost. Nuclites and Palaeoneilo can be compared with Malletia and Yoldia and so thought to have lived deeper infaunally with the posterior end uppermost. All these genera apparently were deposit feeders.

Another element of the Palaeoneilo fecunda assemblage in the Brassfield is Cyrtodonta[?] ferruginea, a member of the family Cyrtodontidae. This family is extinct and has no Recent homologues. However, its shell form is analogous to Recent forms such as Glycymeris and other arcoids (Pojeta, 1971, p. 37). Glycymeris is known to be a shallow burrower with the posterior end of the shell protruding from the sediment (Vlès, 1906 fide Pojeta, 1971, p. 37). Therefore, Cyrtodonta may have been semi-infaunal if the analogy with Glycymeris is correct. The Brassfield species of this genus has a somewhat flattened anterior margin suggesting that it rested on that surface, but the lack of byssal structures (at least an opening reflected in the shell) does not strengthen this hypothesis. This type of broad surface, high position center-of-gravity shell would have been relatively unstable in an epifaunal position (Stanley, 1972). Rather, the general shell shape suggests an upright, semi-infaunal position (Kauffman, 1969). The posterior region is somewhat extended and could have reasonably housed short, broad siphons. It is assumed that Cyrtodonta was a suspension feeder, although only additional morphologic data, such as a pallial sinus scar, could substantiate this.

Lyrodesma sp., also a member of this Palaeoneilo fecunda assemblage, is presumed to have been infaunal based principally on its antero-posteriorly elongate valve shape. Since Pojeta (1971) has reported the presence of a pallial sinus in some Ordovician Lyrodesma species, it is possible that this Brassfield species may also have had a sinus and, hence, retractible siphons. Lyrodesma sp. was probably an infaunal suspension feeder on this basis.

The generalized feeding type and life position of the species in the Actinopteria brisa assemblage of the Brassfield can be characterized as epifaunal-suspension feeding, although there is considerable variation in specific types. Genera in this assemblage include "Mytilarca," Actinopteria, "Cypricardinia," Modiolopsis[?], and Cuneamya, which (with the exception of Cuneamya) have usually been considered as byssally attached epifauna (e.g. Pojeta, 1966, and Kauffman, 1969).

Kauffman (1969) described several categories of epifaunal byssate bivalves. He placed Mytilarca in the "byssate closely attached bivalves in exposed habitats" category. Modiolopsis may also fit into this category or may have been a "byssate epifaunal nestler." Cypricardinia may also be considered "byssate nestlers." The "byssate, closely attached" type of habitus is more of an open, exposed life position than is the "byssate nestler." Differences in shell morphology of these two groups may be quite minor. Most "byssate nestlers" have the byssal apparatus near the mid-line of the valves and have a reëntrant in the shell margin at that point (e.g., Cypricardinia). The shell shape of Cuneamya in the Brassfield is somewhat unlike other species assigned. The Brassfield form has a more erect umbonal ridge, a more subcentral beak and a fairly prominent medial sulcus (byssal?) as compared to other species of the genus. Because of its shell shape, the Brassfield form is reminiscent of some Recent "byssate nesters" such as Anadara or Noetia (Arcoida). Interpretation of life position for this Brassfield Cuneamya must remain tentative until more is known of the shell morphology (especially the pallial line). Pojeta (1966 and written communication) has suggested that Cuneamya may be considered infaunal based on the presence of a distinct lunule and escutcheon. Only a lunule is present in the Brassfield forms, however better preservation of materials may yield substantive morphologic features for life habit interpretation.

The "byssate closely attached" forms may have a byssal apparatus at various positions along the shell margin, although it tends to occupy a position along the anterior half of the shell. The shell margin in contact with the substratum is relatively straight, having only a slight indentation at the position of the byssus.

Pojeta (1971, p. 33) illustrated Modiolopsis in both "closely attached" (to an exposed substrate) and "nestled" (in the branches of a trepostome bryozoan) life positions. He also illustrated two ambonychiid genera, apparently related to Mytilarca in a "closely attached habitus. Because of the shell shape and inferred position of byssal emergence, this is apparently a reasonable interpretation.

Kauffman (1969, p. 144) would probably characterize the pteriid Actinopteria as a "byssate free-swinging bivalve." The traditional life position interpretation of most fossil pteriids is much like that of the modern genus Pteria, commonly depicted as free-swinging, byssally attached to some stalk-like structure (such as gorgoniaceans) above the sediment interface (Stanley, 1970). Stanley (1972) took exception to this and many other traditional inferences about life orientation of fossil byssate bivalves.

Working from the hypothesis that the modern semi-infaunal, byssate genera of the Pinnacea and the Mytilacea are archetypical rather than secondarily modified, Stanley (1972) referred many pterioids, ambonychiids, and modiolopsids to what he called an "endobyssate mode of life" (infaunal or semi-infaunal). However, some modern Mytilacea, such as Arcuatula, that are semi-infaunal, may have secondarily obtained that habit (Kauffman, 1969, p. 163).

Stanley considered most ancient byssate genera that are prosocline and have an anterior auricle to have been semi-infaunal or "endobyssate." More prosocline forms with a less prominent auricle were less deeply imbedded in sediment or may have been epifaunal (for example, Stanley, 1972, text-fig. 17).

As well as using anterior lobation as a criterion for an endobyssate life habit, Stanley used shell inflation (or cross-sectional area) as an interpretive feature reflecting mode of life (for example, see Stanley, 1972, text-fig. 6). Shells with widest cross-section near the substrate he felt were likely to have been "epibyssate" (epifaunal). This morphology provides a lower center of gravity for the shell, thus making it a more stable in exposed habitats. With the thickest part of the shell a greater distance from the substratum, the center of gravity would be high and the shell could be more easily overturned. He commented that shells with their greatest thickness at mid-height, or dorsal to that, are typically burrowers. Much of this interpretation would, of course, depend on the nature of the byssus, its strength, length and substrate attachment.

Stanley's interpretation of the modes of life of most

Brassfield bivalve species varies in great measure from that of Kauffman.

Although Stanley visualized Mytilarca as living much like modern Mytilus edulis ("epibyssate"), a mode of life interpretation much like Kauffman's, his interpretation of other byssate genera (Actinopteria, Cypricardinia, Modiolopsis) was different. Stanley (1972, p. 184) depicted Actinopteria as a shallow endo-byssate form with about one-third of the shell buried.

The species of Actinopteria (A. decussata and A. boydi) used by Stanley are not as inflated as the Brassfield species (A. brisa), which also has a considerably larger anterior auricle. The cross-section area of A. brisa would indicate an epibyssate life habit when compared with other species of Actinopteria. However, analyzing the size of the anterior auricle, A. brisa should be more deeply infaunal.

Using Stanley's technique for A. brisa presents a confusing picture of A. brisa's life habit. It seems more like that A. brisa had a mode of life similar to modern Pteria, which is free-swinging byssate. There are many large, branching trepostome bryozoa which could have served as an attachment site for A. brisa in the Brassfield Sea. Cypricardinia and Modiolopsis probably had a similar mode of life. Stanley correlated the shape of these extinct genera with living Modiolus, and inferred that they were endobyssate of varying burrowing depth. In Stanley's view, the more equidimensional the valves, the shallower the depth. Kauffman (1969) considered these two genera as "byssate nestlers," as did Pojeta (1971, p. 33) in reporting the observed occurrence of a species of Modiolopsis nestled in the branches of a trepostome bryozoan. This probably was the Silurian mode of life for this genus also. "Cypricardinia"'s life habits are still conjectural, but because it has a shell form similar to Modiolopsis (especially with a medial [byssal?] sulcus, "Cypricardinia" may also have had a "nestler" life habit.

If these forms from the A. brisa assemblage are epifaunal as interpreted here, their feeding type would be suspension-feeding. Since they would not be imbedded in the substratum to any appreciable degree in this life position, their opportunity to ingest bottom sediment (deposit-feeding) would be nil. Documentation of suspension feeding awaits morphologic data. The presence of a pallial sinus, indicating siphons (the structures used in suspension feeding) would support the suspension feeding interpretation for these taxa. Even though Cuneamya may eventually be considered infaunal, it is probably still a suspension feeder, because of its elongate posterior region, which may house siphons. Documentation of internal features of Cuneamya is, unfortunately, lacking. Based on the life habits suggested herein, a generalized diagram of life positions for genera in each of the two assemblages of Brassfield bivalves (Text-fig. 10) can be made.

Text-fig. 10--Probable life habit reconstruction for genera of the Actinopteria brisa and Palaeoneilo fecunda faunal assemblages in the Brassfield.

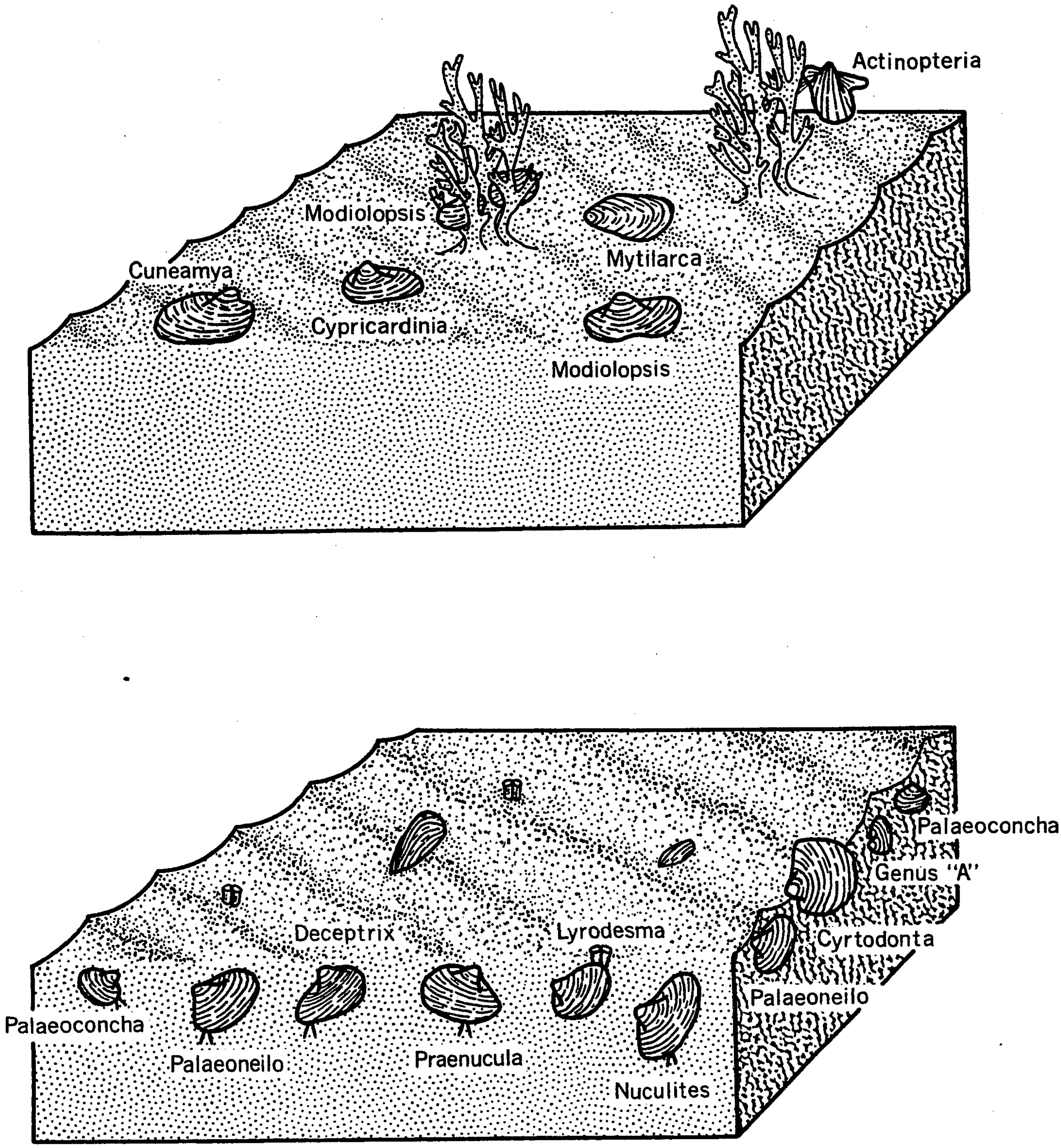
Autecology

Autecology is, in part, the study of the environmental interrelationships of each species with the chemical and physical environment in which it lived. It also includes how organisms respond to these environmental factors. Environmental factors that are critical to organismal life processes are many and varied; and some such factors are salinity, oxygen content and food supply (Snyder and Bretsky, 1971, p. 228).

Autecology usualy includes such factors of a species as growth rate, fecundity, mortality, survivorship. These factors can be deduced from size-frequency data using the technique employed by Levinton and Bambach (1970). A growth model proposed by them can be expressed by the following equation

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

where D is the size, T is time (or age) and s is a constant. Snyder and Bretsky (1971) used this equation to construct life table and survivorhip data for populations of Palaeoneilo fecunda and Nuculites neglectus in the basal Maquoketa Formation at Scales Mound and Mt. Carroll, Illinois.



Text-fig. 10--Probable life habit reconstruction for genera of the Actinopteria brisa and Palaeoneilo fecunda faunal assemblages in the Brassfield (upper and lower, respectively).

The constant *s* is determined from the equation by using the maximum size for *D*, and selecting a value for *T*. The larger the value selected for T, the smaller the resulting *s*. It is clearly important that the selection of *T* be consistent if two populations are to be compared. Snyder and Bretsky were unable to make their values for *T* (and consequently, *s*) available to the author. Following Levinton's (personal communication and Levinton and Bambach, 1970) instructions, the author could not determine a constant value for *s* in all of Snyder and Bretsky's (1971) survivorship curves. Because the author could not be sure that the survivorship curves which he could construct from data in this study would have been constructed as Snyder and Bretsky's were, they are not presented here. Rather, only the histograms (Text-fig. 11) of *P. fecunda* in the Brassfield is presented for comparison with that of Snyder and Bretsky (1971). The Brasssfield population of *Palaeoneilo fecunda* is more like the Scales Mound than the Mt. Carroll populations of Snyder and Bretsky (1971).

Text-fig. 11--Size-frequency distributions of length, height, and anterior length of *Palaeoneilo fecunda* (Hall) from the Brassfield

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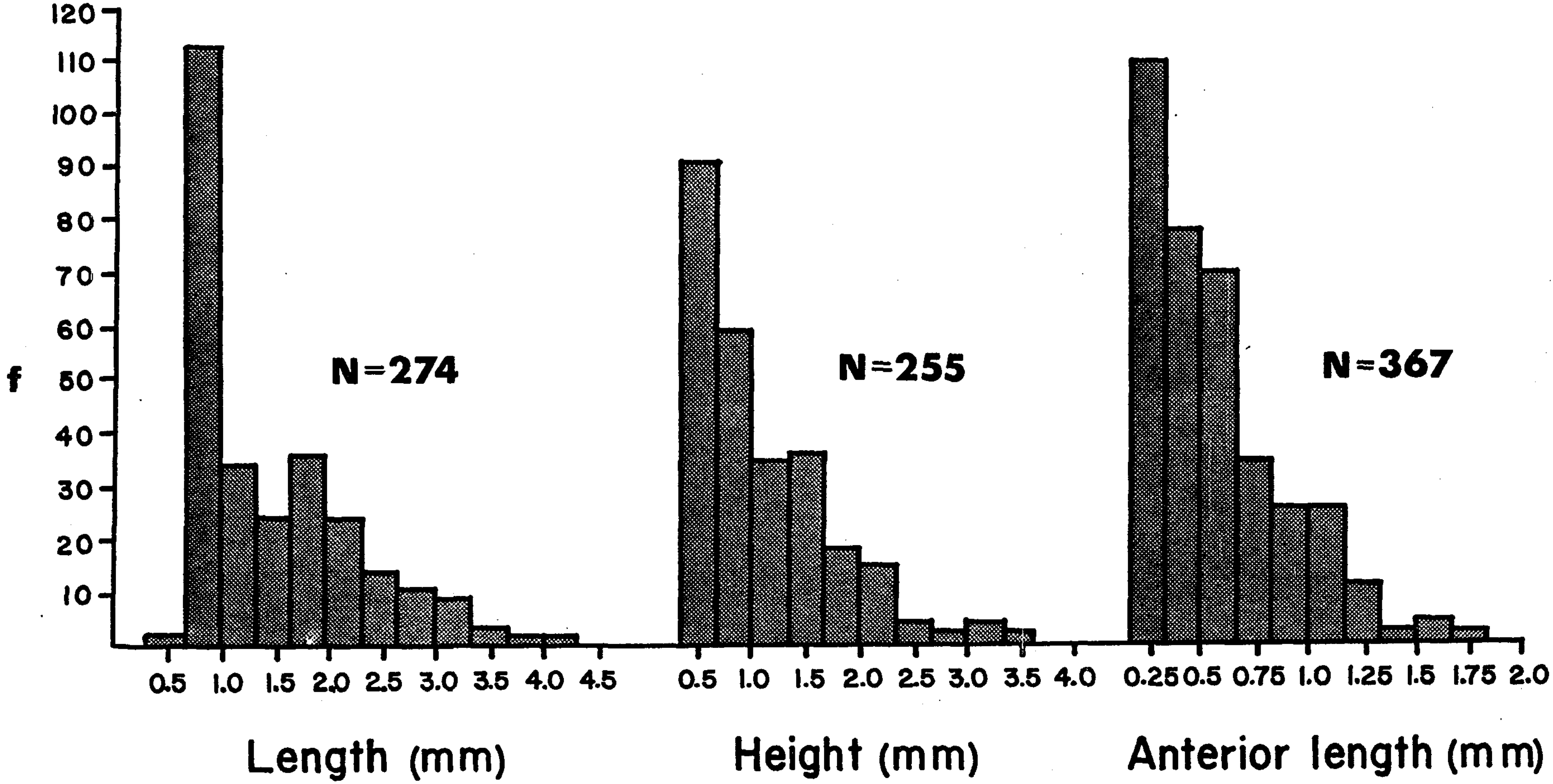
Nuculites neglectus, although the second most abundant nuculoid in the Brassfield was not generally well enough preserved to determine size-freqency data.



Text-fig. 11--Size-frequency distributions of length, height, and anterior length, of Palaeoneilo fecunda (Hall) from the Brassfield.

There is a predominance of small bivalves (especially nuculoids) in the upper thinly-bedded Brassfield in Adams County sections (localities 4, 5, and 6), as exemplified by P. fecunda (text-fig. 10), and also true of all species in the P. fecunda assemblage (described earlier). Because of the restriction of the small organisms to this part of the Brassfield, these horizons (from 28 to 36 feet above the base of the Brassfield at locality 4) are informally designated the "diminutive zone" of the Brassfield. Small-sized or "diminutive" faunas are not unique to the Brassfield. They have been described from many geographic areas and geologic ages. Branson (1930, Phosphoria Formation, Permian, Wyoming), Fisher (1951, Ludlowville Formation, Devonian, New York), Loomis (1903, "Tully limestone," Devonian, New York) and Snyder and Bretsky (1971, Basal Maquoketa Formation, Ordovician, Iowa and Illinois) are some of the authors who have described and analyzed these diminutive faunas. Numerous causes have also been suggested for the small size of these organisms (Tasch, 1953). Environmental "stunting" or "dwarfing" is often used to explain this phenomenon. Physio-chemical hardship in the environment supposedly produced this "stunting." Mechanical sorting may also produce a concentration of certain sized individuals (as suggested for the basal Maquoketa by Tasch, 1953). This process may, in part, be responsible for the size distribution of the fauna in the "diminutive" Brassfield.

Snyder and Bretsky suggested instead of harsh environments producing "stunting," that the environment may have been especially rich in organic matter, providing an excess of nutrient materials. Faunas in these environments, they suggested, might undergo selection for high fecundity, rapid maturation and subsequent high mortality of small, sexually mature (paedomorphic) individuals (Snyder and Bretsky, 1971, p. 228, as suggested for the basal Maquoketa Formation of eastern Iowa and adjacent Illinois). This high mortality provides large quantities of small individuals as potential fossils.

The size distribution of the "diminutive" Brassfield bivalve fauna (especially its dominant element _P. fecunda_) is quite similar to the basal Maquoketa fauna reported by Snyder and Bretsky (1971). The maximum size for _P. fecunda_ in the Brassfield is about 10 to 15 percent less than those in the basal Maquoketa, which may reflect current sorting of the Brassfield specimens. (Detailed comparison of the "diminutive" Brassfield and the basal Maquoketa is given below under a separate subheading.)

POST-MORTEM INFLUENCES

One of the most obvious questions to be answered about any fossil assemblage is how closely it represents a life assemblage. By studying the accumulation of organismal remains in modern assemblages, it is clear that erroneous interpretations of the relative abundances and size (ages) of the community members could be made (Johnson, 1960, Kornicker, Wise and Wise, 1963; Ager, 1963; Hallam, 1967; and Raup and Stanley, 1971). Gross misinterpretations of the living assemblages can be made if the remains are analyzed as representative of those assemblages. Kornicker, Wise and Wise (1963) showed that the percentage of various modern bivalve species in a population, and percentage of right and left valves, varied from month to month in the death accumulations from an offshore, stable community.

Biological factors such as selective mortality or predation on a certain age (size) group cause the fossil accumulation to be unrepresentative of the population as a whole. Various post-mortem effects can alter the original size and species composition of the living population. Sorting and selective destruction are two early taphonomic selective processes that alter the original population. Sorting is probably the most studied (and perhaps the most influential) process. Sorting may be either physical (mechanical) or biological. For example, organisms such as some polychaetes (sabellids) select particular sized shells or fragments to cement to their dwelling burrow. Other examples are cited by Schäfer (1972). Selective destruction by organisms (especially boring types, Ager, 1963) of a particular age group (shell size) is another example of biological sorting. No evidence was encountered in the Brassfield to suggest biologic sorting or destruction.

Mechanical sorting has commonly been cited as having occurred in ancient or modern skeletal assemblages (e.g. Boucot, 1953; Johnson, 1960). This type of sorting, produced by bottom currents in the submarine system, usually forms an assemblage with a disproportionately high number of members of one size group as compared with a living population (e.g. Brace, Boucot and Demar, 1958; Johnson, 1960; and Hallam, 1967).

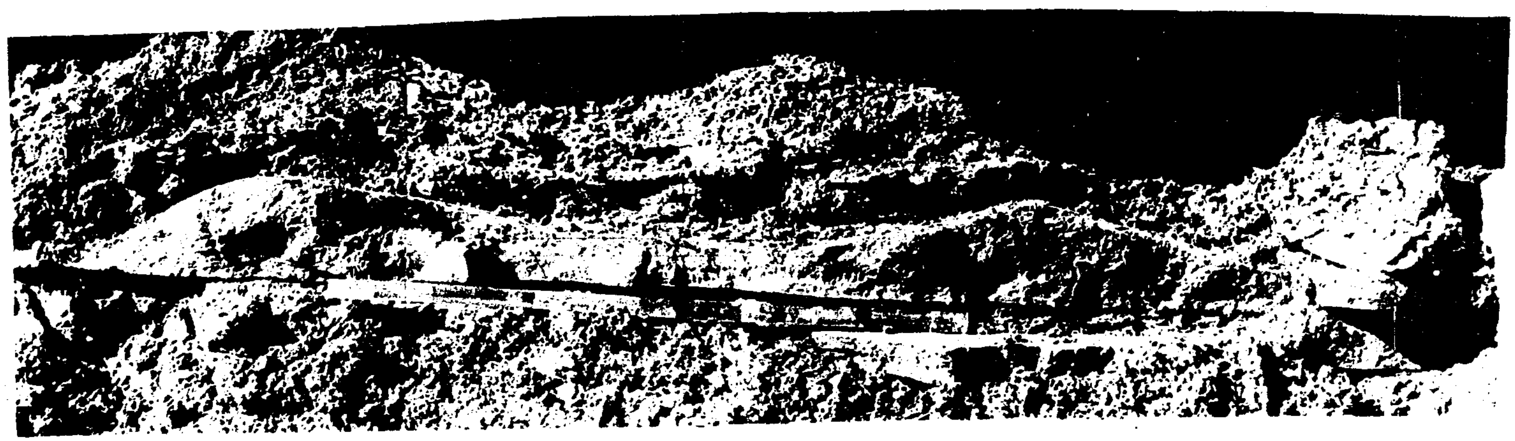
A restricted size distribution for a fossil assemblage alone may not be conclusive evidence for sorting of the population. The larger and smaller members of a species may have lived in separate habitats. The juveniles of *Callianassa major* Say live in an environment separate from the adults of the same species (W. A. Pryor, personal communication). In the estuaries and lagoons near Beaufort, North Carolina, small (approximately 1cm in length) individuals of *Aequipecten irradians* Say live attached to wharf pilings and other substrata, whereas the larger individuals (usually averaging 4 to 5cm in length) live in the more saline subtidal sand flats in the lagoons (personal observation, 1971).

Corroborating sedimentological evidence is essential to any affirmative statement about mechanical sorting of an assemblage. Primary sedimentary structures such as ripple marks, scour and fill features, cross-bedding and narrow grain size distribution could indicate the presence of a current with the potential of sorting the skeletal material of the fossil assemblage.

Segregation according to size is not the only way in which a population or community may be sorted. In organisms with skeletons of two or more articulating parts (*e.g.*, vertebrates, Amphineura, echinoderms, brachiopods, or pelecypods), the parts may become separated during current-induced movement along the bottom, with concomitant size, shape and gravity segregation. There are several reports of assemblages of pelecypods and brachiopods that have been selectively sorted to produce a dominance of one valve (*e.g.* Lever, 1958; Martin-Kaye, 1951; Kornicker, Wise and Wise, 1963). The general conclusion from an assemblage of this type is that sorting has acted to selectively concentrate one valve of these bivalve forms, over their living condition of exactly equal numbers of each valve. Boucot, Brace and Demar(1958) have made several stream-table and flume studies pertinent to this segregation. Several horizons (at sections 4 and 5 in the "diminutive" Brassfield) form which bivalves were recovered show sedimentological evidence of current activity and presumably concomitant sorting of fossil specimens. Rippled beds occur in this sequence (Text-fig. 12).

Text-fig. 12--Rippled limestone bed in section shown in Text-fig. 7.

However, the pelecypods of these layers (members of the *Palaeoneilo fecunda* assemblage) are apparently not sorted



Text-fig. 12--Rippled limestone bed in section shown in Text-fig. 7. This horizon is 36 feet above the base of the Brassfield. A limonite layer (WU-14) is draped above this layer. The wavelngth of this ripple is 42 inches. Thickness at the crest is 6 inches, and at the trough, 3 inches.

as to right and left valves (Table 2), which was not expected, given current movement of the sediment. Data for sample WU-14 for example, shows nearly equal numbers of left and right valves of Palaeoneilo fecunda. There were 323 left valves, 345 right valves and 57 articulated specimens of this species recovered from this sample. In the same sample, there were 65 left, 72 right, and 9 articulated valves of Lyrodesma sp.

Although this assemblage of the Brassfield pelecypod fauna does not appear to be sorted on the basis of right/left valve abundance, the size distribution seems quite narrow

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Table 2. Valve Counts from the Palaeoneilo fecunda assemblage in the Brassfield Formation.

(0.3mm to 6.5mm in length) with over half of the specimens in some species less than 1.5mm in length. This size distribution could be interpreted as a reflection of mechanical sorting which has selectively concentrated the smaller shells. This would seem somewhat peculiar in terms of current sorting processes which usually concentrate larger particles and winnow away those smaller sizes. It sees significant in this connection that there are broken fragments of larger shells of this size range in the assemblage. The selective breakage of larger shells may have produced this relative abundance of small individuals.

Table 2. Valve counts from the Palaeoneilo fecunda assemblage in the Brassfield Formation

Species(sample number)	Right	Left	Articulated
Deceptrix scofieldi (WU-11)	0	1	2
D. scofieldi (WU-14)	3	6	12
D. scofieldi (WU-101-20)	3	8	22
D. scofieldi (WU-1)	3	4	9
Palaeoneilo fecunda (WU-14)	345	323	57
P. fecunda (WU-1)	191	213	18
P. fecunda (WU-11)	117	102	3
P. fecunda (WU-101-20)	1	2	31
Nuculites neglectus (WU-1)	15	18	--
N. neglectus (WU-14)	25	22	--
Lyrodesma sp. (WU-14)	72	65	9
L. sp. (WU-1)	36	24	7
L. sp. (WU-11)	23	18	2
L. sp. (WU-101-20)	--	--	5
Palaeoconcha ohioensis (WU-1)	4	3	11
P. ohioensis (WU-14)	8	10	2
P. ohioensis (WU-11)	2	1	--
Praenucula albertina (WU-1)	11	11	--
P. albertina (WU-14)	1	3	--
P. albertina (WU-11)	6	5	--
P. albertina (WU-101-20)	--	--	7
Genus "A: foerstei (WU-1)	2	2	--
C. longa (WU-14)	11	8	--
C. longa (WU-11)	1	1	--

Nuculites neglectus, which apparently has a thinner, less durable shell than Palaeoneilo fecunda, is commonly found as broken fragments, while P. fecunda is commonly found as intact valves. Broken valves of various sizes are found for all species, but it appears that the larger valves may have suffered most. This breakage probably occurred during transport, but some may have occurred during sample processing. A few posterior hinge plates of P. fecunda have been recovered that are 5.5mm in length. These specimens, when whole, would have measured 8 to 9mm in length. Although larger than any whole specimens from the Brassfield, this size shell is well within the size range of the basal Maquoketa "depauperate" population of this species (Snyder and Bretsky, 1971).

Some workers might also argue that a disparity in the ratio of left to right valves would be present if current sorting had occurred. However, Kornicker, Wise and Wise (1963, p. 706) showed that significant current transport did not always produce a great disparity of valve ratios in the resultant deposit, In fact, a right-left valve disparity might be expected only if there were marked disparity in the valve morpholoy, which in the genera here involved does not exist. Other factors such as the intensity of the current and whether it was unidirectional or oscillatory may also play a role in valve separation and dispersion.

The occurrence of the majority of bivalves in this part of the Brassfield is restricted to rippled and cross-bedded layers of biogenic limestone. It may not be entirely safe to conclude that the small, restricted size distribution of the "diminutive" Brassfield fauna is wholly due to current sorting. Snyder and Bretsky (1971) have described a fauna from the basal Maquoketa "depauperate" zone, that is very similar, both in size distribution and taxonomic composition to this one from the "diminutive" Brassfield. Their explanation of the fauna's small and restricted size merits consideration and may logically apply here, because of the taxonomic similarity of the Brassfield "diminutive" fauna to theirs.

They found very limited physical evidence of bottom current movement and concluded that the assemblage underwent little or no post-mortem transport and sorting (Supporting this interpretaition is the fact that most bivalve individiuals are articulated.) The common explanation of this small-sized assemblage would then involve environmental "stunting" or "dwarfing" (e.g. Ladd, 1929).

Snyder and Bretsky (1971, p. 244) suggested that the small size of this assemblage may be genetically controlled rather than an environmentally controlled phenotypic variation (i.e. "stunting"). They hypothesized that environmental conditions such as a thixotropic, unstable substratum produced high juvenile mortality rates, so that early maturation and high fecundity would be selected for. "Those few, most successful species would flourish at the expense of all the others, dominate the environment, and drastically lower the faunal diverstiy" (Snyder and Bretsky, p. 246). They, then, believed that in the basal Maquoketa natural selection for paedomorphic (sexually mature small-sized "juveniles") individuals had occurred, producing the great quantities of small shells.

The small size of the bivalves in the "diminutive" Brassfield assemblage may also in part be a result of this paedomorphic process. Although the diminutive Brassfield bivalves are obviously sorted, it may be that only the larger members of the "living association" have been removed. Comparison of size-frequency data for Palaeoneilo fecunda (Hall) shows a similar distribution of individuals in the "diminutive" Brassfield (Text-fig. 11) and the basal Maquoketa (Snyder and Bretsky, 1971, text-fig. 4, 5). There are, however, more larger individuals in the basal Maquoketa assemblages.

Comparison of the "diminutive" Brassfield with the basal Maquoketa is based on several factors other than size of the individuals. Several of the bivalve species from the "diminutive" Brassfield (the Palaeoneilo fecunda assemblage) are also found in the basal Maquoketa Formation. Palaeoneilo fecunda (Hall) is the dominant bivalve in the basal Maquoketa; Nuculites neglectus Hall is second greatest in abundance in the Basal Maquoketa. Palaeoneilo fecunda is also the dominant bivalve in the "diminutive" Brassfield, where N. neglectus is again second in abundance in the "diminutive" Brassfield, but relatively less so than in the basal Maquoketa (perhaps because of selective destruction in the higher energy taphocoenose of the Brassfield). Praenucula albertina (Ulrich) occurs in both assemblages but is a relatively minor constituent (1-5 percent).

Other molluscan fauna, associated with the bivalves, in the "diminutive" Brassfield are similar to those in the basal Maquoketa. Several species of archeogastropods, including Liospira micula (Hall) and "Cyclora" depauperata (Hall) and a supposed scaphopod Plagioglypta iowensis (James) occur both in the basal Maquoketa and in the "diminutive" Brassfield zone (L. Harrison, personal communication). A Brassfield hyolithid, Elegantilites? sp. is very similar to "Hyolithes" parviusculus (Hall) from the basal Maquoketa.

Species of mollusks described from the basal Maquoketa and those found in the "diminutive" Brassfield (this study and L. Harrison, personal communication) are listed in Table 3. Those marked with an asterisk are dominant

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Table 3. Basal Maquoketa and diminutive Brassfield Molluscan species

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faunal elements.

The similarity of size-frequency data for P. fecunda, and the overall small size of the two faunal assemblages,

Table 3. Basal Maquoketa and diminutive Brassfield

Molluscan species

Taxa	Maquoketa: Ojakangas (1959)	Maquoketa: Ladd (1929)	Maquoketa: Johnson (1939)	Maquoketa: Snyder and Bretsky (1971)	Brassfield (this study)
"*Ctenodonta*" *pulchella* Ulrich				X	
Deceptrix scofieldi (Ulrich)					X
**Nuculites neglectus* (Hall)	X	X	X	X	X
Lyrodesma sp.					X
Orthdesma approximatum Foerste	X				
Orthodesma triangulata (manuscript type)	X				
"*Palaeoconcha?*" *hamburgensis* (Walcott)				X	
Palaeoconcha obliqua (Hall)	X	X	X	X	
Palaeoconcha ohioensis (Bassler)					X
**Palaeoneilo fecunda* (Hall)	X	X	X	X	X
Praenucula albertina (Ulrich)				X	X
Praenucula sp.				X	
Genus A aff. "*Ctenodonta*" *longa* (Ulrich)					X
Michelinoceras sociale (Hall)	X	X	X		
Orthoconic cephalopod					X
*"*Plagioglypta*" *iowaensis* (James)	X	X	X		X
"*Bellerophon*" *lirata* Hall		X	X		
"*Bellerophon*" *patersoni* Hall		X	X		
Bucanella (*Plectonotus*) *conradi* Hall		X	X		
Bucanella (*Plectonotus*) sp.					X
Bucania? sp.					X
Cyclonema (*Cyclonema*) *humorosum* Ulrich			X		

Cyclonema (Cyclonema) bilex Conrad			X		
Cyclonema (Dyeria?) sp.					X
"Cyclora" depauperata (Hall)		X	X		X
"Cyclora" minuta Hall	X				
"Cyclora" sp.		X			
"Cyclora" cf. "C." pulchella Miller					X
Cyrtolites carinatus Miller	X				
Cyrtolites retrorsus var. fillmorensis Ulrich and Scofield	X				
Holopea symmetrica Hall	X				
Holopea? sp.					X
Holopea cf. H. symmetrica Hall					X
*Liospira micula (Hall)	X	X	X		X
Loxoplocus (Donaldiella) sp.					X
Loxoplocus (Lophospira) milleri	X				
Loxoplocus (Lophospira) tropidophora Meek	X				
Loxoplocus (Lophospira) sp.	X				
Loxoplocus (Lophospira?) sp.					X
Murchisonia (Hormotoma) trentonensis Ulrich and Scofield	X				
Murchisonia (Hormotoma) sp.?			X		
Murchisonia (Hormotoma) sp.		X			
Murchisonia (Murchisonia) sp.					X
Raphistomina rugata Ulrich and Scofield	X				
Tropidodiscus subacutus Ulrich	X				
Tropidodiscus sp.					X
Elegantilites? sp.					X
"Hyolithes" parviusculus (Hall)	X	X	X		

the taxonomic similarity (Table 4) and the presence of the

Table 4. Brassfield and Maquoketa environmental equivalents

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same dominant faunal elements suggest that the fauna of the basal Maquoketa beds of Iowa, Illinois and Missouri is very similar to that of the "diminutive" Brassfield fauna in Adams County, Ohio.

The "diminutive" Brassfield might be described as a "recurrent" assemblage in the sense of Raup and Stanley (1971, p. 229). However, this fauna is only "recurrent" in a stratigraphic sense; it is really a reflection of similar facies which occur in both areas. The facies occurs in the Upper Ordovician basal Maquoketa in Iowa, Illinois and Missouri and apparently migrated eastward, where it is found in the "diminutive" Brassfield in Adams County, Ohio. Some evolution of the fauna occurred during this interval, but the dominant mollusk elements survived relatively unchanged. Other analyses of this sort of facies phenomenon may be found in Williams (1914), Caster (1934, 1938) and Kohut (1960).

The lithologies of the basal Maquoketa and the "diminutive" Brassfield are not so strikingly similar. It should be emphasized, however, that the "diminutive" Brassfield fauna may not now be found in the lithology representative of its living environment. The basal Maquoketa has probably been somewhat altered in lithology from when the fauna

Table 4. Brassfield and Maquoketa environmental equivalents

Major Taxon	Maquoketa/Brassfield
"Scaphopoda"	"Plagioglypta" iowaensis/"P." iowaensis
Cephalopoda	Michelinoceras sociale/
Nuculoid-Bivalvia	Nuculites neglectus/N. neglectus
	Paleoconcha/Paleoconcha
	Palaeoneilo fecunda/P. fecunda
	Praenucula albertina/P. albertina
Archeogastropoda	Bellerophon/Bucania?
	Bucanella (Plectonotus)/B. (Plectonotus)
	Cyclonema (Cyclonema)/C. (Dyeria?)
	"Cyclora" depauperata/ "C." depauperata
	Cyrtolites/Cyrtolites
	Holopea/Holopea
	Liospira micula/L. micula
	Murchisonia (Murchisonia)/M. (Murchisonia)
	Tropidodiscus/Tropidodiscus
Hyolithida	"Hyolithes" parviusculus/Elegantilites? sp.

occupied that environment. Penecontemporaneous[?] dolomitization (Snyder and Bretsky, 1971) of the basal Maquoketa may have accentuated these differences. The original basal Maquoketa environment may have contained silty and clayey sediments rich in organic matter. Interbedded with the bioclastic limestones in the diminutive Brassfield are shale and claystone units (Text-fig. 12) that could represent sediments from the living environment of the bivalves and other mollusks. Since much of this fauna is inferred to have lived at the sediment interface or only a few millimeters below it, they could easily have been eroded by currents and incorporated into the bioclastic sands that compose the rippled limestones.

Only the conodonts (usually considered excellent biostratigraphic indicators) in these two formations are distinctly different and provide a partial key to the different chronologic ages of the basal Maquoketa and "diminutive" Brassfield. The basal Maquoketa contains characteristically Ordovician conodonts (Glenister, 1957), while this assemblage in the Brassfield contains Lower Silurian forms such as Icriodina irregularis (Rexroad, 1967).

Bivalves, other than those in the "Paleoneilo fecunda assemblage" are in such low abundance that inferences about their post-mortem history is unsafe. It should be noted, however, that all of the 50 specimens of Actinopteria brisa were left valves. This distribution might imply selective separation of the two valves; however, examination of specimens of other species of *Actinopteria* indicates that the right valve is much thinner and flatter than the left and is probably more susceptible to selective destruction *in situ*, and quite likely responded quite differently hydrodynamically.

CONCLUSIONS

The pelecypod taxa occurring in the Brassfield Formation of Ohio, Indiana and Kentucky have been revised to reflect current taxonomic concepts. The following additional information has been gathered pertaining to this fauna:

1) The local abundance, with limited regional distribution of this Early Silurian fauna, as compared with the more widespread, abundant occurrence of pelecypods in the underlying Upper Ordovician has direct implication on the phylogeny and evolution of bivalves in the Cincinnati Arch area.

Bivalve fossils were found in locally abundant assemblages in several places in Ohio, including localities in the Dayton area and in Adams County, but none were found in the Indiana and Kentucky exposures. The great variety of taxa, including numerous genera of ambonychiids, cyrtodontids, and modiolopsids known in the underlying Ordovician strata is much reduced in the Brassfield. Only one genus each of those above listed groups is found in the Brassfield.

Nuculoids, however, at least on a geographically restricted scale, are abundant. This restricted geographic and taxonomic distribution of pelecypods in the Silurian Brassfield, as compared with the underlying Ordovician, suggests a marked unsuitability of the Brassfield environment for the bivalves (except perhaps nuculoids). In the Cincinnati Arch region, then, the end of the Ordovician marks a change in environmental conditions that extinguished or forced immigration of a taxonomically diverse, regionally extensive bivalve fauna and encouraged its replacement in the Silurian by a taxonomically meager and extremely localized fauna.

2) Several taxa previously unknown in the Silurian are described herein. These forms, mostly nuculoids, are conspecific with nuculoids from the Upper Ordovician "Depauperate Zone" of the basal Maquoketa Formation (Snyder and Bretsky, 1971). These taxa are: Palaeoneilo fecunda (Hall), Nuculites neglectus Hall, Praenucula albertina (Ulrich), Deceptrix scofieldi (Ulrich), Palaeoconcha ohioensis (Clarke and Ruedemann). This study represents the first documented occurrence of Lyrodesma, Palaeoconcha and Praenucula in rocks other than Ordovician in age.

3) The distribution of pelecypods in the Brassfield is in two distinct faunal associations. These are the "Palaeoneilo fecunda assemblage" in which all species are infaunal, and the "Actinopteria brisa assemblage" where all species are probably epifaunal.

The "Palaeoneilo fecunda assemblage" appears to be a stratigraphically recurrent assemblage of the "Depauperate Zone" of the basal Maquoketa Formation in the Upper Ordovician. Other elements of the Brassfield fauna of this community (e.g. gastropods, cephalopods, "scaphopods" and hyolithids) are also very similar to the "Depauperate Zone," reinforcing this interpretation. The "Actinopteria brisa assemblage" is taxonomically similar to the younger Silurian or Devonian faunas, but cannot be correlated with any assemblage based on present data.

SYSTEMATIC PALEONTOLOGY

Subclass PALAEOTAXODONTA Korobkov

Order NUCULOIDA Dall

Description

Bivalves of this order possess taxodont dentition often distinguishable as to posterior and anterior series. They are commonly small compared with other bivalves. Muscle scars left on the shell consist of nearly equal sized (isomyarian) adductors and often several pairs of pedal muscle scars in the dorsal region of the shell. The shell microstructure may be either nacreous or cross-lamellar. Living representatives show protobranchiate gill development.

Superfamily NUCULACEA Gray

Description

All forms included herein are nuculoids that are truncate posteriorly and elongate anteriorly. A pallial sinus does not occur. The positioning of the ligament (internal or external) has historically been the basis for familial discrimination.

Family PRAENUCULIDAE McAlester

Description

Genera included in this family are nuculacean bivalves with an external ligament positioned posterior to the beak. The umbones curve toward the elongate anterior region of the shell (prosogyrous). The surface prosopon consists exclusively of comarginal growth varices.

Genus *Deceptrix* Fuchs, 1919

1852 *non* *Ctenodonta* Salter, p. 64

1894 *Ctenodonta* Salter, Ulrich, p. 578 (*partim*: most of the species of the *Ctenodonta* *levata* group)

1919 *Deceptrix* Fuchs, p. 79

1934 *Praeleda* Pfab, p. 231

1968 *Deceptrix* Fuchs, McAlester, p. 25

1969 *Deceptrix* Fuchs, McAlester, p. 229

1970 *Praeleda* Pfab, Bradshaw, p. 636

1971 *Deceptrix* Fuchs, Pojeta, p. 16 (*partim*)

Type Species

Deceptrix *carinata* Fuchs (1919) is the type species by monotypy. The lectotype was designated by Dahmer (1951, p. 67) as the right valve illustrated by Fuchs on his Plate 7, figure 2. The lectotype and three paralectotypes are well illustrated by McAlester (1968, Plate 6, figures 1-10). The type suite is from the Lower Devonian of Germany.

Diagnosis

Anteriorly elongate praenuculid bivalves with dental series differentiated into a few large anterior teeth and numerous smaller posterior teeth.

Description

These are medium sized (adults generally 10-20mm in length), equivalved, subcircular to subquadrate, anteriorly elongate and posteriorly truncate, prosogyrous bivalves with numerous taxodont teeth which are commonly differentiated into an anterior and posterior series. The hinge plate is slightly arched with the anterior dental series containing fewer and substantially larger teeth than the posterior series. The number of teeth in each series is variable with ontogenetic age and from species to species, but there are commonly 3 to 10 anterior teeth and perhaps twice that many posterior ones. The teeth are commonly chevron-shaped, but may be long, straight or undulose in some species (Bradshaw, 1970, p. 232 and Babin, 1966, p. 47). Rounded adductor scars are moderately impressed into the shell, with scars of well-developed pedal muscles dorsal to the adductors. Anterior pedal protractor and retractor muscle scars are usually confluent with the adductors, but posterior pedal retractor muscle scars may be free or partially fused to the adductors. The pallial line is entire and nonsinuate. Numerous, small magnitude, comarginal growth varices mark the external shell surface.

The ligament is external as shown by Pojeta (1971, Pl. 5, fig. 9, 17, 20) and by the continuance of dentition beneath the beaks, which precludes the presence of a resilifer.

Discussion

Most early Paleozoic nuculoid bivalves from North America have been referred to the genus *Ctenodonta* Salter (1852). *Ctenodonta*, however, as represented by *C. nasuta*, its type species from the Upper Black Riverian (Middle Ordovician) of Ontario, Canada, establishes much more restrictive features for the genus than traditional assignments. Use of the name *Ctenodonta* should be restricted to bivalves with the general morphology of _C. nasuta_ as indicated by McAlester (1968, 1969), Bradshaw (1970) and Pojeta (1971).

Ulrich (1894) recognized that usage of this genus was as a kind of "_omnium gatherum_" for a heterogeneous group of species. Although hesitant to erect new genera, which he seems to have felt were someday required, he did divide the species assignable to "_Ctenodonta_" into six groups. (For further discussion see section entitled "Classification.") Ulrich's _Ctenodonta levata_ group (1894, p. 581) was composed of nuculoids that were predominantly posteriorly truncate and anteriorly elongate. Some of the species described by Ulrich that are assignable to this form group are "_Ctenodonta_" _socialis_, "_C._" _nitida_, "_C._" _medialis_, "_C._" _scofieldi_ and "_C._" _albertina_ (all authored by Ulrich). At least three generic names have been proposed for these early Paleozoic nuculoids: _e.g._, _Deceptrix_ Fuchs (1919), _Praeleda_ Pfab (1934) and _Praenucula_ Pfab (1934). _Deceptrix_ is more or less equilateral than _Praeleda_ which is elongated antero-posteriorly (Bradshaw, 1970). The dentitions of these two genera are similar, and they are considered synonymous by some authors (McAlester, 1969, and Pojeta, 1971). _Praenucula_ and _Praeleda_ are similar in elongate shell outline and may be satisfactorily separated only by differences in dental arrangement (McAlester, 1969). _Praeleda_ and _Deceptrix_ each have an anterior dental series with relatively few and rather large chevron-shaped teeth and a posterior series with more and smaller chevron or straight teeth. In _Praenucula_ the teeth are of similar size throughout and are equal in number anterior and posterior. Pojeta (1971) pointed out the essential intergradation of shell shape in these three "genera." Text-figure 13 illustrates the outline of some Ordovician and Silurian species of the "Ctenodonta levata group" and demonstrates the likelihood of a gradational series of "species" which are based on shell outline alone. On the basis of dentition,

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Text-fig. 13--Valve outlines of several Ordovician and Silurian species of the Deceptrix-Praeleda-Praenucula form group (not to scale)

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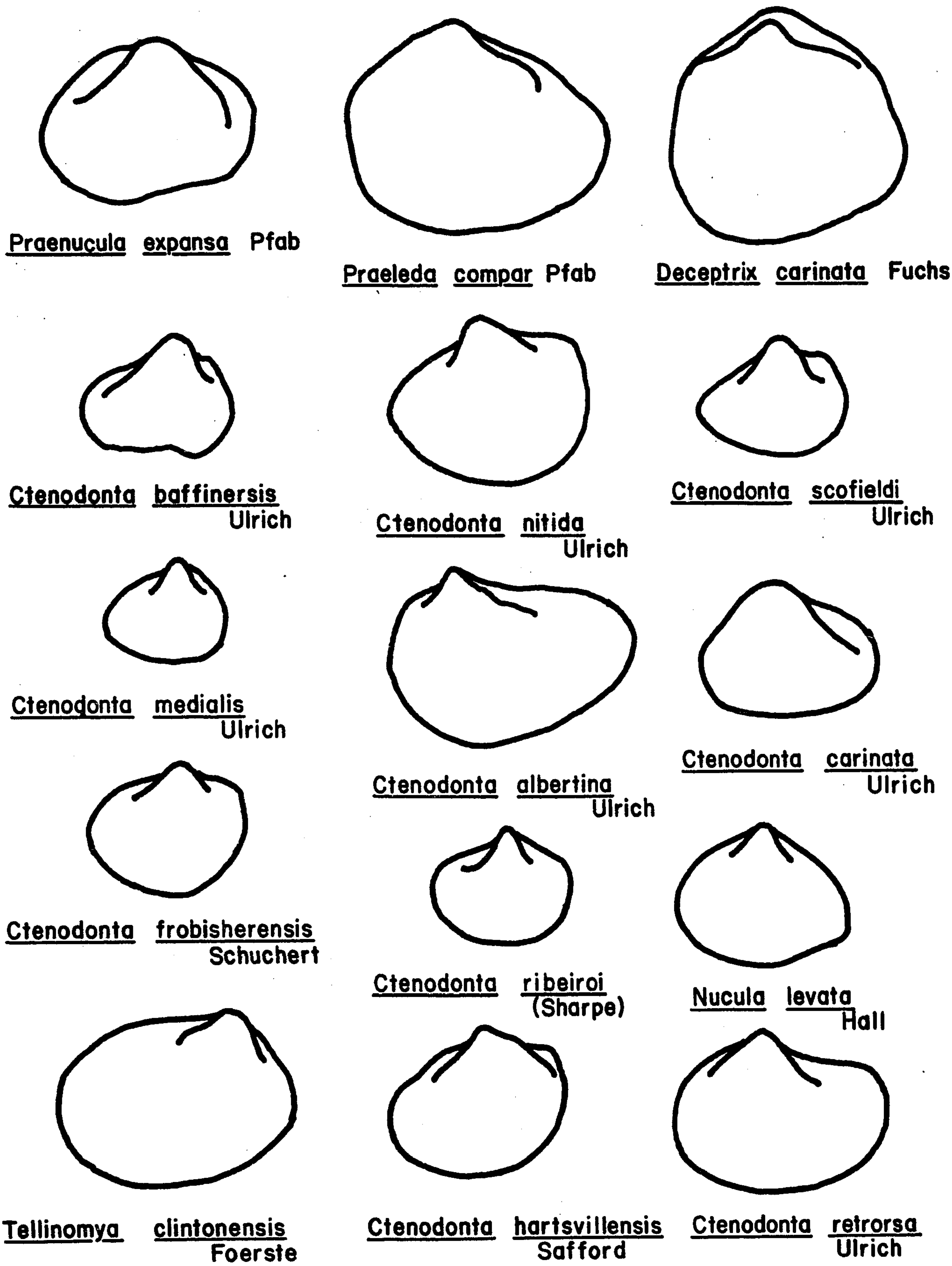
however, some of these "species" can be referred to Praenucula, while others must be considered of the Praeleda-Deceptrix type. The two types of dentition do not intergrade and are the valid taxobasis. Shell shapes are apparently homeomorphic.

A few specimens with the Praenucula dental type were encountered in this study, and further analysis of these forms may be found in the discussion of Praenucula. There are numerous specimens from the Brassfield Formation with Deceptrix-Praeleda dentition. Deceptrix Fuchs (1919) has priority over Praeleda Pfab (1934).

Distribution

The assignment of species to Deceptrix is based on the arrangement of dentition (large, few anterior and many smaller posterior teeth). Because dentition is not commonly



Text-fig. 13--Valve outlines of several Ordovician and Silurian species of the Deceptrix-Praeleda-Praenucula form group (not to scale) preserved, only a few species of the Deceptrix-Praenucula shape group can be definitely assigned to either genus. The majority of species assignable to the Deceptrix-Praenucula shape group have been described from the Ordovician of North America (Ulrich, 1894, 1895; Stewart, 1920; Pojeta, 1971). Several species have also been described from Ordovician through Devonian in northern France (Babin, 1966).

Deceptrix scofieldi (Ulrich)

Pl. 1, fig. 1-17

1894 Ctenodonta scofieldi Ulrich, p. 593, Pl. 42, fig. 53-58.

1895 [?] Ctenodonta perminuta Ulrich, p. 680, Pl. 46, fig. 11-14.

Type Specimen

This species is represented by two vials of syntype specimens deposited in the National Museum of Natural History (USNM 46150-46151). No lectotype has yet been designated; however, designation for all Ordovician species without holotypes is forthcoming in a monograph on Ordovician pelecypods by John Pojeta (manuscript in preparation). One syntype is figured herein (Pl. 1, fig. 1-2). The type material of "C." scofieldi was collected from the "Trenton shales" (Middle Ordovician) near Cannon Falls, Minnesota. "Ctenodonta" perminuta (USNM 46145) was collected from Upper Ordovician rocks in the Cincinnati, Ohio region.

Diagnosis

Deceptrix with a large, high beak and an attenuated anterior region which comprises two-thirds of the total length.

Description

Specimens assignable here are small to average size for the genus (adults range from 5 to 10mm in length) equivalved and markedly inequilateral. The shell outline is suboval to subquadrate with a prominent, high and erect prosogyrous beak situated in the posterior third of the shell (Pl. 1, fig. 1, 5, 13). The anterior region of the shell is elongate and attenuated at the anterior margin.

The anterior teeth are larger and fewer than the posterior. Generally, there are three to five anterior teeth although there may be twice that many posterior teeth (Pl. 1, fig. 6, 15). Although the dentition is continuous beneath the beak on a gently arching hinge plate, there is little difficulty distinguishing the anterior from the posterior dental series: in addition to number and size of the teeth, the anterior series occurs in front of the beak on the elongate portion of the shell.

The adductor muscles left impressed, oval scars on the shell near the anterior and posterior margins slightly above the shell mid-height (Pl. 1, fig. 1) Several pairs of accessory muscle scars occur near the hinge in the dorsal part of the shell. Although smaller than the adductors, the pedal muscles are prominent and well impressed. The anterior protractor and retractor scars are confluent and merge with the dorsal portion of the adductor near the hinge line. The anterior protractor muscle leaves a slightly larger scar that is nearer the adductor than the retractor scar (Pl. 1, fig. 12, 14). Posteriorly, only a retractor muscle scar is present. It is slightly larger than the anterior one. Circular to suboval in outline, the posterior retractor scar is near the hinge line, dorsal to, but distinctly separated from the posterior adductor scar (Pl. 1, fig. 16). Another set of two or three accessory muscle scars occurs in the umbonal region of the shell, on the underside of each beak; they cannot be certainly ascribed to muscles of any particular function, but are probably homologous with those called "dorso-median" and "ventro-median" by Heath (1937, p. 14) and Driscoll (1964, p. 62) (Pl. 1, fig. 15). The most probable function of the muscles is either attachment of dorsal viscera to the shell or of an accessary pedal mechanism. Heath (1937, p. 14) indicates that fibers of these muscles, in Recent protobranchs, extend into both the visceral mass and the foot.

The pallial line is rarely observable in specimens of this species, but it appears to be entire and integripalliate (non-sinuate).

Since specimens of this species are usually preserved as Steinkerns, there generally is little evidence of a ligament. In some specimens, however, the ligament appears to have occupied a slit beneath and slightly posterior to the beak. Whatever its placement, the ligament must certainly have been external, as the dentition and hinge plate are continuous beneath the beak, precluding the presence of a resilifer.

The mode of preservation generally limits knowledge not only of the ligament structure but also of external surface features. The prosopon is, however, preserved on some of the specimens from the Brassfield Formation. It consists of uniformly spaced, very fine varices of growth (Pl. 1, fig. 17).

Discussion

Deceptrix scofieldi is distinct, especially in the Brassfield association, because of its high beak and long anterior region. These and other traits, which appear to be diagnostic for large (presumably adult) specimens assigned here, appear to change substantially during ontogeny. What are assessed to be juveniles and adults from the Brassfield Formation are dissimilar in morphology, but a relatively continuous range of constantly varying morphologies from small (0.60mm) to medium (4.5mm in length) specimens supports placing them in an ontogenetic series of this species. Morphology of the various sized individuals is discussed below in the section on ontogeny.

Deceptrix perminuta (Ulrich) originally described from Upper Ordovician strata in the Cincinnati, Ohio area, is thought to be conspecific with *D. scofieldi* because several small specimens which occur in the Brassfield and seem to belong to the *D. scofieldi* ontogenetic series, are virtually identical with syntypes of *D. perminuta* (Pl. 1, fig. 3, 4)

Ulrich felt that Ctenodonta scofieldi was most closely related to Ctenodonta medialis which can also be assigned to Deceptrix. D. medialis is at present differentiable from D. scofieldi principally in the shorter, truncate anterior region of D. medialis, giving it a much more equilateral shell outline. The D. medialis beak is more central to the dorsal area and is seemingly not as prominent as in D. scofieldi. The anterior-dorsal slope is less convex upward in D. scofieldi than in D. medialis.

Ontogeny

In the samples collected for this study, D. scofieldi occurs in variable abundances but usually comprises less than 10 percent of the bivalves recovered (Table 2). For example, one sample (WU-14) contained 21 specimens of D. scofieldi of the total 982 bivalves. Another sample (WU-101-20) contained 33 D. scofieldi of 79 total bivalves. Table 2 presents data on abundances of D. scofieldi in two other samples. Seventy-three specimens of D. scofieldi were collected in this study; of these, only 41 were complete enough to measure some size parameters (these data are presented in Text-figs.14, 15, 16). It should be remembered that these data are from samples from four separate horizons and it is hazardous to unconditionally draw conclusions about ontogeny from several samples (populations?). The specimens from these samples are so similar that it seems reasonable to discuss them as a morphologic continuum (bearing in mind their heterogenous, but superjacent horizons).

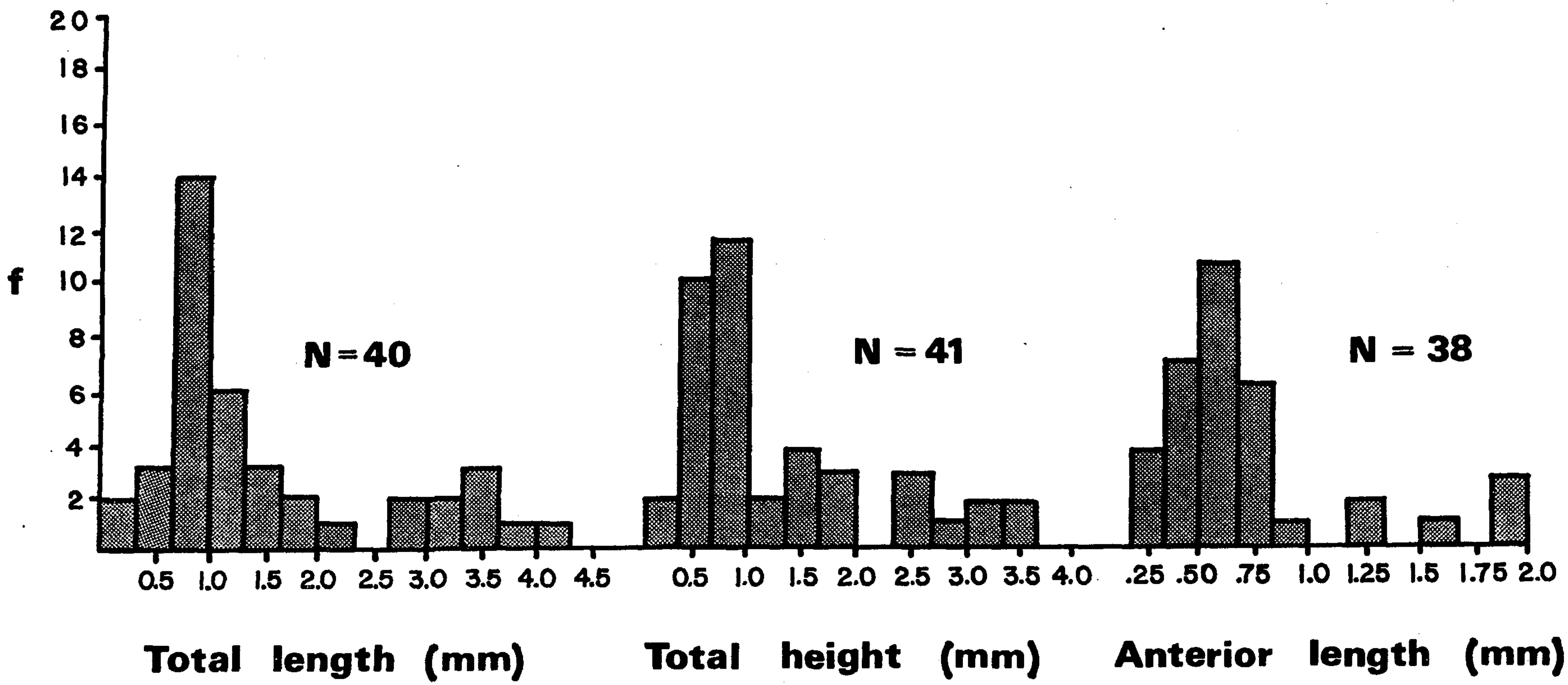
Text-fig. 14--Size-frequency distribution of length, height, and anterior length of Deceptrix scofieldi (Ulrich) from samples WU-14 and WU-101-20.

Text-fig. 15--Length to height plot for Deceptrix scofieldi (Ulrich) populations at West Union, Ohio (combined data from WU-14 and WU-101-20).

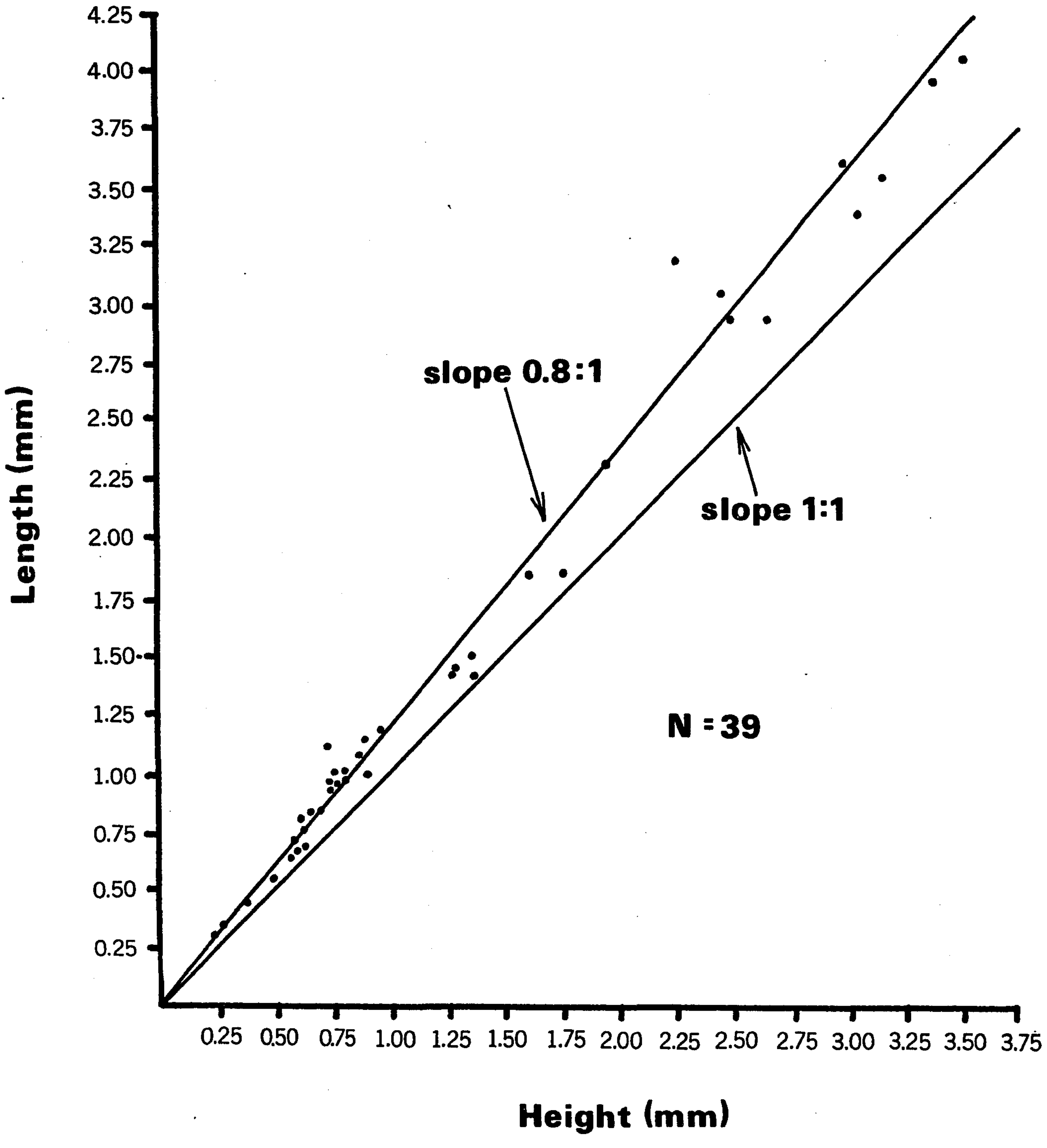
Text-fig. 16-- Anterior to posterior length plot for Deceptrix scofieldi (Ulrich) populations from West Union, Ohio (WU-14 and WU-101-20).

Text-figures 15 and 16 show the change in various shell parameters with increasing size. There seems to be little change in length to height ratios. All individuals plot very close to a straight line, with the length slightly greater than height. The data imply growth of length and height at the same rate. A plot of anterior/posterior length (Text-fig. 16) yields a more diverse pattern, and it can be concluded only that there is considerable diversity in the growth rate of the longer anterior region compared to the posterior. This species, as several others in the WU-1, 11, 14, and 101-20 samples, is represented by a large relative abundance of small specimens (42% being less than 1.00mm in length).

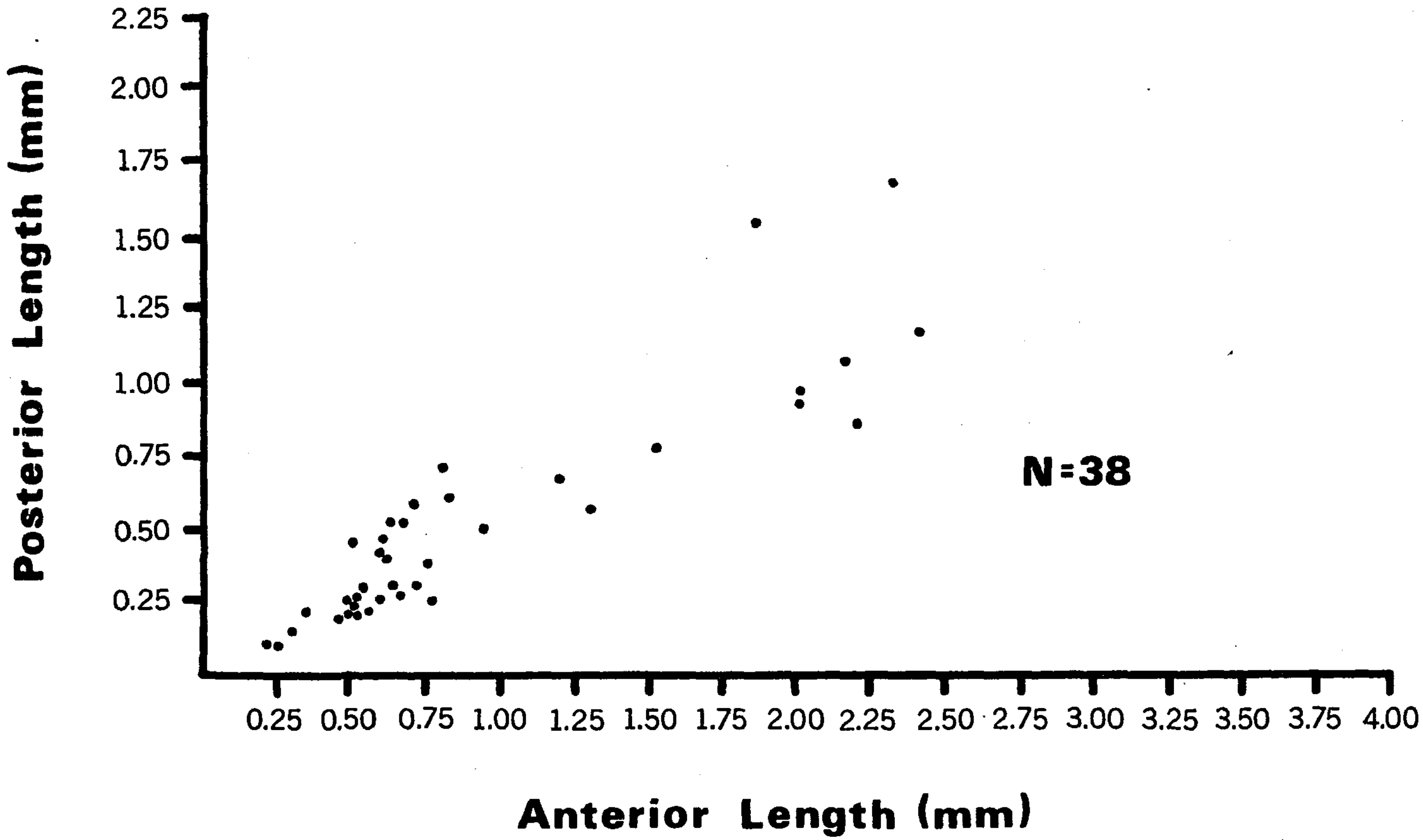
The anterior teeth appear first and are preserved in the smallest individuals known. The posterior teeth are never found in individuals smaller than 0.90mm, and are rarely seen



Text-fig. 14--Size-frequency distribution of length, height, and anterior length of Deceptrix scofieldi (Ulrich) from samples WU-14 and WU-101-20.



Text-fig. 15--Length to height plot for Deceptrix scofieldi (Ulrich) populations at West Union, Ohio (combined data from WU-14 and WU-101-20).



Text-fig. 16--Anterior to posterior length plot for Deceptrix scofieldi (Ulrich) populations from West Union, Ohio (WU-14 and WU-101-20).

even in larger ones. In specimens where posterior teeth can be observed, there are twice as many as anterior teeth (Pl. 1, fig. 15). With an increase in shell size, additional anterior teeth are added at the anterior margin of the hinge plate. New anterior teeth are added first to the left valve, then a corresponding tooth is formed in the right valve. Specimens in one sample (WU-101-20) range from 1 to 3 anterior teeth in each valve. When there is an unequal number of teeth, the extra one is in the left valve. The maximum number of anterior teeth (five in each valve) occur in specimens greater than 4.0mm in length (Pl. 1, fig. 6). There is one anterior tooth in each valve of specimens less than 0.40mm in length, and two in each valve of shells about 0.80mm in length. Those greater than 1.0mm in length have three anterior teeth in each valve. In larger shells, posterior teeth are rare so as to make generalizations about later stages of development hazardous.

Figured Specimens

USNM 46151, 46145; UCGM 42619-42626.

Genus *Praenucula* Pfab, 1934

1799 *non Nucula* Lamarck, p. 87

1852 *non Ctenodonta* Salter, p. 64

1881 *Nucula* Lamarck, Barrande Pl. 269, 273, 274 (*partim*)

1894 *Ctenodonta* Salter, Ulrich, p. 578 (*partim*)

1934 *Praenucula* Pfab, p. 234

1966 *Ctenodonta* Salter, Babin, p. 41 (*partim*)

1968 *Praenucula* Pfab, McAlester, p. 46

1969 Praenucula Pfab, McAlester, p. 229

1971 Praenucula Pfab, Pojeta, p. 16

Type Species

Praenucula expansa Pfab (1934, p. 234) is the type species by original designation. A lectotype for the type species was selected by McAlester (1968, p. 46). This left valve (Pfab, 1934, Pl. 3, fig. 10 and 11), together with paralectotypes are well illustrated by McAlester (1968, Pl. 8, fig. 3-9). These specimens in the Barrande collection at the Narodni Museum, Prague, Czechoslovakia, were collected from the Bohemian Ordovician near Osek, Czechoslavakia.

Diagnosis

Anteriorly elongate praenuculid bivalves with dental series containing numerous, nearly uniform anterior teeth and an equal or smaller number of similar posterior teeth.

Description

Species of this genus are of small to medium size for the family (5mm to 20mm in length), anteriorly elongate, and posteriorly truncate. Each valve is subtriangular to suboval, with many species having an outline similar to Deceptrix. The beak is rather prominent and pointed. There is a distinct anterior umbonal ridge extending from the beak at least half way to the ventral margin and a more weakly developed, shorter posterior ridge. These ridges accentuate the inflated umbonal region. Relatively undifferentiated anterior and posterior dental series occupy a hinge plate which is dorsally concave anteriorly and convex posteriorly.

Numerous, small uniform chevron-shaped teeth, with the chevron apexes directed toward the beak, compose each dental series. The number of posterior teeth may be equal to or fewer than the anterior ones.

The muscle scars of this genus are lightly impressed. Oval adductor scars are located near the shell margins, ventral to the anterior and posterior ends of the hinge plate and slightly dorsal to the mid-height of the shell. Anterior and posterior pedal retractor muscles are reflected in the shell as small circular pits dorsal to the adductor scars. The anterior retractor is broadly fused to the adductor, while the posterior one is separated from the corresponding adductor. Other accessory muscle scars are rarely preserved, although some specimens have two or four pairs of small scars in the umbonal region just below the beak. These umbonal scars may reflect muscles described as dorso- and ventro-median by Heath (1937) for Recent nuculoid bivalves. The pallial line is poorly preserved but appears to be entire and integripalliate. The ligament occupies a short, narrow slit along the dorsal margin of the hinge plate, beneath and posterior to the beaks. While most representatives of this genus are preserved as molds of the valve interior as Steinkerns, a few show shell exterior features. The type of prosopon preserved on these forms consists of very fine and closely spaced comarginal varices of growth.

Discussion

Praenucula is very similar to *Deceptrix* in general shell topography and outline. The teeth of Praenucula are similar in size anteriorly and posteriorly, with an equal or greater number anteriorly. Deceptrix has a few large teeth anteriorly and numerous smaller teeth posteriorly.

Ulrich (1894, p. 581) listed a number of species in his "Ctenodonta levata group," most of which can be placed in Deceptrix; however, C. fecunda and C. calvini are assignable to Palaeoneilo and C. albertina, C. filistriata and C. hartsvillensis may be placed in Praenucula. Ctenodonta ciae Sharpe (1853) as cited by Babin (1966, p. 49) and Bradshaw (1970, p. 633) also seems to fit into Praenucula.

Distribution

The type species occurs in Middle Ordovician strata near Osek, Czechoslovakia. Other species occur in various Middle and Upper Ordovician strata of North America (Hall, 1862b; Ulrich, 1894, 1895; Stewart, 1920; Pojeta, 1971).

Ordovician rocks of northern France (Massif Armoricain, Babin, 1966) contain species of Praenucula. The known Brassfield distribution of this genus is restricted to the ferruginous and crystalline limestone layers 35 to 37 feet above the base of the formation in several sections along State Road 41, 2.5 miles north of West Union, Adams County, Ohio (WU-14, WU-1, WU-11, WU-101-20).

Praenucula albertina (Ulrich)

Pl. 2, fig. 1,2

1847 non Nucula levata Hall, p. 50, Pl. 34, fig. 1a-i

1875 [?] Tellinomya levata (Hall), Hall and Whitfield, p. 82

1894 Ctenodonta albertina Ulrich, p. 598, Pl. 42, fig. 76-80

1894 Ctenodonta filistriata Ulrich, p. 599, fig. 44

1920 Ctenodonta albertina Ulrich, Stewart, p. 9

1970 Praenucula levata (Hall), Bretsky, p. 114

Type Specimen

Ulrich (1894, p. 598) described and figured (Pl. 42, fig. 76-82) several specimens of this species. Three of these specimens (USNM 46122) are illustrated by Pojeta (1971, Pl. 5, fig. 14, 16 and 18). No specimen was designated holotype by Ulrich (1894) and a lectotype will be designated by Pojeta (manuscript in preparation). The type material of "Ctenodonta" albertina is from the Upper Ordovician near Clarksville, Ohio (Richmondian). The type of "C." filistriata is from the Upper Ordovician near Covington, Kentucky Edenian).

Diagnosis

Praenucula with more teeth anteriorly (usually 5 to 15 anterior teeth). A nearly vertical posterior margin and elongate anterior region with gently rounded margin. The beak is essentially orthogyrous and rather small relative to rest of the shell, and the anterior and posterior hinge plates meet at a very obtuse angle (greater than 120°).

Description

Individuals of this species are average to large size for the genus (large inviduals are about 15mm long). The shells are equivalved and very inequilateral with the beak in the posterior third of each valve. Subtriangular to subrectangular in outline, the shells of this species are elongate anteriorly and truncate posteriorly, with the posterior margin being nearly vertical to the shell's antero-posterior axis. The beak is low, rounded and orthogyrous or slightly prosogyrous. The many small chevron-shaped teeth that occupy the anterior and posterior hinge plate are variable in number, but usually are more numerous in the anterior series. The apexes of the chevrons point toward the beak. The total number of teeth is greater with increasing age (size).

Oval adductor muscle scars are situated just below the ends of the hinge plate near the anterior and posterior margins in each valve. Accessory muscle scars are not well preserved in most of the specimens of the type suite, or on the Brassfield specimens.

The anterior retractor is inserted very near to the scar produced by the adductor and appears fused to it, but the posterior pedal retractor is widely disjunct from the posterior adductor scar and appears as a lobe on the dorsal margin of the adductor between the pedal retractor and the adductor. Two to four pairs of small muscle scars are located in the umbonal region just beneath the beak; they are probably muscles of the dorso-median group (Heath, 1937). The pallial line and ligament are not preserved on any of the Brassfield specimens.

The external surface is marked by very fine, uniformly spaced growth varices.

Discussion

Ulrich's (1894, p. 598, 599) Ctenodonta albertina and C. filistriata (both from Upper Ordovician strata of southwestern Ohio) were distinguished on the basis of finer growth lines in the latter and some minor differences in shell shape. Ulrich's distinctions (p. 599) between these two "species" seem to be within the range of interspecific variation. The dentition of the two appears to be identical: Ulrich (1894, Pl. 42, fig. 80 and text fig. 44e) and Pojeta (1971 Pl. 5, fig. 14-16) figure the hinge plates of C. albertina and C. filistriata and there appears to be little difference between these specimens.

Tellinomya levata (Hall) of Hall and Whitfield (1873, p. 82) (from the Richmondian of Ohio) seems also to belong in this species primarily on the basis of their illustrations of similar dentition. However, Nucula levata Hall (1847, p. 150) (from the New York, Trenton, Middle Ordovician) is probably a Deceptrix.

Ulrich (1894, p. 599) made the following comment in comparing Ctenodonta filistriata and Tellinomya levata (Hall).

> This species [C. filistriata] is generally identified with Hall's Nucula or Tellinomya levata, originally described from the Trenton limestone of New York, and closely resembles C. nitida of this report. The error of this identification is so palpable that it is really

not worth the while to refute it. Anyone at all capable of distinguishing species must, now that attention has been directed to the matter, see at once that the two shells are very different.

Praenucula albertina was compared by Ulrich (1894, p. 597-8) to Ctenodonta madisonensis from the Upper Ordovician (Richmondian) near Madison, Indiana. However, internal structures of C. madisonensis are not known, and eventhough external features of the two species are similar, the lack of internal morphology leaves the matter unsettled.

Specimens of Praenucula ciae (Sharpe, 1853) from the Middle Ordovician of northern France figured by Babin (1966, Pl. 1, fig. 9 and text-figures 10-12) and Bradshaw (1970, text-figures 11, 12) are very similar to P. albertina, differing mainly in the shape of the posterior teeth which are straight or only slightly chevron-shaped in P. ciae (see Babin, 1966, p. 49 and Bradshaw, 1970, p. 633 for complete description of P. ciae).

Distribution

Type material of Ctenodonta albertina was collected from the "upper beds of the Cincinnati Group [Upper Ordovician] at Clarksville and other localities in Ohio." This species may also occur "in Minnesota . . . in the Hudson River strata [Upper Ordovician] near Spring Valley" (Ulrich, 1894, p. 599). These strata are now considered Richmondian in age in Ohio and probably so in Minnesota.

Ctenodonta filistriata types were collected in "the lower beds of the Cincinnati group at numerous localities in and near the city of Cincinnati" and occur also in "equivalent beds at Granger, Minnesota." These beds are probably of Edenian age in the Cincinnati area.

Numerous specimens were recovered from samples collected 35 to 37 feet above the base of the Brassfield Formation at several sections on State Road 41, 2.5 miles south of West Union, Adams County, Ohio (WU-1, 11, 14, 101-20).

Figured Specimens

OSU 2975, UCGM 42627

Genus Palaeoconcha Miller, 1889

1852 non Ctenodonta Salter, p. 64

1889 Palaeoconcha S. A. Miller, p. 498

1894 Ctenodonta Salter, Ulrich, p. 578 (partim)

1968 Palaeoconcha Miller, McAlester, p. 40

1969 Palaeoconcha Miller, McAlester, p. 229

1971 Palaeoconcha Miller, Pojeta, p. 16

Type Species

Palaeoconcha faberi (Miller, 1889) is the type species by original designation. There are three syntypes of this species in the Walker Museum Collection at the Chicago Natural History Museum (WM 8870). McAlester (1968) did not designate a lectotype as these specimens were unavailable to him. Likewise, Pojeta (1971) failed to specify a lectotype for this species, although he illustrated one of the syntypes (Pl. 6, fig. 608). Pojeta (1972, personal communication) is presently preparing a monograph on Ordovician pelecypods which will contain lectotype indications for all undesignated Ordovician species.

P. faberi was collected from the Upper Ordovician (Richmondian) near Versailles, Indiana.

Diagnosis

Very small (consistantly less than 5mm in length), nuculacean bivalves with a markedly triangular dorsal outline and a rounded, hemispherical ventral outline. Numerous, small blocky taxodont teeth uniformly compose the anterior and posterior dental series.

Description

Species assignable to Palaeoconcha are equilateral and nearly equidimensional bivalves which are consistantly less than 5mm in length. Individuals placed here show a distinctly triangular outline of the dorsal half of the shell and a rounded, hemispherical outline of the ventral half.

The anterior-dorsal margin is slightly excavated and a posterior auricle may be developed to varying degrees. Straight, prominent, elevated beaks are erect or somewhat prosogyrous. The hinge plate is arched or bent at an obtuse angle with the angulation just below the beaks. No differentiation of anterior and posterior dental series was noted within the generally obscure and extremely fine taxodont teeth. Although diminishing somewhat in size, the dental series is continuous beneath the beaks, making the presence of a resilifer unlikely. The anterior adductor impressed a prominent rounded scar on the shell, while the posterior adductor is larger, dorso-ventrally elongate, and weakly impressed. Occasionally pedal muscle scars are preserved dorsal to the adductors. The pallial line is entire and nonsinuate, but is rarely preserved. Since all known specimens assignable here are preserved as internal molds, surface features of the shell are unknown. There is a faint indication of fine comarginal prosopon on the surface of some Steinkerns.

The absence of a resilifer may indicate an external ligament, but it is not preserved on the internal molds.

Discussion

In 1889, S. A. Miller described *Palaeoconcha faberi* as the type of his new genus *Palaeoconcha*. It was based on specimens of very small internal molds from Cincinnatian rocks at Versailles, Indiana and Butler County, Ohio (Pl. 2, fig. 3, 4). James Hall (1845) had previously described a species of diminutive bivalve from the Cincinnati rocks as *Nucula obliqua*, which Ulrich (1894) synonomized with *P. faberi*.

F. B. Meek (1873) described and figured a specimen from "near the middle of the Cincinnati group, at the tops of the hills at Cincinnati, Ohio," which he felt was referrable to Hall's *Nucula obliqua*, and that the probable generic placement was in *Tellinomya* Hall (1847). Meek commented, however, that this specific identification lacked certainty because of Hall's figure-less and brief description. He then provided for any contingency by suggesting that should his specimen (Meek, 1873, Pl. 11, fig. 11a-c) ever prove to be distinct from Hall's, "it may take the name T. microsperma." Meek's specimen is certainly congeneric (and probably conspecific) with Hall's Nucula obliqua.

Ulrich (1894) regarded Palaeoconcha as a synonym of Ctenodonta, stating that Miller's genus was "wrongly conceived" and that these forms could be accommodated within Ctenodonta (p. 580, 605).

Nucula obliqua Hall (which Ulrich (1894) considered synonomous with P. faberi) is, however, separated from most other Ctenodonta by placement in Ulrich's informal "Ctenodonta recurva group." This informal group, that also includes species of "Ctenodonta" which are presently included under Similodonta, is one of six which Ulrich proposed in 1894. He considered members of each group to be closely related to one another and intimated that subsequent generic segregation of the groups might be desirable.

Although Palaeoconcha and Similodonta do appear to be very closely related because of similar shell outline, they are now considered to be valid genera. Consistant difference in the size of these two forms notwithstanding, Palaeoconcha has a posterior auricle variably developed, whereas none occurs in Similodonta. The hinge plate in both genera is angular (bent at an angle averaging 90°), but the area beneath the beak of Similodonta, where the anterior and posterior dental series meet, shows a gap in the dentition between the offset tooth rows (Ulrich, 1894, Pl. 42, fig. 39). The dental series seems to be continuous under the beak in specimens of Palaeoconcha (Pl. 2, fig. 10). A striking difference, which may be more apparent than real, is the mode of preservation of these two genera. Similodonta is usually found as replaced shell material, while Palaeoconcha commonly occurs only as internal molds of the shells. This preservation could, however, indicate a fundamental difference in shell composition of these two forms, since shells of similar physical and chemical structure would be expected to be preserved similarly. Species of these two genera are not known to occur together (Ulrich, 1894).

Examination of a series of 280 specimens of P. obliqua from the Faber Collection (UCGM 19292) from a single locality near Oxford, Ohio (Upper Ordovician, Richmondian) suggests that a wide range of shell shape may be allowable within a single species of Palaeoconcha (see discussion of P. ohioensis). The three types of P. faberi show a strongly developed posterio-dorsal auricle, a relatively small beak and greater height than length (Pl. 2, fig. 3). Although Hall's types of P. obliqua were not examined, Ulrich's

(1894) figures of the species probably indicate its general form. There seem to be sufficient differences in the shell configuration to consider these two separate species. (See the discussion under P. ohioensis for a detailed analysis of the variation in the species of Palaeoconcha.

Pojeta (1971, p. 7) lists two species of Palaeoconcha in the Ordovician. While these two are not specified, it is here assumed that they are P. faberi and P. obliqua. A third species assignable to this genus is the Brassfield Ctenodonta ohioensis Bassler (1915) (formerly Tellinomya (Nucula?) socialis Foerste, 1893 [1895], p. 563; not Ulrich 1894 [1897], p. 594). It is discussed below.

Distribution

The type suite of P. faberi which was collected from the "Hudson River Group [Richmondian?] at Versailles, Indiana and in Butler County, Ohio." The species also occurs in other horizons in the Cincinnatian Series (Edenian through Richmondian) of the Cincinnati Arch area. This genus is also known from the Maquoketa Formation of Late Ordovician age, in Iowa, Illinois, Wisconsin, and Minnesota. Lower Silurian occurrences in the upper Brassfield are reported by Foerste (1895) from several quarries in the vicinity of Dayton, Ohio. Additional Brassfield specimens (P. ohioensis) have been recovered from ferruginous and associated calcareous limestones, 35 to 37 feet above the Brassfield base in several road cuts on State Road 41, 2.5 miles north of West Union, Adams County, Ohio. (WU-1, 11, 14, 101-20).

Palaeoconcha ohioensis Bassler

Pl. 2, fig. 6, 9-17

1894 non Ctenodonta socialis Ulrich, p. 594, Pl. 42, fig. 59, 60

1895 Tellinomya (Nucula?) socialis Foerste, p. 563, Pl. 37, fig. 12a-c.

1915 Ctenodonta ohioensis Bassler, p. 308 (new name for Tellinomya socialis Foerste, 1895)

Type Specimen

This species was originally proposed as Tellinomya (Nucula?) socialis Foerste (1895) (non Ctenodonta socialis Ulrich, 1894). Since Ctenodonta and Tellinomya are synonyms, these two species are homonyms. Bassler (1915) therefore proposed Ctenodonta ohioensis to replace Foerste's species name.

This species is represented by a series of syntypes in the collections of the National Museum of Natural History (USNM 88538). Of the eleven specimens in this suite, seven are reasonably similar to Foerste's illustration (Foerste, 1895, Pl. 37, fig. 12a-c), three are fragments of claystone and are probably not fossils, and one is another species of bivalve most probably Palaeoneilo fecunda (Hall). The syntypes have been mounted on a 60-space microfaunal slide. Specimens referrable to this species are in spaces fourteen through twenty. The three claystone particles are at squares 25-27 and the Palaeneilo fecunda specimen is in space 37.

Neither Foerste (1895) nor Bassler (1915) designated any particular specimen as type for the species. The lectotype, designated herein, is the specimen in space number 15 on the microfaunal slide (USNM 88358) (Pl. 2, fig. 6, 9). This specimen is the second largest of the syntypes and most closely resembles Foerste's (1895) figures, although those figures (Pl. 37, fig. 12a-c) appear to be somewhat schematic. The type suite is from the upper shaley beds of the Brassfield Formation (Lower Silurian) from Huffman's Quarry near Dayton, Ohio.

Diagnosis

Palaeoconcha with moderate development of posterior auricle, beak low and rounded, shell length is equal to or slightly greater than height.

Description

Average size for the genus, but small as compared with other nuculoids (1 to 3mm in length). This species possesses a characteristic palaeoconchid shape, with triangular dorsal and semi-circular ventral outlines. A posterior auricle is developed (Pl. 2, fig. 6) but not nearly so prominently as in *P. faberi* Miller (Pl. 3, fig. 6). Low, rounded beaks are erect, or show slight curvature anteriorly. The internal casts of the syntype suite reflect a shell that was inflated (Pl. 2, fig. 9) compared to the *P. faberi* type (Pl. 2, fig. 4).

The general state of preservation of the syntypes of this species is inferior to that of specimens examined from

Cincinnatian strata (especially Faber Collection, UCGM 19292). Those collected for this study are much better, showing some dentition and musculature.

The narrow, small taxodont teeth, characteristic of the genus, are not preserved in any of the syntypes, and are uncommonly represented in the Brassfield specimens obtained in this study. When preserved, the teeth are straight, blocky and there is little differentiation between the anterior and posterior series (Pl. 2, fig. 10, 15). Lack of dentition is a relatively common preservational feature for palaeoconchids, indicating that the teeth are rather frail, and their absence on molds is common.

Muscle scars are also poorly preserved on the syntypes. On these specimens, the anterior adductor leaves a shallow impression on the shell; other species characteristically have well impressed anterior adductor scars (as seen in P. obliqua (Hall) (Pl. 2, fig. 7). Anterior and posterior accessory muscle scars are present on one paralectotype (Pl. 2, fig. 14). These small, elliptical scars are probably produced by the pedal retractors. These scars are better seen in some (Pl. 2, fig. 12) Brassfield specimens collected in this study (WU-1 and WU-11) and are very similar to a series of scars along the hinge plate in P. obliqua (Pl. 2, fig. 8) from Upper Ordovician strata near Oxford, Ohio (UCGM 19292). Both the anterior and posterior pedal scars seem to be disjunct from the adductor scars.

The posterior retractor scars are elongate and located at the posterior end of the accessory muscle scar series along the hinge line (Pl. 2, fig. 12).

Morphology of the pallial line and ligament is unknown from the specimens at hand. The prosopon consists of very fine comarginal varices of growth (Pl. 2, fig. 17).

Discussion

This species as represented by its type material seems to be distinctly different in outline and shell configuration from the type species of Palaeoconcha (P. faberi) as represented by one of the P. faberi syntypes illustrated by Pojeta (1971, Pl. 6, fig. 6-8). Palaeoconcha faberi Miller has a prominent postero-dorsal auricle which is only weakly developed in P. ohioensis. The antero-dorsal region of P. faberi is straight or slightly convex dorsally, while P. ohioensis shows a somewhat concave dorsal outline in front of the beaks. P. faberi is compressed; P. ohioensis is robust and comparably quite gibbous. The ratio of valve height to thickness of articulated valves is 2.50 for the specimen of P. faberi illustrated by Pojeta (1971, Pl. 6, fig. 6-8) but only 1.55 for the lectotype of P. ohioensis.

The third "species" of Palaeoconcha, Nucula obliqua Hall (1845, p. 294), from Upper Ordovician Maquoketa strata in Iowa, and oldest named entity of the genus, may conceptually embrace both of the other species. Unfortunately, the type material (at the American Museum of Natural History) of this species is not available at this time. Illustrations of plesiotypes (also not seen) by Ulrich (1894, Pl. 42, fig. 83-87) from Upper Ordovician (Richmondian) Cincinnati Ohio, are the basis for present understanding of the species.

Ulrich's P. obliqua (Hall) type differs in shell shape and outline from P. faberi types by the absence of a postero-dorsal auricle that is prominent in P. faberi (Pl. 2, fig. 5). P. obliqua also has larger beaks and umbones and a dorsally concave antero-dorsal margin in contrast to the slightly convex antero-dorsal margin in P. faberi (Pl. 2, fig. 3).

Specimens illustrated by McAlester (1968, Pl. 11, fig. 11-24) as P. faberi Miller are virtually indistinguishable from Ulrich's drawings, and should be assigned to P. obliqua (Hall). McAlester's entire suite, including the nine illustrated specimens was examined in this investigation. It consists of 280 specimens collected by C. L. Faber from "Oxford" (Ohio), i.e. Richmondian, (UCGM 19292) and show considerable variation in shell shape. They all have a markedly triangular dorsal outline; however, there are several specimens in the suite which are quite similar to P. faberi in possessing a moderately well developed postero-dorsal auricle and relatively smaller beaks, with a subrectangular dorsal outline. (None of these were illustrated by McAlester (1969). If this sample of 280 specimens were considered a "population" of Palaeoconcha obliqua, variations of morphology within this one species could include forms presently assigned to P. faberi and P. ohioensis. Because little is known of the exact locality or precise stratigraphic position of these specimens, few inferences can be drawn concerning morphologic variation within the species. However, the chances are very good that the Faber suite represents a very circumscribed area and horizon in the Richmond sequence of the Oxford area, since bivalve occurrences of abundance in the Cincinnatian tend to be of this nature. Although it is reasonable to suspect from this collection that the three species of Palaeoconcha may represent intraspecific variations within a single long-lived species, other comparable suites with precise provenance are required to clinch the argument. Meanwhile, the three species are regarded as distinct Palaeoconcha ohioensis being the only Silurian (Brassfield) representative of this otherwise Ordovician genus.

Distribution

Specimens in the syntype suite are from the Beavertown Marl (Upper clayey units of the Brassfield Formation) in the area around Dayton, Ohio (Huffman and George Young Quarries). Numerous individuals were also found in acid residues from several ferruginous layers 35 to 37 feet above the base of the Brassfield at two sections on State Road 41, 2.5 miles north of West Union, Adams County, Ohio (WU-14, WU-11).

<u>Ontogeny</u>

In sample WU-14, 10 left, 8 right and 2 articulated valves were recovered. The smallest valve is 0.61mm long and 0.60mm high, while the largest valve in this sample has a length of 0.95mm and height of 0.90mm. Another sample, WU-1, contained a larger specimen that had a length of 1.10mm and height of 1.00mm. Two other specimens of this species were recovered from acid residues of WU-T.S., and were the largest individuals obtained from the West Union (WU) localities. Specimens from the WU-T.S. and WU-1 samples were Steinkerns of articulated shells. The WU-T.S. specimens are 1.98mm and 2.90mm in length and 1.95mm and 2.65mm in height, respectively. Five of the seven cotypes (USNM 88538) were complete enough to measure, and their sizes ranged from a length of 1.6mm and height of 1.55mm to 3.30mm in length and height.

No one sample had many specimens of this species, therefore, the data presented herein are taken from 42 valves and Steinkerns from several samples. In almost all the specimens, the length is slightly greater than the height. The length to height ratio does not vary significantly through ontogeny. The data concerning anterior and posterior proportions do not support such clear-cut analysis. The anterior length is always greater than the posterior length. In the small individuals of sample WU-14, the anterior length increased much faster than posterior length.

Individuals that range in anterior length from 0.36mm to 0.71mm have a corresponding posterior length of only 0.25 to 0.39mm. Larger specimens, such as those from the type suite (USNM 88538) and from sample WU-T.S., have anterior/posterior length dimensions that are subequal.

The lectotype has an anterior length of 1.7mm, and a posterior length of 1.0mm. The smallest specimen of the type suite has an anterior length of 1.1mm and posterior length of 0.5mm.

The use of samples from several localities may reflect genetic or environmental differences of separate populations or may represent an alteration of growth at some stage during ontogeny. The small number of specimens available for study precludes a complete and accurate description of changes in anterior/posterior proportions.

Variation of dentition through ontogeny is not known.

Figured Specimens

P. faberi WM 8870; *P. obliqua* UCGM 19292, I, P, Q; *P. ohioensis* USNM 88538 #14, 15, 16; UCGM 42628-42631.

Superfamily NUCULANACEA Adams and Adams

Description

Members of this superfamily are posteriorly elongate nuculoid bivalves, usually with a pallial sinus developed. The position of the ligament and curvature of beak and umbone are criteria for separating families.

Family MALLETIIDAE Adams and Adams

Description

The ligament of genera assigned here is predominately external, usually occupying a narrow slit posterior to the beak. The beak and umbo are curved toward the shorter anterior end of the shell (prosogyrous). The genera assigned here by McAlester (1969, p. 233-235) are quite variable in shell prosopon, outline and dentition. The teeth vary from genus to genus, being vertical (Malletia DesMoulins), inclined (Koenenia Beushausen and Dysodonta Mansuy) and chevron-shaped (Neilo Adams). In Palaeoneilo, the anterior teeth are inclined, while the posterior ones are chevron-shaped. The large amount of morphlogic variability in this family implies heterogeneity. Further study of these forms should yield a very different family level taxonomy. The only constant features of morphology for genera assigned here by McAlester (1969) are posterior elongation and taxodont dentition.

Genus Nuculites Conrad, 1841

1841 Nuculites Conrad, p. 49 (partim)

1847 Cleidophorus Hall, p. 300

1851 Cucullella M'Coy, p. 50

1852 non Pyrenomoeus Hall, p. 87

1856 Nuculites Conrad, Hall, p. 394

1871 Clidophorous (sic) Hall, Hall, p. 228

1885 Nuculites Conrad, Hall, p. xxvi

1889 Clidophorus (sic) Hall, Miller, p. 471

1889 Nuculites Conrad, Miller, p. 496

1895 Cucullella M'Coy, Beushausen, p. 97

1899 Nuculites Conrad, Grabau, p. 254

1916 Cleidophorus Hall, Williams and Breger, p. 159

1917 Nuculites Conrad, Williams, p. 29

1963 Nuculites Conrad, Babin, p. 55

1966 Nuculites Conrad, Babin, p. 94

1968 Cucullella M'Coy, McAlester, p. 23

1968 Nuculites Conrad, McAlester, p. 37

1969 Nuculites Conrad, McAlester, p. 233

1971 Cleidophorus Hall, Pojeta, p. 15

1971 Nuculites Conrad, Pojeta, p. 15

Type Species

The type species is Nuculites oblongatus Conrad (1841, p. 50) by subsequent designation of Miller (1889, p. 496). No holotype was designated by Conrad. Because Conrad's original specimens appear to have been lost, no lectotype can be designated. No specimens have since been discovered from Conrad's site, and with no topotype material available, no neotype can be designated. Hall (1862b) reproduced Conrad's (1841) illustration but is so generalized that it cannot be shown to represent any single specimen (McAlester, 1968, p. 37). Conrad's description, however, is adequate so that specimens of the species can be recognized. It is from the Hamilton (Middle Devonian) of New York State.

Diagnosis

Malletiidae with internal septum bordering the posterior edge of the anterior adductor muscle. Chevron-shaped teeth of nearly uniform size occur along the length of the posterior hinge plate; slightly larger undulose teeth occur anteriorly.

Description

These are medium to large (10 to 30mm in length), posteriorly elongate nuculacean bivalves with the beak near the anterior third of the shell. The shell outline is generally suboval to subrectangular or may be subtriangular in a few species. Prosogyrous beaks are low and rounded, standing barely above the dorsal margin. Many long, narrow taxodont teeth occupy the gently arched hinge plate along one-half to two-thirds of the shell's dorsal length. The teeth may be straight, inclined or slightly chevroned. While nearly uniform along the hinge plate, the teeth become slightly longer beneath the beak and for a short distance anteriorly. The teeth of the anterior series are not markedly set off from the comparatively greater number in the posterior series. In at least some species (including the type species, N. oblongatus) several of the teeth in the umbonal region bifurcate dorsally.

Perhaps the most diagnostic feature of this genus is the ridge on the interior surface of each valve, slightly anterior to the beak and extending from the underside of the hinge plate at least halfway to the ventral margin. This ridge, referred to as an anterior "myophoric buttress" by Pojeta (1971) borders the posterior margin of the anterior adductor. Called a "septum" by McAlester (1968), this interior ridge is vertical in some forms (N. oblongatus) or may slant or curve anteriorly (as in the Brassfield forms, among others). There are several accessory muscles. Scars of pedal protractors and retractors occur along with several other muscle impressions in the umbonal region. These umbonal muscles served an unknown function but may be called "dorsal-median" and "ventro-median" muscles in the terminology of Driscoll (1964) and Heath (1937). (For more information on accessory muscle scars, see the text discussion of accessory muscle morphology).

The pallial line is not often preserved, but appears to be slightly sinuate (McAlester, 1968, p. 37).

The external surface of these shells is marked by numerous fine comarginal varices. Some specimens may possess a slight posterior umbonal ridge, but never a sulcus as seen in Palaeoneilo Hall and Whitfield. The ligament is external and occupies a long narrow groove dorsal to the posterior dental series.

Discussion

Several generic names have been proposed for lower Paleozoic nuculoid forms that are posteriorly elongate and possess a prominent anterior septum. Nuculites Conrad has been used almost exclusively for Devonian species of this general type. On the other hand, most Ordovician forms in North America have been grouped under the genus Cleidophorus

Hall. Ordovician and Silurian European bivalves with this morphology have been attributed to M'Coy's genus Cucullella.

Some authors have suggested that these three genera may be synonymous (McAlester, 1968, and Pojeta, 1971). Comparison of photographs of the type species of each genus (McAlester, 1968) indicates that the difference in morphology of these species is not of great consequence and can be tolerated within the single genus under current concepts. Present criteria for assignment of nuculoid species to these genera is the possession of an anterior septum and a posteriorly elongate shell.

Hall (1847, p. 300) originally thought Cleidophorus was edentulous but later assigned a dentate species to the genus (C. neglectus Hall, 1862a, p. 55). The original material (Nuculites planulata Conrad, 1841) upon which Hall based his new genus was not very well preserved (McAlester, 1968) and quite probably the teeth were simply not preserved.

Although Cleidophorus Hall, Nuculites Conrad and Cucullella M'Coy are indistinguishable on the basis of known morphology, it is likely that new morphologic characteristics will be discovered in this form group that may allow separation of this group. Richard Bambach (Virginia Polytechnical Institute) has been studying species of this group, particularly in the Appalachian Silurian, and has defined some morphologic structures (such as the presence of a posterior septum in some species) that may serve to break down this group into several new taxa (J. Pojeta, personal communication). Bambach's conclusions are not published yet, but should provide much needed new information about this morphologically conservative, long-ranging group.

Nuculites Conrad is the oldest name (1841) and therefore has priority.

Pyrenomoeus Hall (1852) has been considered synonymous with Nuculites by McAlester (1969). This genus is based on relatively poor material, and specimens of the type suite lack dentition. The presence of an anterior septum is questionable and if present is not developed to a degree approaching that in Nuculites. The outline of Pyrenomoeus can perhaps be accommodated within Nuculites; however, the umbones of some specimens curve toward the longer end of the shell (a feature not possessed by other members of Nuculites). Because of these morphologic differences, Pyrenomoeus will not be considered a synonym of Nuculites in this study.

Distribution

The type material was probably from the Middle Devonian (Hamilton group) near Smyrna, Chenango County, New York. Species of Nuculites occur in marine sediments of Middle Ordovician through Devonian age in North America, and northern Europe (Germany, France, British Isles) and Devonian of South America (Clarke, 1900).

Nuculites neglectus (Hall)

Pl. 3, fig. 1-4, 7-8, 10-18

1862a Clidophorus neglectus Hall, p. 55, fig. 2,3 (figure only)

1894 *Clidophorus neglectus* Hall, Ulrich, p. 607, Pl. 42, fig. 20-25.

1895 *Cleidophorus* (*Nuculites*) *ferrugineum* Foerste, p. 564, Pl. 37, fig. 2a,b

1903 *Clidophorus neglectus* Hall, Weller, p. 165, Pl. 2, fig. 16

1909 *Nuculites neglectus* (Hall), Grabau and Shimer, p. 397, fig. 508a-c

1970 *Nuculites neglectus* (Hall), Snyder and Bretsky, p. 239, Pl. 1, fig. h-j.

Type Specimen

Hall (1862a, p. 55 fig. 2 and 3) figured two specimens of *Nuculites neglectus* but did not describe them. These two specimens are in two suites of specimens in the American Museum of Natural History (AMNH 1362/1 and 1362/2).

No specimen was designated as the type by Hall or subsequent workers. Pojeta, as stated previously, will establish lectotypes for North American Ordovician pelecypods without type designations (manuscript in preparation). Several of Hall's syntypes, including his two originally figured specimens are illustrated here (Pl. 3 fig. 1, 3). Hall's type material is from the Maquoketa Formation (Upper Ordovician) near Dubuque, Iowa.

Diagnosis

Nuculites with a relatively long anterior septum, dorsal and ventral posterior margins are nearly parallel for half their length then rapidly converge to form an attenuated posterior tip. Juveniles show blunter anterior and posterior margins. There are numerous, fine, chevroned teeth with the apex of the chevronspointing toward the beak.

Description

The size is small to medium for the genus (less than 2mm to not greater than 15mm). Equivalved and strongly inequilateral, the shell is posteriorly elongate with the anterior and posterior marginal outline rather pointed in larger individuals and blunter in smaller forms. A slight posterior wing is present in most larger specimens of the syntype suite (Pl. 3, fig. 2). The prosogyrous beak is high and somewhat pointed, in the anterior half to third of the shell (Pl. 3, fig. 2, 4).

The anterior septum is well developed (elevated), long and rather narrow (Pl. 3, fig. 2, 4). Having a general anterior declination, the septum curves even more anteriorly in its lower half (Pl. 3, fig. 2, 4). Septum length is at least half the shell height.

The dental series is differentiated into a posterior and anterior series. The anterior series contains fewer (usually less than 7 or 8) and slightly larger teeth than the posterior series. Anterior teeth are undulose with the dorsal ends slanted anteriorly (Pl. 3, fig. 16, 17). Posteriorly there are perhaps twice as many teeth (12 to 16 in large specimens). The posterior teeth are chevron shaped with the point of the chevron pointing toward the beak (Pl. 3, fig. 11). The apex of the chevrons is at the ventral edge of the teeth farthest from the beak and becomes gradually more dorsal in position in teeth closer to the beak. This pattern is very similar to that shown in Text-fig. 3. In general, the teeth are thin and small. The hinge plate occupies about half the shell length.

Several sets of muscle scars are reflected in the shells and on internal casts of this species. The adductors are the largest and generally most prominent scars on the shell. Oval and slightly impressed, the adductors are inserted beyond and ventral to the anterior and posterior end of the hinge plate (Pl. 3, fig. 10, 12). The anterior adductor, as well as the anterior pedal muscles, are bounded by the prominent septum characteristic of the genus. Two smaller, well impressed scars are situated near the hinge plate, anterior to the septum and dorsal of the adductor. The dorsalmost one is probably the retractor; and the other, a protractor scar (Pl. 3, fig. 13). A prominent long, narrow scar is observed on the underside of the posterior hinge plate about half-way between the adductor and beak. This scar is most likely reflective of the posterior retractor (Pl. 3, fig. 14). There are two or three dorso-ventrally elongate scars in the umbonal region just beneath the beak; these are probably produced by the dorso- and ventro-median muscles (see Heath, 1937, p. 14) (Pl. 3, fig. 10, 13). The pallial line was not preserved in any of the specimens studied here.

The ligament occupies a long, narrow groove along the dorsal margin of the hinge plate beneath and posterior to the beak (pl. 3, fig. 17).

Numerous low magnitude, thin, closely spaced comarginal growth varices mark the external surface of the shell in this species.

Discussion

Hall (1862a, p. 55) figured two specimens of his new species *Clidophorus* [*sic*] *neglectus* from the Maquoketa near Dubuque, Iowa. Since *Cleidophorus* Hall is considered synonymous with *Nuculites* Conrad (see generic discussion), *C. neglectus* is placed in *Nuculites*.

Ulrich (1894) reported occurrence of this species in the "Depauperate zone" of the basal Maquoketa Formation (Upper Ordovician) of Minnesota and other midwestern states and was apparently the first to carefully describe the species and figure the shell's morphology in detail. Snyder and Bretsky (1970) studied large numbers of this species from several populations. They analysed intraspecific variation of the populations, constructing growth and mortality curves. Their interpretation of the paleoecology of this species is discussed here under "Bivalve ecology and paleoecology."

Ulrich (1894, p. 607) and Bassler (1915, p. 232) suggested that *Nuculites fabula* (Hall, 1847) from the Upper Ordovician (Cincinnatian) of Cincinnati, Ohio area, might be a "dwarfed" form of *N. neglectus* (Hall). Comparison of type specimens of both species indicates that there are some differences other than size between the two. N. fabula is more rounded at the anterior and posterior margins and although smaller overall, N. fabula has a relatively more prominent beak. The shape and position of the anterior septum and the type of dentition are virtually indistinguishable in types of these two species. Two of the syntypes of Nuculites fabula (AMNH 1361) are illustrated here (Pl. 3, fig. 5, 6). Young individuals of N. neglectus have an outline more like N. fabula than adults (Pl. 3, fig. 4).

Several specimens from the Brassfield (Pl. 3, fig. 8, 10, 15, 18) have an outline intermediate to N. fabula (Pl. 3, fig. 6) and N. neglectus (Pl. 3, fig. 4). The fact that small (juvenile) individuals of N. neglectus more closely resemble N. fabula than do N. neglectus adults suggests that N. fabula may represent the phylogenetic stock out of which N. neglectus evolved. N. fabula is known to occur throughout the Upper Ordovician (Cincinnatian series) while N. neglectus is known only from the upper stage of the Cincinnatian (Richmondian) and the lowest Silurian (Brassfield Formation). Although morphologically similar, these two species are probably distinct.

Although N. neglectus is an abundant element of the bivalve fauna in the basal Maquoketa Formation, it is relatively less abundant in the Brassfield. This species composes up to 40% of the nuculoid bivalves in the basal Maquoketa. In one sample (WU-14) from the Brassfield, 6.5

pounds of bulk sample was acified and yielded 902 individual valves and 80 articulated bivalve shells. Of these 982 specimens, only 47 (about 5 percent) were Nuculites neglectus. All of these are disarticulated, 22 left, and 25 right valves.

Nuculites ferrugineum (Foerste, 1895, p. 564) was described from the Brassfield ferruginous zone at Todd's Fork Creek, Ohio. The only known specimen, the holotype (OSU 8207), is a poorly preserved internal mold of a right valve (Pl. 3, fig. 18). The shape of the beak, anterior outline and anterior septum of N. ferrugineum is very near that of the other Brassfield Nuculites collected for this study and to the type material of N. neglectus from the Maquoketa Formation. N. ferrugineum is therefore synonymized with N. neglectus.

Distribution

The N. neglectus type suites are from the "Hudson River group" of "Sinsinnewa, Wisconsin" and "near Dubuque, Iowa," according to the museum labels. These type suites are presumable from rocks which are now included in the Upper Ordovician Maquoketa Formation. This species is abundant in many outcrops of the Maquoketa Formation in Iowa, Illinois and Wisconsin (Snyder and Bretsky, 1971).

The Brassfield occurrences are restricted to the numerous ferruginous layers and do not occur in the crystalline limestone layers 35 to 37 feet about the base of the Brassfield in several road cuts along State Road 41, 2.5

miles north of West Union, Adams County, Ohio (localities WU 14, 1, and 11).

Figured Specimens

N. fabula AMNH 1361, OSU 8081; *N. ferrugineum* OSU 3207; *N. neglectus* AMHN 1362/1, 1362/2; UCGM 42632-42637.

Genus *Palaeoneilo* Hall and Whitfield, 1869

1842 *Nuculites* Conrad, p. 249 (*partim*)

1847 *non Tellinomya* Hall, p. 151

1852 *non Ctenodonta* Salter, p. 64

1869 *Palaeaneilo* Hall and Whitfield, p. 6

1885 *Palaeoneilo* Hall and Whitfield, Hall, p. xxvii

1888 *Palaeoneilo* Hall and Whitfield, Oehlert, p. 653

1889 *Palaeoneilo* Hall and Whitfield, Miller, p. 499

1889 *Tellinomya* Hall, Miller, p. 514 (*partim*)

1894 *Ctenodonta* Salter, Ulrich, p. 578 (*partim*)

1895 *Ctenodonta* (*Palaeoneilo*) Hall, Beushausen, p. 77

1899 *Palaeoneilo* Hall and Whitfield, Grabau, p. 256

1962 *Palaeoneilo* Hall and Whitfield, McAlester, p. 16

1966 *Ctenodonta* Salter, Babin, p. 41 (*partim*)

1966 *Palaeoneilo* Hall and Whitfield, Babin, p. 72 (*partim*)

1968 *Palaeoneilo* Hall and Whitfield, McAlester, p. 41

1969 *Palaeoneilo* Hall and Whitfield, McAlester, p. 233

Type Species

The type species for this genus is *Nuculites constricta* Conrad (1842) by subsequent designation of Hall (1885, p. xxvii). Provisional lectotype of the type species was designated by McAlester (1962, p. 18) as the right valve figured by Conrad (1842, Pl. 15, fig. 8). The whereabouts of Conrad's types is unknown, and they are assumed to be lost (McAlester, 1968, p. 41). Because the species can apparently be recognized from Conrad's figure, it was McAlester's thought that no neotype need be designated. This procedure is open to question. Conrad's type material is from the Middle Devonian (Hamilton group) of New York.

Diagnosis

Malletiidae with anterior and posterior dental series composed of similar size teeth on an arcuate dental plate containing teeth regularly diminishing in size toward the beak. Anterior teeth are vertical or inclined while the posterior ones are chevron-shaped, with the apexes of the chevrons pointing toward the beak and located at the venter of the dental plate posteriorly and becoming more dorsal anteriorly (Text-fig. 3). Posterior flank marked by a faint radial sulcus, extending from the umbo to the postero-ventral margin.

Description

These are medium to large sized (10-30mm in length), posteriorly elongate nuculoid bivalves that are equivalved and vary from oval or suboval to subrectangular in outline. The low, rounded, prosogyrous beak is located near the anterior third of the shell and rarely extends much above the dorsal margin. The posterior margin of the shell may be slightly attenuated.

The thin taxodont teeth are distributed uniformly along a gently arched hinge plate. Dentition is continuous beneath the beak. The anterior teeth may be vertical or inclined, while those posteriorly are chevron-shaped. Both series diminish in size toward the beak. The posterior series occupies at least half of the hinge-plate length, with at least twice as many teeth as in the anterior series. The chevrons of the posterior dental series are assymetrical with the apex of the posterior teeth near the hinge venter and becoming more dorsal in position nearer the beak (Text-fig. 3).

The adductor muscles are moderately impressed, and appear as suboval scars occurring just ventral to the terminal regions of the dental series. Accessory muscle impressions can also be observed dorsal to the adductors, near the hinge, and in the umbonal region. These scars are interpreted as reflecting pedal protractor and retractor and "dorsal-median" muscles respectively (Heath, 1937). The pallial line of this genus is entire. It is not certain whether a pallial sinus is present since preservation is not optimum in most specimens. McAlester (1968) showed a slight sinus in one Devonian species of this genus. The type species (*P. constrictus*) is not known to have a sinus.

The exterior surface of *Palaeoneilo* is marked by fine, closely spaced, uniform comarginal varices. An external ligament occupies a long narrow groove, posterior to the beak, along the dorsal margin of the dental plate.

Discussion

The spelling of this genus as originally proposed was Palaeaneilo, in an anonymous (1869) New York State Museum publication, but was soon changed to Palaeoneilo (Hall and Whitfield, 1873). Most subsequent authors used the emended spelling. As Stoll (1961) was of the view, however, that the new spelling was an unjustified emendation, the original spelling should be retained. Because the emended spelling had been so widely used, a decision was requested of the International Commission on Zoological Nomenclature. In a controversial decision, Opinion 215, the Commission ruled that the emended spelling and the original date be retained. The opinion attributed the authorship of the anonymous 1869 paper to James Hall. Cooper (1931), however, endeavored to show that the authorship should belong to Hall and Whitfield. Cooper's evidence seems valid; therefore, Palaeoneilo is here attributed to Hall and Whitfield, 1869.

Several authors have suggested that Palaeoneilo is a subgenus of Ctenodonta and is probably synonymous (Beushausen, 1895; Pfab, 1934; and Babin, 1966). However, the types of these two genera are sufficiently distinct that their synonymy seems unwarranted.

As with Nuculites, most Ordovician and Silurian species within this morphologic group are given different generic names from their Devonian and Carboniferous counterparts, which are usually called Palaeoneilo. Ordovician and

Silurian members are most often placed in Nucula, Tellinomya or Ctenodonta (Hall, 1857, 1862; Miller, 1889; Ulrich, 1894; Foerste, 1895; and others). Frankly, much of this taxonomy appears to have had more stratigraphic than morphologic basis. Pojeta (1971) suggested that certain small Ordovician nuculoids are morphologically best placed in Palaeoneilo. In the present work, morphology is the sole basis for taxonomic assignment. As with Nuculites, the present criteria for this form group are such that a relatively large group of species through a long period of time can be placed here.

Palaeoneilo, as conceived by McAlester (1969, p. 233) is an extremely long ranging genus with generalized suboval or subrectangular outline, and uniform dental series as described above. McAlester (1969) synonymized nine other genera with Palaeoneilo.

It seems unlikely that this form group should be included in only one genus with such a long geologic ("Ordovician to Mesozoic") and wide geographic range ("cosmopolitan"). Although no one has yet tackled the task of sorting out the taxa in this group, it seems likely that detailed examination of morphologic features (particularly dentition and musculature) should yield criteria to separate taxa in this group.

The Paleozoic taxa included in the Malletiidae by McAlester (1969) seem to be a heterogenous group of genera that should be separated in the future. In this family, Nuculites is perhaps the most closely related to Palaeoneilo.

Both have similar shell outlines (posteriorly elongate), similar, but not identical dentition (see generic discussion of both). Palaeoneilo is readily distinguishable from other nuculaceans (such as Praenuculidae members) in that Palaeoneilo is posteriorly elongate, while Praenuculidae genera (such as Deceptrix or Praenucula) are anteriorly elongate. This shell shape represents a fundamental biologic difference between these two families. In modern nuculoids, anteriorly elongate forms such as Nucula Lamarck have unfused mantle lobes and are deposit feeding; while posteriorly elongate types, such as Malletia desMoulin or Yoldia Möller, have partially or completely fused posterior mantle lobes that form siphons for a suspension feeding supplement to a deposit feeding habit.

Distribution

The type species was described from the Middle Devonian (Hamilton group) near Moravia, Cayuga County, New York. McAlester (1969, p. 233) placed nine genera in synonomy with Palaeoneilo and gave its consequent range as "Ordovician to Mesozoic" and its occurrence as "cosmopolitan." Most species have been described from the Devonian of eastern North America (Hall, 1885; McAlester, 1962, and others).

The Lower Palaeozoic distribution of this genus closely parallels that of Nuculites, predominantly in continental Europe, British Isles and North America, in Middle Ordovician through Devonian strata.

Palaeoneilo fecunda (Hall)

Pl. 4, fig. 1-13; Pl. 5, fig. 1-13, Pl. 6, fig. 1, 6

1847 Nucula levata Hall, p. 150 (partim), Pl. 34, fig. 1f-i

1862a Nucula (Tellinomya) fecunda Hall, p. 55 (figure only)

1870 non Palaeoneilo fecunda Hall, p. 8 (first illustrated by Hall (1889) Pl. 49, fig. 13

1894 non Ctenodonta simulatrix Ulrich, p. 600, Pl. 42, fig. 74, 75

1894 Ctenodonta fecunda (Hall), Ulrich, p. 595, Pl. 42, fig. 67-73.

1894 [?] Ctenodonta calvini Ulrich, p. 596, Pl. 42, fig. 61-64

1923 Ctenodonta cf. simulatrix Ulrich, Foerste, p. 87, Pl. 14, fig. 19a, b

1946 [?] Ctenodonta cf. calvini Ulrich, Reed, p. 702 (no figure)

1971 Palaeoneilo? fecunda (Hall), Snyder and Bretsky, p. 237

Type Specimens

Hall (1862a p. 55) figured a single specimen of this species. This specimen is the largest of a large suite of Hall's type specimens from the Upper Ordovician, Maquoketa Formation of Iowa which are in the collections of the American Museum of Natural History (AMNH 1360/5). In a manuscript in preparation, Pojeta will designate a lectotype. This illustrated specimen would seem automatically to be the best candidate for lectotype. The specimen figured by Hall (1862a) as well as several other specimens from the syntype suite are illustrated herein (Pl. 4, fig. 1, 2, 4, 5, 6, 9).

Diagnosis

Small, oval Palaeoneilo, with posterior radial sulcus poorly developed or obsolete. Beak and umbo relatively large, rounded and blunt, and only slightly prosocline. Hinge plate is uniformly curved and teeth are of nearly equal size, decreasing only slightly in size toward the beak.

Description

Small (usually less than 20mm in length) equivalved, and only slightly inequilateral, posteriorly elongate Palaeoneilo. The low rounded, slightly prosogyrous beak is variably located in the anterior half of the shell. There is a faint radial sulcus, variably developed to absent, extending from the umbonal region to the postero-ventral margin. This sulcus is often identifiable only through the presence of a reentrant in the shell outline at the postero-ventral margin (Pl. 4, fig. 1, 10).

There are fewer anterior teeth than posterior. In smallest individuals (9.3 to 0.7mm in length), there are three to four anterior teeth and four to five posterior teeth (Pl. 5, fig. 1,2); however, in larger shells (4 to 6mm in length), there are eight or nine anterior teeth and 15 to 20 posterior teeth (Pl. 5, fig. 8, 13). Intermediate sized individuals have numbers of teeth correlative with their size (Pl. 5, fig. 6, 7, 9). The number of posterior teeth increase at a greater rate than the anterior teeth during ontogeny. Inclined teeth occupy the anterior hinge plate, while the posterior teeth are chevron-shaped with the points of the chevron toward the beak. Additionally, the apex of the chevron is at the base (ventral on hinge plate) of posteriormost teeth and is in a successively more dorsal position in each tooth closer toward the beak. The posterior teeth nearest the beak have the chevron apexes near their dorsal margin (Text-fig. 3).

Scars of musculature are usually preserved on the interior of shells or the surface of Steinkerns. The most prominent scars are those of the adductor muscles. Both anterior and posterior scars are roughly oval in outline, with the anterior adductor scar somewhat more impressed (Pl. 4, fig. 13 and Pl. 5, fig. 5). The adductors were attached to the shell just below the anterior and posterior ends of the hinge plate.

Accessory scars, probably associated with pedal muscles are also preserved on the shell. A short elongate scar (pedal retractor) is present on the underside of the hinge plate dorsal to, but distinctly separated from the anterior adductor (Pl. 4, fig. 7). In a similar posterior position is a more elongate scar (pedal retractor) (Pl. 4, fig. 11). It is also discrete from the adductor. In a few Steinkerns, there are two or three dorso-ventrally elongate muscle scars in the umbonal region under the beak of each valve (Pl. 4, fig. 12). These scars are most likely reflective of dorso- and ventro-median muscles (as described by Heath, 1937, p. 14).

The pallial line is rarely preserved. An occasional specimen shows a pallial line which appears to be nonsinuate (Pl. 5, fig. 6). The opisthodetic ligament is seen in many shells as a long, narrow groove on the hinge plate, dorsal to the teeth, below and posterior to the beak (Pl. 4, fig. 9, Pl. 5, fig. 11, 12).

The shell surface is marked by numerous closely spaced, fine, comarginal growth varices (Pl. 4, fig. 1, 2; Pl. 5, fig. 10). An occasional more widely spaced varix is also observed (Pl. 4, fig. 2).

Discussion

In 1847 James Hall described a series of specimens collected from the Middle Ordovician "Trenton Limestone" of New York and Wisconsin as *Nucula levata*. Clarke and Ruedemann (1903b, p. 521) designated the specimen represented by Hall in Plate 34, fig. 1a, b, a specimen from New York, as the lectotype. Specimens figured by Hall as the "western specimens" (Pl. 34, fig. 1f-i) are distinctly different from the lectotype, which is anteriorly elongate, while the "western specimens" are posteriorly elongate. One of these specimens (Fig. 1g, h) is figured herein (Pl. 4, fig. 7, 10, 11) and may readily be placed in *Palaeoneilo fecunda*. The lectotype and specimens figured by Hall (1847) in figures 1c, d and e are now considered as belonging to *Deceptrix*

(Pojeta, 1971) because of the elongate anterior region.

Hall (1862a, p. 55) first used the name Nucula (Tellinomya) fecunda for a small nuculoid from the Upper Ordovician, Maquoketa Formation in Iowa, which he figured but did not describe.

In his monograph on "Lower Silurian [Upper Ordovician] Lamellibranchiata of Minnesota," Ulrich (1894, p. 595) figured and described additional specimens which he attributed to Hall's species, while assigning them to Ctenodonta (in his C. levata group). Ulrich also created Ctenodonta calvini for forms very similar to C. fecunda. He distinguished C. calvini from C. fecunda by lesser convexity of the valves, greater size and greater posterior height in C. calvini.

In one sample (WU-14) analyzed in this study, considerable variability was observed in shell shape (especially outline) with increasing size. Specimens (WU 1, 14) show that in smallest individuals of P. fecunda, the anterior and posterior lengths are about equal (Pl. 5, fig. 1); but as individuals grow larger, the posterior length increases more rapidly, thus producing an elongate posterior region (Pl. 5, fig. 6, 8). The variation in height, compared with length, is less dramatic with the length generally being about 1.4 times the height. Comparing individual specimens, however, there is considerable variation in the relative height of the valves. Several small valves (WU-14, WU-1) have a height much less than the average ratio (length greater than 1.4 times height) (Pl. 5, fig. 2, 6). While larger valves (WU-1) have a height that is greater than the average (length less than 1.4 times height) (Pl. 5, fig. 8). These specimens of *P. fecunda* with a relatively greater posterior height are quite similar to Ulrich's types of *P. calvini* (compare (Pl. 4, fig. 8 and Pl. 5, fig. 8). Since nothing is known about the ontogeny of *P. calvini*, it would not be wise to unconditionally synonymize *P. fecunda* and *P. calvini*. However, because the morphology (particlarly posterior height ratio) of *P. calvini* is within the morphological range of *P. fecunda* from the Brassfield, it seems reasonable to at least questionably assign *P. calvini* to *P. fecunda*.

Snyder and Bretsky (1971) studied large numbers of specimens of "*Palaeoneilo*? *fecunda*" from the Maquoketa in an attempt to establish ecological parameters (mortality and survivorship curves, size frequency distributions, etc). Results of their analyses are further discussed herein under "Bivalve Ecology and Paleoecology." This was the first published reference to *Ctenodonta fecunda* as a *Palaeoneilo*. Pojeta (1971, Pl. 1, fig. 8-11), in figuring one of Ulrich's plesiotypes, also referred this species to *Palaeoneilo* (Hall). These specimens figured by Snyder and Bretsky and Pojeta have an outline, shape and position of the beak that is very close to Hall's types of *P. fecunda*.

Foerste (1923, p. 87) reported the occurrence of bivalves from the Centerville shale (lowermost Brassfield Formation) near Dayton, Ohio, which he questionably assigned to Ctenodonta simulatrix Ulrich; however, reexamination of Foerste's specimens (USNM 72031) and Ulrich's type of C. simulatrix (USNM 46153) indicates Foerste's specimens compare more favorably with the types of Nucula (Tellinomya) [now Palaeoneilo] fecunda and are thus reassigned to that species. Ctenodonta simulatrix Ulrich is probably assignable to the Deceptrix-Praenucula form group. Ulrich's holotype (USNM 46153) is elongate anteriorly with the beak curving slightly toward the elongate end. In P. fecunda (Hall) and Foerste's specimens, the beak curves toward the shorter anterior region, while the posterior is elongate. The teeth of Ulrich's "C." simulatrix are straight both anteriorly and posteriorly (Ulrich, 1894, Pl. 42, fig. 75); while those of P. fecunda are inclined anteriorly and chevron-shaped posteriorly (Pl. 5, fig. 13). Some of Foerste's specimens are illustrated herein for comparison (Pl. 6, fig. 1, 6).

Placing Nucula (Tellinomya) fecunda Hall (1862) in Palaeoneilo creates a nomenclatural conflict. Hall (1870, p. 9) proposed the name Palaeoneilo fecunda for a different group of shells from the "Hamilton group" (M. Devonian) of New York state. This species was not figured until much later (Hall, 1885, Pl. 49, fig. 13, 15-24). The morphology of this Hamilton species is documented by Hall (1885, p. 336) and should suffice to describe the species. These two species have, thus, been made homonymous. The name belongs to the 1862a species, and the 1870 species becomes a junior subjective homonym. Some of Hall's original specimens of Palaeoneilo fecunda Hall (1870, p. 8) are reillustrated (Pl. 2, fig. 4, 7) and the new name for this Middle Devonian species, proposed here, is Palaeoneilo halli. The specimen figured by Hall (1885, Pl. 49, fig. 15) and reillustrated here is designated the lectotype (Pl. 6, fig. 3).

The morphology of Palaeoneilo fecunda (Hall, 1862a) has previously been known almost exclusively from articulated specimens preserving external features and from Steinkerns. Most of the individuals assigned to this species from the Brassfield are, however, limonite replaced, disarticulated valves and some show a quality of preservation (interior and exterior features) comparable to Tertiary and Recent shells.

Distribution

Hall's syntype suite of P. fecunda (Hall) was collected from the "Hudson River Group, Scales Mound, Illinois" (probably Maquoketa Formation, Upper Ordovician). This species is also reported from the Maquoketa Formation of Wisconsin and Iowa (Ulrich, 1894 and Snyder and Bretsky, 1971).

It is known also from the same horizon in Wisconsin an Iowa (Ulrich, 1894, Snyder and Bretsky, 1971); as "Nucula" levata "western syntypes" also from the Wisconsin Maquoketa (Hall, 1847); from the Maquoketa, near Graf, Iowa (the types of Ctenodonta calvini Ulrich, 1894) and Scales Mound, Illinois (Ulrich, 1894, p. 597). John Pojeta (personal communication) has found P. fecunda in the Middle Ordovician of Kentucky, the oldest report of the species. Reed (1946) identified a single specimen of C. calvini Ulrich from the Hill Quarry Beds (Upper Ordovician) of Girvan, Scotland. There are several Lower Silurian Brassfield occurrences: the Centerville Shale (Lower Brassfield) near Centerville, Ohio (Foerste, 1923); from the present study, at Todd Fork Creek near Wilmington, Ohio and from the ferruginous and associated calcareous limestone layers 35 to 37 feet above the base of the Brassfield in several road cuts on State Road 41, 2.5 miles north of West Union, Adams County, Ohio (WU-14, 1, 11, and 101-20).

Ontogeny

Specimens of Palaeoneilo fecunda occur in all the samples etched with acid from the West Union, Ohio, area. This is by far the most abundant species in every sample. For example, sample WU-14 (a sample used for quantitative data presented in this study) has a total of 894 valves and 78 shells, of which 668 valves and 56 shells are assignable to P. fecunda. Three hundred eighty-three well preserved specimens were measured.

The lengths of specimens in this species range from 0.55mm to 5.40mm. The heights of 252 specimens measured range from 0.45mm to 3.50mm. Of these specimens, 114 (45%) are less than 0.75mm high. In 277 individuals where length could be measured, 120 (43%) were less than 1.0mm long.

This large number of small individuals may be explained in several ways (discussed in the paleoecology section), including mechanical sorting, high juvenile mortality, and paedomorphism. Several histograms (Text-fig. 14) show the size distribution of P. fecunda based on several parameters. The marked left skew of these graphs reiterates the large number of small individuals in this sample.

The number of teeth in the anterior and posterior dental series varies, with consistently more in the posterior series. The fewest teeth occur in the smallest individuals; as the shell grows larger, more teeth are added to each series at its distal (farthest from beak) margin.

The average number of anterior teeth for the smallest specimens (0.34 to 1.00mm long) is 4, while larger valves (greater than 3.00mm) have 9 teeth. There are 5 teeth in the posterior series of the smallest valves. Intermediate sized shells have numbers of teeth commensurate with their size, with more posterior teeth being added during growth (Table 5).

Table 5. Number of teeth per valve in Palaeoneilo fecunda (Hall) of the "diminutive" Brassfield

In addition to the considerable change in number of teeth, there is a change in tooth shape as more teeth are added and the teeth become larger. Both anterior and posterior teeth of very small (less than 0.75mm in length) valves of P. fecunda are inclined, straight teeth, and new teeth are added with straight, inclined orientation (tooth slopes away from beak). However, posterior teeth nearer the beak (older teeth) are more symmetrically chevron-shaped

Table 5. Number of teeth per valve in _Palaeoneilo fecunda_ (Hall) of the "diminutive" Brassfield (samples WU-1, 11, 14, 101-20)

Length(mm)	Number of Anterior teeth	Number of Posterior teeth
0.00-0.33*	--	--
0.34-0.67	3	4-5
0.68-1.00	4-5	6-8
1.01-1.33	4-5	7-9
1.34-1.67	4-6	8-11
1.68-2.00	5-6	11-13
2.01-2.33	6-8	12-14
2.34-2.67	7-8	12-15
2.68-3.00	7-8	12-14
3.01-3.33	7-10	14-16
3.34-3.67	7-9	14-17
3.68-4.00	8	18
4.00-4.33	8	15-19

*No specimens in the size class were found.

than those farther away. Text-fig. 3 illustrates the change in tooth shape of the posterior dentition from beak to posterior margin. Apparently, secondary addition of material to the ventral portion of older teeth in an increasingly posterior direction produces the chevron effect, and younger posterior teeth (distal) have not had time to be formed into symmetrical chevrons as have the ones near the beak. There is no change in the shape of the anterior teeth in right valves less than 1.50mm in length. There is a tooth directly below the beak that is conspicuously larger than other teeth and is erect (nearly vertical to the hinge plate) (Pl. 5, fig. 7, 12). In the left valve, there is a correspondingly large socket. This socket is in such a position that it could be mistaken for a resilifer. This large tooth cannot be distinguished in larger valves because of the greater relative growth rate of adjacent teeth.

The position of the beak varies through ontogeny. Beak position is reflected by the anterior/posterior lengths. Text-fig. 17 is a plot of anterior length versus posterior

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Text-fig. 17 --Anterior to posterior length and length to height ratios of Palaeoneilo fecunda (Hall) population at West Union, Ohio (WU-14).

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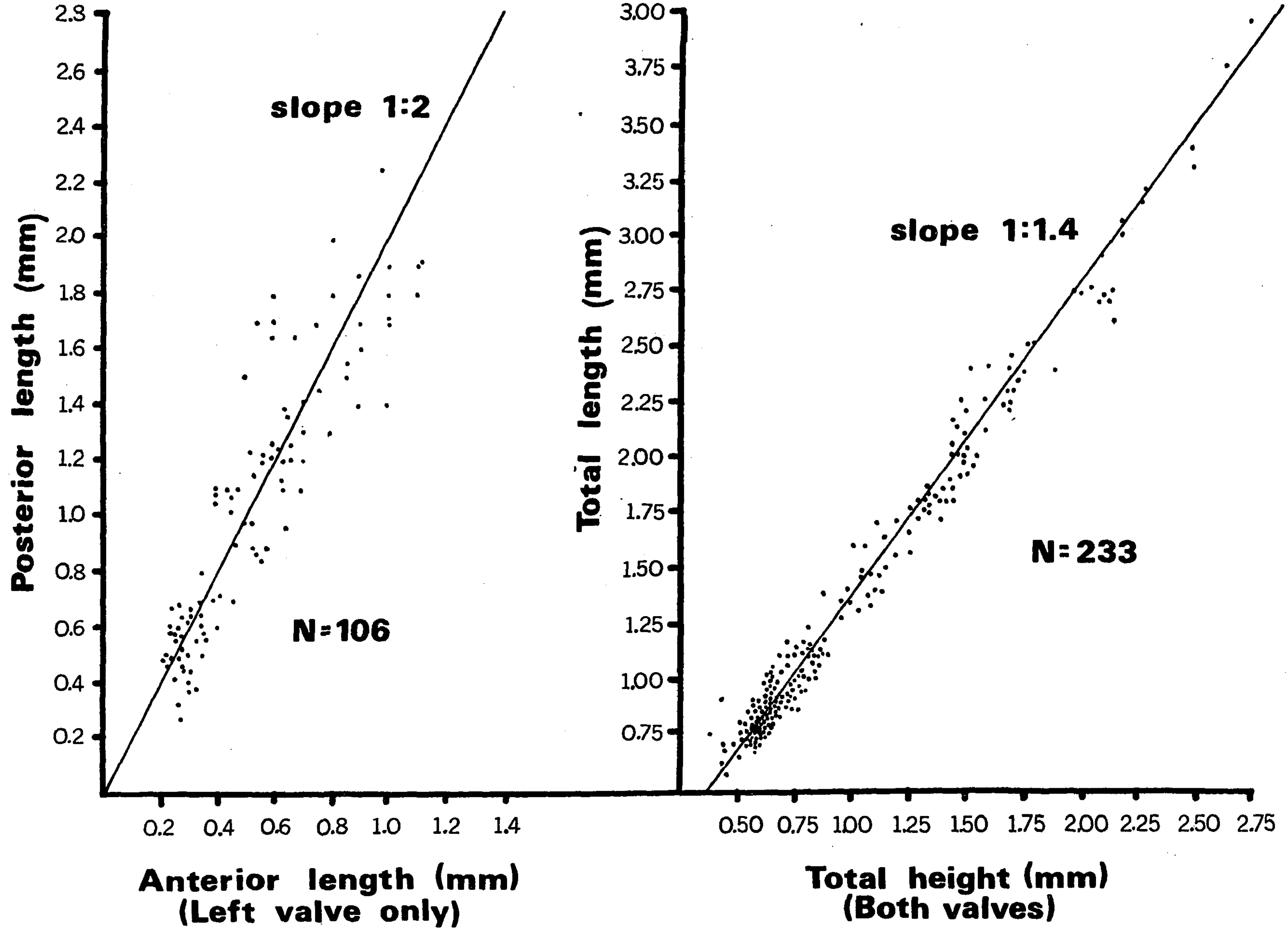
length. A reference line of an anterior/posterior ratio of 1:2 is included on this graph.

The smallest valve has an anterior length of 0.27mm and a posterior length of 0.28mm. This yields an anterior/posterior length ratio of nearly 1.00, indicating a centrally



Text-fig. 17--Anterior to posterior length and length to height ratios of Palaeoneilo fecunda (Hall) population at West Union, Ohio (WU-14).

placed beak. Most valves with a posterior length of less than 0.5mm have an anterior/posterior length ratio greater than 0.5 (that is, to the right of the 1:2 line). In these valves, the beak is therefore subcentrally located. However, as the valves grow larger, the beak becomes relatively closer to the anterior end of the shell (although there is considerable variability in larger individuals). The apparent movement of the beak probably reflects a more rapid relative growth rate of the posterior region of the shell (see Pl. 5, fig. 1-10 for a growth series of specimens of this species).

Figured specimens

Palaeoneilo constricta OSU 12968; *Palaeoneilo calvini* USNM 46124; "*Nucula levata*" AMNH 1362/3; "*Ctenodonta* cf. *simulatrix*" USNM 72031; *Palaeoneilo fecunda* AMNH 1360/5, 1360/5A, 1360/5E, 1360/5G; UCGM 42638-42649.

New Genus "A"

Type Species

New genus "A" *foerstei* n. sp. is the type species of this genus. It is known only from the upper thinly-bedded unit of the Brassfield (Lower Silurian) in Adams County, Ohio.

Diagnosis

Malletiidae with erect beak and dental plate differentiated into an unequal anterior and posterior rectilinear series that meet with a sharp angulation beneath the beak (angle of 140° to 150°). The posterior series is longer and has more teeth. The posterior teeth are chevron-shaped, while the anterior teeth are straight or slightly undulose.

Description

Fossils assignable here are small for this family (probably not exceeding 3 to 4mm in length). The shell appears to be posteriorly elongate with the beak within the anterior one-third of the shell. The beak is distinct, rounded and erect (orthogyrous). The posterior dental series is longer than the anterior one and the teeth are chevron-shaped, with the apex of the chevrons pointing toward the beak. The anterior teeth are straight or slightly undulose with the long axis of each tooth perpendicular to the ventral margin of the hinge. No evidence of the musculature, ligament or body of shell is preserved.

Discussion

The Malletiidae as presently conceived can accommodate this genus, but should this family be re-evaluted, with close attention paid to the dentition types, this genus may be assigned to a new family. The angulation of the hinge in this genus is unlike any other palaeotaxodont. Only Tancrediopsis Beushausen (Family Ctenodontidae) has a strongly angulated hinge plate but in Tancrediopsis, the anterior and posterior series are equal in length and number of chevron-shaped teeth. The dentition of this new genus is very similar to that of some species of Nuculites.

Nuculites have an elongate posterior series with chevron-shaped teeth and fewer slightly undulose anterior teeth. The *Nuculites* anterior teeth are not, however, perpendicular to the venter of the hinge and are often more undulose. This new genus also lacks the anterior septum characteristic of *Nuculites*. The hinge of *Nuculites* is not angulated, but gently convexly curved dorsally.

Distribution

The type suite was collected from the upper thinly-bedded unit of the Brassfield Formation near West Union, Adams County, Ohio (WU-1, 11, 14)

New Genus "A" *foerstei* n. sp.

Pl. 6, fig. 9-11

Type Specimens

The holotype (UCGM 42651) and the paratypes (UCGM 42650, 42652) are from the upper thinly-bedded Brassfield Formation (Lower Silurian), near West Union, Adams County, Ohio.

Diagnosis

Because this species is the only one assignable to New Genus "A", the diagnostic characteristics of the genus, including chevron-shaped posterior teeth and straight or slightly undulose anterior ones on a distinctly angulated hinge plate, apply here as well.

Description

Descriptive characteristics are also presented in the systematics of this new genus. Let it suffice here to say that shells of this species are small, posteriorly elongate, nuculoids with an erect, rounded beak and a posterior series of chevron-shaped teeth (usually 6-8 teeth) and an anterior series of straight or slightly undulose teeth with their long axes perpendicular to the ventral margin of the hinge plate. The anterior and posterior regions of the hinge plate and contained dental series meet at a distinct angle beneath the beak (angle of 140-150°).

Discussion

As mentioned in the generic discussion of New Genus "A", there are virtually no Paleozoic nuculoids exactly like New Genus "A" *foerstei* n. sp. However, there is one form group of palaeotaxodonts that has some similar morphological features: "*Ctenodonta*" *longa* (Ulrich, 1892) (Pl. 6, fig. 5, 8). "*C.*" *longa* is posteriorly elongate and has the distinctly angulated hinge plate and dental series. The posterior series is longer and has more teeth just as in the specimens of New Genus "A" *foerstei* n. sp. The tooth shape in "*C.*" *longa* is substantially different from that in New Genus "A" *foerstei*. "*C.*" *longa* has only straight teeth that have their long axes perpendicular to the anterior/posterior adductor scar axis rather than to the base of the hinge plate. The teeth of the anterior and posterior series of "*C.*" *longa* are very similar in shape, a few may be slightly undulose, but none show any tendency toward a chevron shape. "*C.*" *longa* was collected from the middle (stratigraphically) Trenton Shales (Middle Ordovician) at Goodhue County, Minnesota. John

Pojeta (personal communication) has recovered large accumulations of several species similar to "C." longa in the Middle Ordovician of Central Kentucky.

It seems reasonable, therefore, that a consistent development of straight teeth in the Middle Ordovician forms like "C." longa represents a separate genetic entity from those nuculoids in the Lower Silurian Brassfield that have chevron-shaped posterior teeth and straight but differently oriented anterior teeth.

This difference in these two taxa is perhaps presently best ascribed to a generic level taxobasis. The uniquely similar angulated hinge does, however, imply that the "C." longa form group is more closely related to New Genus "A" foerstei than to any other Paleozoic nuculoids. This affinity might be indicated by grouping these two in a subfamilial category. However, since strict re-evaluation of the Malletiidae and concomitant taxobases is greatly needed, the familial structure of these posterior elongate Paleozoic nuculoids should be held in abeyance.

Distribution

All specimens from the Brassfield Formation were recovered from acid residues of samples collected from the ferrugenous and associated calcareous limestone 35 to 57 feet above the base of the Brassfield at several road cuts on the west side of State Road 41, 2.5 miles north of West Union, Adams County, Ohio.

Figured specimens

"Ctenodonta" longa USNM 46135; New Genus "A" foerstei UCGM 42650-42652.

Subclass HETEROCONCHIA Hertwig

Order TRIGONIOIDA Dall

Diagnosis

Shell triangular to subtriangular, posteriorly elongate, with two or more ventrally diverging cardinal teeth in each valve. The shell exterior is differentiated into a lateral portion (flank) and a postumbonal region (area) separated by an umbonal ridge extending from the beak to the postero-ventral margin (marginal carina).

Superfamily LYRODESMATACEA Ulrich

(nom. trans. Lyumkevich, et al.)

Family LYRODESMATIDAE Ulrich

Diagnosis

Trigonioida with a semicircular hinge plate possessing four to nine transversely striated, ventrally diverging teeth, more or less symmetrically arranged beneath the beak.

Discussion

The systematic position and composition of the Lyrodesmatidae has been subject to question since the family was first proposed. Ulrich (1894, p. 486) originally conceived the family (his Lyrodesmidae) as containing Lyrodesma, Allodesma, Ischyrina and Technophorous (all Ordovician), but later in the same paper (p. 608) removed all genera except Lyrodesma. Ulrich was undecided about the higher level taxonomic relations of the Lyrodesmatidae and balked at any concrete statements of relationships.

Dall (1895, p. 524 and 1900, p. 378) questionably placed Actinodonta along with Lyrodesma in the Lyrodesmatidae. This family, together with the Trigonidae, he placed in the superfamily Trigoniacea. Lyumkevich, et. al. in the Osnovii Palaeontologie (1960, p. 93) assigned Lyrodesma and Actinodonta to the Lyrodesmatidae of the Lyrodesmatacea in the order Schizodonta Steinmann which is equivalent to Trigonioida Dall (1889) as used by Newell (1965).

Vokes (1967, p. 225) divided the order Trigonioida into two superfamilies--the Lyrodesmatacea and the Trigoniacea. To the Lyrodesmatacea he assigned one family (Lyrodesmatidae) with the genera: Actinodonta, Actinodontophora, Honeymania, Ischyrodonta, Palaeopteria and Lyrodesma, among others.

Cox (1960, p. 73) grouped Actinodonta, Allodesma, Cycloconcha, Ischyrodonta, Redonia and Lyrodesma in the Lyrodesmatidae, but placed them in the order Pantodontida, a little known suborder of Dall (1895, p. 537). The order Actinodontoida Douvillé (1912, p. 438) has often been used to include the genus Actinodonta and miscellaneous other genera. Cox showed preference for Pantodontida over Actinodontoida because of what he called confusion over the definition of the Actinodontoida. His concept of the order was, however, significantly broader than Dall's, as evidenced by the genera he included.

Newell and LaRocque (1969, p. 471) reverted to Ulrich's original revised idea and placed only Lyrodesma in the Lyrodesmatidae and questionably put the family in the superfamily Trigoniacea and order Trigonioida.

Pojeta (1971, p. 9) favors the use of Actinodontoida for the ordinal taxon containing the Lyrodesmatidae. He noted (p. 10) that at present the Lyrodesmatidae is monogeneric but will probably be subdivided when the group is more intensely studied. The argument used by Pojeta for classifying Lyrodesma with actinodonts is based on dentition. Comparison of dentition of the French Early Ordovician (the oldest lyrodesmatid) Lyrodesma armoricana de Tromelin and Lebesconte (1876) with Cycloconcha (an actinodont) of Middle and Upper Ordovician age) indicates that there may be a relationship between these two genera. Long posterior teeth of the Early Ordovician Lyrodesma are similar to those of some actinodonts (Pojeta, p. 10). Pojeta also noted that the posterior teeth are reduced to virtually the same length as the anterior ones in Middle and Upper Ordovician forms. In Early Silurian (Brassfield) specimens, the teeth are nearly all the same length.

Although Pojeta would agree that Lyrodesma is the most probable known genus ancestral to the Trigoniaceans (p. 28) it is not a trigoniacean per se. If the elongate posterior teeth of L. armoricana are homologous with the posterior lateral teeth of Cycloconcha, Lyrodesma should be classified in the Order Actinodontoida.

There seems little doubt that lyrodesmatids are related to actinodonts, and the Early Ordovician members are quite probably evolutionary derivatives from them. But it is equally reasonable to assume that lyrodesmatids are the stock form which trigonids and myophorids (trigoniaceans) evolved. The Order Trigonioida contains four families, the Lyrodesmatidae, Trigoniidae, Myophoriidae and Scaphellinidae. All have the characteristic subtrigonal valve outline, with flank and area differentiated. Members of each also have ventrally diverging cardinal teeth. Teeth of the Lyrodesmatidae and Trigoniidae are always transversely striated while those of the Myophoriidae are not commonly striated and striation is absent in many genera assigned here. No striation has been observed on any members of the Scaphellinidae. The stratigraphic range of the Lyrodesmatidae is Lower Ordovician to Lower Silurian, the Myophoridae from Lower Devonian to Upper Triassic, the Scaphellinidae (monogeneric) is Lower Permian, and the Trigoniidae Middle Triassic to Recent.

The later members (Middle and Upper Ordovician) of the Lyrodesmatidae are morphologically much more like Trigoniaceans than actinodonts, based on the total aspect of their morphology, which is summarized under the generic systematics of Lyrodesma. Lyrodesmatids are, thus, placed in the order Trigonioida, but the differences from other trigoniids seem to warrant their assignment to a separate superfamily. Lyumkevich et al (1960) elevated Ulrich's family to superfamilial status. It is monotypic, containing the single family Lyrodesmatidae and genus *Lyrodesma*.

Distribution

Lyrodesma occurs in Lower, Middle and Upper Ordovician strata, with a cosmopolitan distribution. The genus is also reported from the Welsh Lower Silurian.

Genus LYRODESMA Conrad, 1841

1841 *Lyrodesma* Conrad, p. 51

1851 *Lyrodesma* Conrad, M'Coy, p. 272 (*partim*)

1871 *Lyrodesma* Conrad, Hall, p. 227

1889 *Lyrodesma* Conrad, Miller, S. A. p. 487

1894 *Lyrodesma* Conrad, Ulrich, p. 608 (*partim*)

1895 *Lyrodesma* Conrad, Dall, p. 524 (*partim*)

1909 *Lyrodesma* Conrad, Grabau and Shimer, p. 481

1960 *Lyrodesma* Conrad, Lyumkevich, *et al*. p. 93 (*partim*)

1966 *Lyrodesma* Conrad, Babin, p. 237

1969 *Lyrodesma* Conrad, Newell and LaRocque, p. 471

1971 *Lyrodesma* Conrad, Pojeta, p. 10

Type species

Lyrodesma planum Conrad (1841, p. 51) from the Middle Ordovician of New York state, is the type species by monotypy. No figure accompanied Conrad's original description in most copies of the Fifth Annual Report. However, Hall (1862b, Pl. 11, fig. 5) published a plate, supposedly belonging to Conrad, which he said was distributed with some copies of the Fifth Annual Report. Figure 5 of this plate is labeled, "*Lyrodesma*: Conrad, Annual Report 1841, p. 51."

Diagnosis

At present, *Lyrodesma* is the only representative of the Lyrodesmatidae; therefore, the diagnostic features of the genus are the same as for the family.

Description

These are medium-sized (rarely exceeding 30mm in length), inequilateral bivalves with the beak near the anterior third of the shell. Most forms are subtrigonal, with a rounded anterior and ventral outline. The posterior region is elongate but somewhat obliquely truncate, and often attenuated posterior-ventrally with a postumbonal region (area) separated from the main body (flank) of the shell by a sharp umbonal carina. The flank contains only numerous, very fine, comarginal varices; the area may be smooth or longitudinally striated.

There are four to nine cardinal teeth on a semicircular hinge plate arranged symmetrically directly beneath the beak. In most species, teeth are of equal length, but at least two species (Early Ordovician, Europe), *L. acuminata* Barrois (1891) and *L. armoricana* de Tromeline and Lebesconte (1876), show some elongation of the posterior teeth. In juveniles of this genus from the Brassfield, as few as two cardinal teeth are known and the tooth display may be interpreted as similar to *Trigonia* (Text-fig. 4). A distinctive feature of *Lyrodesma* teeth is the presence of numerous gently curving transverse striae on the lateral articulating surface of each tooth.

The two subequal adductor scars are moderately impressed into each valve and bounded on their inner margins by a slightly elevated buttress. The adductor muscles are located in the dorsal one-fourth of the valve and are attached near the shell margin slightly below the hinge plate. Pedal muscle scars are small circular pits, deeply impressed at the ventro-lateral edges of the hinge plate and just dorsal to the adductor scars. Because the anterior pedal and adductor scars are not distinctly separate, the pedal retractor and protractor muscles appear confluent with the adductor muscle, while the posterior retractor and adductor muscle scars are separate, probably indicating disjunct muscles. There are also several small muscle scars impressed on the underside of the hinge plate and in the umbonal region. These scars reflect muscles of uncertain function, but may be accessory pedal muscles.

The pallial line of Lyrodesma is entire but only faintly impressed and preserved in only a few specimens. Where present, however, the pallial line shows a slight sinus (Ulrich, 1893 [1895], p. 684, Pl. 47, fig. 9 and Pojeta, 1971, p. 11, Pl. 3, fig. 16-18).

Little mention is made of the ligament in published accounts of this genus. It is most probably located in a short narrow slit just posterior to the beak along the dorsal margin. This is the position it occupies in all other trigonids.

Discussion

A discussion of the history of higher level taxonomy of this genus is presented under the family Lyrodesmatidae. The general subtrigonal outline, the differentiation of the shell surface into a lateral flank, a postumbonal area separated by a carina and the presence of ventrally diverging cardinal teeth are aspects of Lyrodesma's morphology which indicate similarity to trigonids and myophorids. The musculature of Lyrodesma and the trigonids and myophirids are also similar. The adductors of each are small prolate and well impressed in the shell just beneath the anterior and posterior ends of the hinge plate. The posterior pedal retractor is also deeply impressed, about one-third the adductor size and located on the posterior ventral margin of the hinge plate. Lyrodesma does, however, show less similarity to trigonids and myophorids than they do to each other. While adult Lyrodesma have 4 to 9 cardinal teeth in each valve, all trigonids and myophorids have two main in the right valve and three in the left. Lyrodesma has an unsculptured flank while the flank of myophorids and trigonids commonly show prosopon with costae, plicae or comarginal rugae. Hence the conclusion here is that trigonids and myophorids belong to the same superfamily (Trigoniacea) and lyrodesmatids to another superfamily (Lyrodesmatacea) of the same order (Trigonioida).

Approximately 26 species (Early to Late Ordovician) have been assigned to Lyrodesma (Pojeta, 1971, p. 7).

Species taxonomy has been based mainly on the number of cardinal teeth and shell outline. The number of cardinal teeth, however, apparently varies with ontogentic stage of the individuals. Examination of more than twenty-five specimens of Lyrodesma subplanum Conrad of varying sizes etched from a sample of the lower Clay's Ferry Limestone (Middle Ordovician) collected at Cynthiana, Kentucky (U. S. Geological Survey locality 6146, CO, UCGM 42667) shows that smaller individuals have fewer teeth: the smallest complete specimens from this sample (6.5mm) possess four cardinal teeth while the largest (21.0mm) have nine. Individuals intermediate in size possess five to eight teeth. Variation in ontogeny has apparently not been taken into account when these species were erected. Because one major taxobasis (number of cardinal teeth) can be shown to vary through ontogeny, it seems reasonable that these previously erected species should be re-evaluated to see if some (those with fewer teeth) may be juveniles of other existing species.

Distribution

The genus was heretofore known from Middle and Upper Ordovician beds in North America and Europe, particularly in the eastern United States and adjacent Canada. Although Ziegler, Cocks and Bambach (1968) cite the occurrence of Lyrodesma in the Welsh Lower Silurian, they give no species identification nor present any aspects of morphology for their material. The occurrence of Lyrodesma in the upper thin-bedded unit of the Brassfield provides an additional, better documented reference of this genus in Lower Silurian rocks.

Lyrodesma sp.

Pl. 9, fig. 4, 6-10

Description

Material upon which this species is based consists of partial and complete molds of hinge plates, molds of isolated denticles, Steinkerns, and limonite coated or permineralized valves of small individuals (0.60mm to 2.0mm) that are equivalved and slightly inequilateral, being elongate posteriorly. Most of the following details of morphology are based on these small specimens. The shell outline is subtrigonal, with the anterior and posterior margins quite rounded. An umbonal ridge extends from the beak to the postero-ventral margin delineating an area and flank, although the separation of these regions on the shell is less distinct than in adult individuals of the genus (for example, see Nucula [Lyrodesma] poststriata Hall, 1847, Pl. 82, fig. 10a, from the Upper Ordovician of New York State). The umbo of each valve is considerably inflated making the beak region appear relatively large. The blunt beak is erect and extends only slightly above the dorsal margin.

The dentition consists of two to four ventrally diverging cardinal teeth in individuals less than 2mm long (Pl. 9, fig. 6, 7, 9, 10). Most of these small shells are from

0.60mm to 0.90mm in length and bear two teeth in the right valve and three in the left. These teeth do not appear to be striated. However, the teeth of the complete dental plates (2.7mm in length of plate) and the isolated teeth are all transversely striated (Pl. 9, fig. 4, 8)

Muscle scars are sometimes preserved in these specimens and more commonly on Steinkerns. The adductors are small, oval and located under the dorsal margin at the anterior and posterior ends of the shell. Two or three pairs of smaller accessory scars occur beneath the beak and are particularly obvious in the Steinkerns. No pallial line is preserved on any specimens studied here. The shell exterior is marked by faint, fine comarginal growth varices. The ligament apparently occuped a short, narrow rarely preserved groove just posterior to the beak.

Discussion

This uncertain species is known mainly from juvenile individuals, disarticulated dental elements and two complete hinge plates of larger specimens with 6 teeth. No complete adult valves were recovered, however, the morphology of these hinge plates (semicircular with ventrally diverging striated dental elements) is characteristic of Lyrodesma. One complete hinge plate (2.7mm long) has six teeth (Pl. 9, fig. 8) and by comparison with the Clay's Ferry sample, would have a shell about 7 or 8mm long. The smallest complete specimen from this Clay's Ferry (Middle Ordovician) sample is 6.5mm long and has a hinge plate 2.5mm long. A specimen 8.5mm long has a hinge plate length of 4.0mm; and the largest valve of this suite is 21.0mm long, with a hinge plate 7.5mm long. The smallest complete hinge plate recovered was 2.2mm long and contained five teeth. The 2.5mm hinge plate had six teeth; the 4.0mm hinge, seven teeth, and the 7.5mm hinge, nine. Transverse striations were not seen on teeth of the smallest hinges, but this may be a factor of the coarse silicification of these specimens.

Complete or nearly complete shells of small specimens from the Brassfield range in size from about 0.6mm to 2.0mm. The hinge plates of these smaller specimens are only about 0.1 to 0.5mm long. They have 2 or 3 teeth (depending on the valve, see ontogeny) in the smaller sizes and 3 to 4 teeth in the larger. Because of the increase of teeth with size, the ventrally diverging cardinal type of teeth. and the subtrigonal shell, with flank and area regions, it is believed that these small specimens are juveniles of Lyrodesma. There are no specimens (valves or hinge plates) collected in the size range between the largest (about 2.0mm) complete small specimen (valves) and the postulated length (about 8mm) of the specimens from which the complete hinge plates originated. However, the trend of increasing number of teeth with increasing size, would lead one to conclude that if these intermediate sizes were found, a complete gradation would exist from the vary small specimens with two teeth to those with six teeth.

The gap in this size distribution is in part produced by the current sorting that has acted upon these particles; particles larger than 3mm are uncommon. Additionally, the complete hinge plates are preserved differently from the small whole specimens. Since the hinge is the most massive part of the shell, it is more likely to be preserved than the much thinner shell. While the small, complete shells are coated or infiltrated with fine-grained iron oxide (limonite?), the larger hinge plates are apparently molds in a fine-grained matrix of iron oxide or silty dolomite. This molding process may not have preserved the thin shell as well as it did the hinge and subsequent diagenesis or sample processing could have destroyed these larger shells leaving only the durable hinge structure.

Species of this genus are defined on the number of teeth and shell shape in adult individuals. Since no complete adult specimens were recovered, it is deemed unwise to erect a new species on juveniles and fragments of adults. To the author's knowledge, this is the only description of specimens of Lyrodesma of this small size. Most individuals previously described (presumably adults) are rarely less than 10mm in length.

Distribution

All of the specimens of this species were collected from acetic acid residues of samples of the ferruginous and associated limestone layers 35 to 37 feet above the base of the Brassfield Formation in several sections on the west side of State Road 41, 2.5 miles north of West Union, Adams County, Ohio (WU-1, 11, 14 and 101-20).

Ontogeny

Description of ontogeny for this species is based on 137 individuals and 9 articulated valves etched from a 6.5 pound block of ferruginous limestone (sample WU-14). Many of the valves were broken; however, 61 were complete enough to measure some parameters. The smallest shell is a right valve with a length of 0.61mm and a height of 0.53mm. The largest complete valve is 1.65mm long and 1.27mm high (a left valve). A broken right valve, 1.9mm long was recovered. About 70% of all valves recovered are between 1.65mm and 0.95mm in length.

Shells less than 0.9mm in length usually have 2 teeth in the right valve and three in the left. Within the size range of 1.00mm to 1.60mm in length, there are 3 teeth in the right valve and 4 teeth in the left valve. A right valve 1.90mm long has 4 cardinal teeth. What is judged to be an adult complete hinge plate has 6 teeth and 5 sockets. This hinge plate is 2.7mm in greatest dimension.

The shell shape of these small individuals changes slightly with increasing size, the posterior becoming more elongate in larger individuals (1.0mm and larger). Text-fig. 18 is a plot of length versus height of 43 valves (4 articulated) from sample WU-14. This graph illustrated that the shell has a relatively greater length in larger individuals (compare slope of points to a line representing a length/height ratio of 1 to 1). This type of allometric

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Text-fig.18--Length to height plot for _Lyrodesma_ sp. (WU-14) and _Actinopteria brisa_ (all samples).

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growth is relatively common in bivalves, particularly those whose ontogenies have been studied herein.

Figured specimens

UCGM 42658-42661, 42666.

Sublcass PTERIOMORPHIA Beurlen

Order [?]ARCOIDA Stoliczka

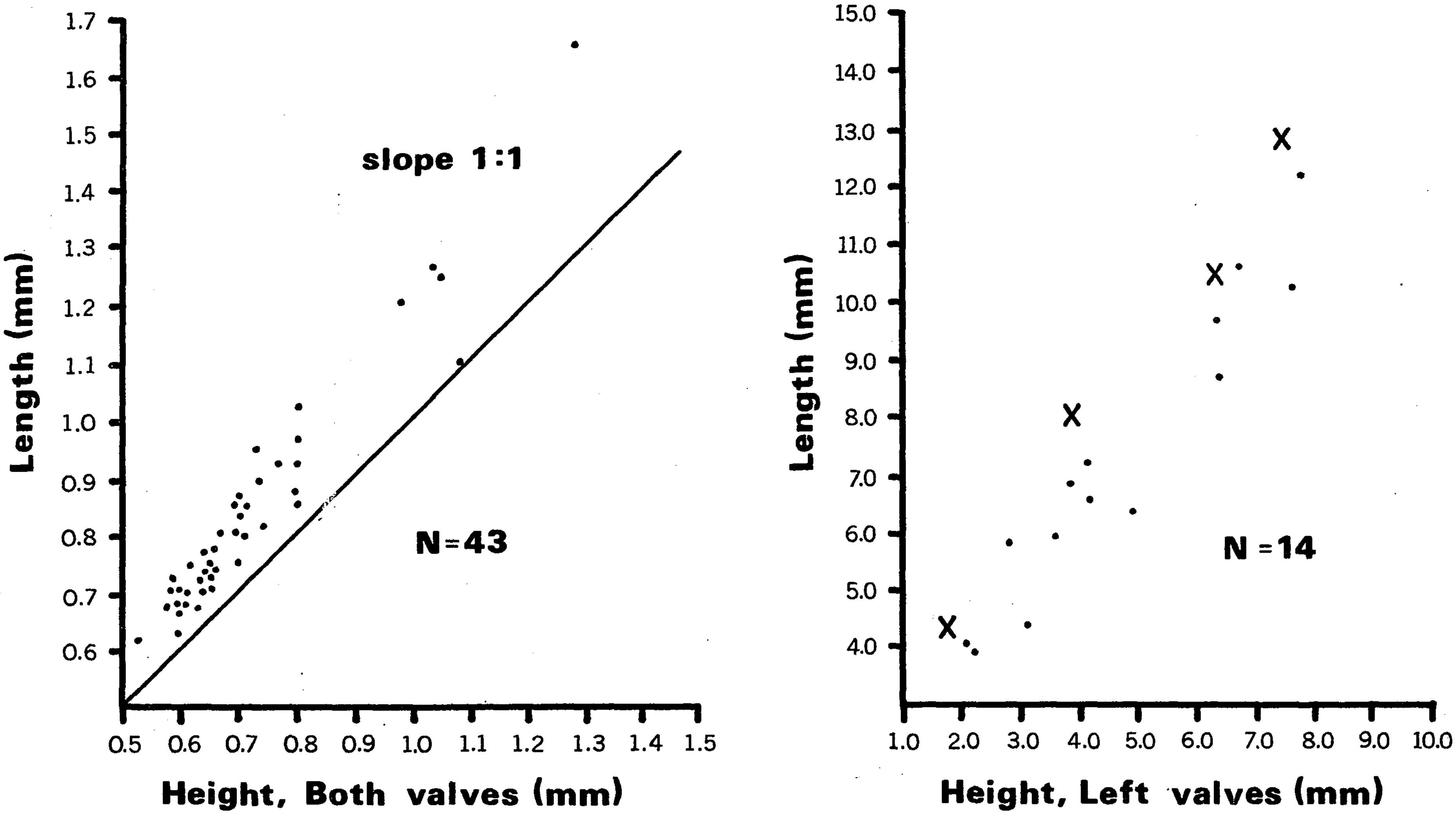
Superfamily [?]CYRTODONTACEA Ulrich

(_Nom. trans_. Newell)

Family [?]CYRTODONTIDAE Ulrich

Description

Genera assignable to this family are avoid and gibbous, prosocline bivalves with comarginal growth varices or rugae. Most are equivalved with a prominent duplivincular ligament and commonly well-developed cardinal and posterior lateral dentition. The adductor muscle scars are subequal in size and usually nearly circular, with the anterior one often deeply impressed into a platform or area of shell thickening (callous) at the anterior margin of the hinge plate. This type of anterior adductor occurrence is apparently restricted to byssally attached types of bivalves (Pojeta, 1971, p. 18). There is no byssal gape seen in forms assigned here. The



Text-fig. 18--Length to height plot for Lyrodesma sp. from sample WU-14 (left and Actinopteria brisa from all samples (right).

beak is situated within the anterior one-third of the shell (it may be terminal in some genera), is prosocline and usually relatively large and rounded. The anterior region of the shell is often reduced and the anterior margin may be somewhat flattened.

Genus [?]CYRTODONTA Billings 1858

1841 [?]*Cypricardites* Conrad, p. 51 (*partim*)

1858 *Cyrtodonta* Billings, p. 179

1859a *Palaearca* Hall, p. 71

1859b *Palaearca* Hall, p. 270

1862b [?]*Cypricardites* Conrad, Hall, p. 192

1889 *Cypricardites* Conrad, Miller, p. 476 (*partim*)

1889 *Cyrtodonta* Billings, Miller, p. 477

1894 *Cyrtodonta* Billings, Ulrich p. 534

1916 *Cyrtodonta* Billings, Williams and Breger, p. 147

1934 *Cypricardites* Conrad, Isberg, p. 231

1934 *Cyrtodonta* Billings, Isberg, p. 240

1956 *Cyrtodonta* Billings, Wilson, p. 29

1969 *Cyrtodonta* Billings, LaRocque, p. 248

1971 *Cyrtodonta* Billings, Pojeta, p. 36

Type species

Cyrtodonta rugosa Billings was one of ten species listed by Billings (1858) when proposing *Cyrtodonta* and was subsequently designated the type species by Williams and Breger (1916, p. 144). Billings (1858, p. 180) stated that *C. rugosa* was found in the Trenton and Black River Formations

(Middle Ordovician) at Pauquette's and LaPetite Chaudière Rapids, Ottawa, Canada.

Diagnosis

Species of this genus have the beak situated in the anterior half of the shell, but never terminal. The anterior adductor is also never on a platform and shell thickening in that region is minimal. The cardinal teeth are all situated anterior to the beak. The posterior lateral teeth are subparallel and occupy only a short stretch of the hinge plate near its posterior terminus, producing an edentulous region along the hinge plate posterior to the beak.

Description

This genus contains species of medium to large size for the family (20 to 50mm in greatest dimension) with low, rounded, prosogyrous beaks placed in the anterior half of the shell, but never terminal. Shells of Cyrtodonta are ovoid in outline and each valve in uniformly thick shelled (areas of callous deposition are rare) and quite inflated. A prominent, broad, rounded umbonal ridge extends from the beak to the postero-ventral margin. The anterior region is reduced and somewhat flattened. No byssal gape is apparent. The dentition consists of 2 to 4 irregularly shaped (straight, curved or sinuous) anterior teeth and 2 or 3 subparallel posterior lateral teeth. There is often an edentulous hiatus on the hinge plate between the anterior and posterior teeth. Subcircular adductor scars occur just below the teeth near the anterior and posterior margins of the shell. The anterior adductor is usually well impressed, but the posterior is not.

The ligament is of the duplivincular type and occupies an area posterior to the beak. The exterior surface is marked by fine comarginal varices and rugae.

Discussion

C. curtus Conrad is the type species of *Cypricardites* by designation of Miller (1889, p. 476). This species is from Richmondian (U. Ordovician) strata near Richmond, Indiana and near Rome, New York. *Palaearca ventricosa* Hall (1859b, p. 271) was designated by LaRocque (1969, p. 248) the type species of *Palaearca*. *P. ventricosa* was described from the "Trenton Limestone in Tennessee" (Middle Ordovician).

Shells of the *Cyrtodonta* type are usually common in Middle Ordovician rocks (Pojeta, 1971, p. 18), and are conspicuous elements of some other Upper Ordovician and Lower Silurian faunas. Although this group of mainly Middle and Upper Ordovician shells has long been recognized as composing a distinct generic entity, considerable confusion has attended its recognition and limitations. Williams and Breger (1916, p. 147) gave a detailed discussion of the taxonomy and history of classification of cyrtodontids. The genera *Cypricardites* Conrad (1841), *Palaearca* Hall (1859) and *Cyrtodonta* Billings (1858) have been employed variously since Conrad's day, for species which he was striving, with imprecision, to create a genus.

Conrad (1841, p. 51) proposed Cyrpicardites for a group of 16 Ordovician and Silurian species. Of these, all except C. curtus Conrad, which Miller (1889b p. 476) designated the type, have now been placed in other genera. Conrad's description was somewhat undiagnostic and the figure accompanying it (see discussions by Hall, 1860 and 1862b) was schematic. Billings (1858, p. 179) described and illustrated Cyrtodonta for which Williams and Breger (1916, p. 149) designated C. rugosa the type.

Hall (1859, p. 8) described and figured Palaearca ventricosa from the Middle Ordovician of Tennessee (type species of Palaearca designated by LaRocque, 1969, p. 248) as one of two species of his new genus Palaearca. This genus was again published as "new" by Hall (1860b p. 270).

Hall (1859b p. 524; 1862b, p. 164) referred to Conrad's genus Cypricardites and gave a figure saying that, "this figure is copied from the original figure of Mr. Conrad, accompanying his description of the genus in 1841. The plate upon which this occurs was engraved to accompany the Annual Report [5th] of 1841; but, unfortunately, only a small number were ever distributed, so far as known to the writer." The plate was completely reproduced by Hall in the 15th Annual Report (1862b, Pl. 11).

Although the figure of Cypricardites reproduced by Hall (1859b p. 524 and 1862b, Pl. 11, fig. 4) resembles Cyrtodonta, this resemblance is mainly based on shell outline, position of the beak and cardinal teeth. Conrad illustrated no posterior lateral teeth for C. curtus. Because of Conrad's brief description and poor line drawing, LaRocque (1969, p. 249) commented that Cypricardites seems "presently unrecognizable from available evidence." Williams and Breger (1916) and Ulrich (1894), however, concluded that Cypricardites was distinct from Cyrtodonta and that both names were valid. Ulrich, however, employed Cyrtodonta for his species of this form group.

Williams and Breger citedthe lack of posterior dentition and the distribution of cardinal teeth both fore and aft of the beak in Cypricardites curtus Conrad as characteristics separating C. curtus (and thus Cypricardites) from Cyrtodonta rugosa, which has cardinal teeth only anterior to the beak and lamellar teeth along the posterior part of the hinge. Judging from Conrad's description and illustration, other characteristics (such as shell shape, musculature, ligament placement or beak position and orientation) of Cypricardites (C. curtus) are not distinguishable from Cyrtodonta (C. rugosa) Billings. Despite the lengthy explanation provided by Williams and Breger (1916), the relationship of Cyrtodonta and Cypricardites is still confused. Based on the morphology cited, the two should be considered separate genera; however, there are those who, because of the undiagnostic nature of Conrad's (1841) description and poor quality line drawing, want to restrict Cypricardites to the type species until more information about C. curtus can be obtained (such as by recovery of Conrad's types which appear to have been lost).

Palaearca Hall has often been synonymized with either Cypricardites or Cyrtodonta. Even Hall (1859b, p. 524) remarked that his new genus (Palaearca) was probably synonymous with Cypricardites Conrad. As mentioned, shell shape is of little use in this from group, although Palaearca ventricosa is oval shaped with a general prosocline orientation of the umbones, and so is more like Cyrtodonta types of species. The dentition of Palaearca is much like Cyrtodonta (subparallel posterior teeth and cardinals only anterior to the beak) and provides the basis for synonymizing these genera.

Although there has been voluminous discourse on the systematics of genera in this form group, there has been relatively little satisfactory solution provided. A complete study of type and supplementary specimens of species assignable here would certainly help resolve the question. Of paramount importance is the certification of morphology for Cypricardites curtus, so poorly described by Conrad (1841).

Distribution

Species of this genus are found in Middle Ordovician through Lower Middle Silurian of North America and Lower Silurian of Europe.

Cyrtodonta[?] ferruginea (Hall and Whitfield)

Pl. 7, fig. 1-3

1875 *Cypricardites ferrugineum* Hall and Whitfield, p. 116, Pl. 5, fig. 11

1895 *Avicula whitfieldi* Foerste, p. 558, Pl. 37, fig. 5 (*non Avicula ferruginea* Conrad, 1848) (new name for *Cypricardites ferrugineum*)

Type specimen

Hall and Whitfield (1875, Pl. 5, fig. 11) based their species on the natural external mold of a single specimen. This holotype is in the collections at Ohio State University (OSU 3208). It was collected from the upper ferruginous beds of the Brassfield at Todd Fork Creek, near Wilmington, Ohio.

Diagnosis

Equidimensional, suberect shells with the beak one-third the hinge length from the flattened anterior margin. There is a moderately developed "wing" or flange posterior to the beak, the distal tip of which makes nearly a right angle with the posterior margin.

Description

Medium sized (length 30 to 35mm) nearly equidimensional shells (height slightly greater than length) that are slightly prosocline, but with a general erectness to the shell which is accentuated by the nearly straight dorsal margin (Pl. 7, fig. 1-3). Most data presented is from the left valve, as only a fragment of the posterior dorsal region of a right valve was collected in this study.

The beak is within the anterior third of the dorsal length, low, rounded and projecting just above the hinge line (Pl. 7, fig. 3). Based on a poorly preserved specimen recovered in this study (locality WU-14), the dorsal hingeline meets the anterior and posterior margins at nearly right angles. The anterior margin is short and flattened while the posterior side of the shell has a moderate "wing" or flange. The umbonal ridge is broad, extending from the beak to the postero-ventral margin and becomes obscure in the ventral half of the shell.

Evidence of the dentition, musculature and ligament is lacking on all specimens of this species. The exterior of the valves is marked by strong comarginal growth varices and rugae (Pl. 7, fig. 1, 2).

Discussion

Hall and Whitfield (1875) originally assigned their Brassfield species to *Cypricardites* Conrad, but as stated within the generic discussion of *Cyrtodonta*, herein, it is felt that no species can be certainly assigned to that genus (*Cypricardites*) until more is known of its type species. Foerste (1895) commented that Hall and Whitfield's illustration of the holotype was from a very poor guttapercha cast and did not represent the shell's true morphology. Foerste's illustration (1895, Pl. 37, fig. 5) was much more like the actual specimen. The presence of a slight posterior "wing" or flange led Foerste to place this species in

Avicula. Conrad (1848) had previously proposed the name Avicula ferruginea for another species from the Middle Silurian, Clinton Formation of New York, hence Foerste proposed Avicula whitfieldi to obviate the homonymy. This species is not, however, an Avicula (which is considered a junior synonym of Pteria Scopoli by Hertlein and Cox, 1969), on the basis of shell shape and outline. The posterior "wing" region of C.? ferruginea is not homologous with the wing or auricle of Pteria. The pteriid wing is distinct from the main body of the shell (as in Pl. 7, fig. 6, 9) while the posterior flange of C.? ferruginea merges imperceptibly with the shell body. In Pteria, there is also an anterior auricle or ear and a byssal sinus or notch ventral to this ear.

Hall and Whitfield (1875) remarked that C.? ferruginea was most like Palaearca saffordi Hall (1859a, p. 11 and 1859b, p. 271) in its external configuration.

Cypricardites grandis Ulrich (1890, p. 387) is considered a Cyrtodonta (Pojeta, 1971) on the basis of dentition, as is P. saffordi (see generic discussion). C. grandis, particularly as illustrated by Ulrich (1894, Pl. 40, fig. 9-14) and Pojeta (1971, Pl. 6, fig. 21-23) shows a shell outline similar to C.? ferruginea and has a posterior "wing" that is poorly developed (Ulrich, 1894, Pl. 40, fig. 14) or only slightly less prominent than that in C.? ferruginea (Ulrich, 1894, Pl. 40, fig. 9). P. saffordi is from the Trenton limestones (Middle Ordovician) of Tennessee and *C. grandis* is from the Trenton limestones of Kentucky and Minnesota. Because of the absence of dentition, muscle scars and ligamental grooves, it is impossible to assign this species to any genus with certainty. Foerste's species is herein questionably assigned to *Cyrtodonta* Billings because of its superficial resemblance to *C. grandis* and *C. saffordi*, but it should be kept in mind that distribution of dentition and musculature are critical aspects of morphology needed for proper taxonomy in this form group.

Distribution

Cyrtodonta? ferruginea has been collected from the Brassfield Formation at Todd Fork Creek, near Wilmington, Ohio (the holotype) and two poorly preserved specimens (a right and left valve) were collected in this study from the ferruginous limestones 36 feet above the base of the Brassfield in a road cut on State Road 41, 2.5 miles north of West Union, Adams County, Ohio. Both of these occurrences are in the upper 10 feet of the formation.

Figured specimens

OSU 3208; UCGM 42653, 42654.

Order PTERIOIDA Newell

Superfamily AMBONYCHIACEA Miller

Family AMBONYCHIIDAE Miller

Description

This family contains equivalved mytiliform bivalves that are anisomyarian or monomyarian, with the anterior adductor, when present, much smaller than the posterior one and located near the umbonal region of the shell (Pojeta, 1966). Genera in this group are thought to have a byssus (on the basis of byssal retractor muscle scars) but not all show a byssal gape. The ligament is duplivincular and attached to the valves in a series of parallel striations or grooves posterior to the beak and usually on the dorsal side of the hinge plate (Pojeta, 1966, Pl. 28, fig. 8). There is apparently no consistent type of dentition displayed, although either cardinal or lateral teeth are often present.

Genus Mytilarca Hall and Whitfield, 1869

1870 Mytilarca Hall and Whitfield, p. 19

1883 Plethomytilus Hall, p. 4

1884 Mytilarca Hall and Whitfield, Hall, p. xiv and 253

1884 Mytilarca (Plethomytilus) Hall, Hall, p. xiv and 253

1886 Mytilarca Hall and Whitfield, Fischer, p. 963

1904 Streptomytilus Kindle and Breger, p. 452

1909 Mytilarca Hall and Whitfield, Grabau and Shimer, p. 432 (partim)

1934 Mytilarca Hall and Whitfield, Isberg, p. 107

1937 Plethomytilus Hall, Maillieux, p. 81

1937 Mytilarca Hall and Whitfield, Maillieux, p. 84

1962 Mytilarca Hall and Whitfield, McAlester, p. 38

1966 Mytilarca Hall and Whitfield, Pojeta, p. 185

1966 Plethomytilus Hall, Babin, p. 174

1969 Mytilarca Hall and Whitfield, Newell and LaRocque, p. 287

Type species

Inoceramus chemungensis Conrad (1842, p. 246) from the Upper Devonian (Chemung) of New York state is the type species of Mytilarca by original designation of Hall and Whitfield (1869, p. 20). Pojeta (1966) and McAlester (1962) illustrated several of Hall's (1883) plesiotypes and other specimens that they considered representative of this species. The type species of Streptomytilus is Mytilarca wabashensis Kindle and Breger (1904) from Niagaran (Middle Silurian) strata of Indiana. The type species of Plethomytilus is P. ponderosa, as designated by Miller (1889, p. 423).

Diagnosis

Mytiliform dentate Ambonychiidae with one to three cardinal teeth and two to four short lateral teeth, comarginal growth varices and no apparent byssal gape. The beak is terminal at the anterior margin.

Description

Species of this genus are medium to large size for the family (generally 20 to 60mm in length). Equivalved and inequilateral, Mytilarca shells have a subtriangular or tear-drop shaped outline, reminiscent of Mytilus edulis. These strongly prosocline shells have a terminal beak and short dorsal hinge line that generally makes an acute angle with the convex, straight or concave anterior shell margin. The absence of a byssal gape is conspicuous in most species of this genus.

There are one to three cardinal teeth just beneath the beak, while two to four short lateral teeth occur on the posterior edge of the hinge plate. Muscle scars are unknown in specimens presently assigned to this genus. The ligament area consists of numerous ridges and grooves of a duplivincular type. Surface sculpture consists exclusively of very fine comarginal growth varices.

Discussion

Mytilarca was originally proposed in an anonymous publication (New York State Museum, 1869). The authorship of this paper has been subject to much debate (see discussion of genus *Palaeoneilo*, herein). The recommendations of Cooper (1931) are followed in this study, and the new names proposed in the anonymous paper are attributed to Hall and Whitfield.

There has been considerable confusion as to the generic placement of early Paleozoic ambonychiid species with comarginal ornament. *Mytilarca* has served as a type of *omnium gatherum* for Silurian and Devonian ambonychiids with comarginal growth varices being the only type of ornamentation. Species assigned here are poorly preserved, most lacking dentition and some even lacking ornamentation (see Pojeta 1966, Pl. 37-41). It seems likely that more than one genetic lineage may be represented in this form group, however, attempts to subdivide these forms have met with little success. *Streptomytilus* Kindle and Breger (1904) was erected for a Niagaran (Middle Silurian) species (S. wabashensis) from Indiana, but was based on poor material with no dentition preserved. Similar problems are encountered with Plethomytilus Hall and Whitfield (1869). Its type species, P. ponderosa Hall and Whitfield (1869), is known only from Steinkerns and internal molds not preserving the dentition. Some other species assigned to this genus by Hall (1883) possess posterior dentition (Plethomytilus cuneatus Kindle and Breger, 1904 from the Indiana Niagaran and Plethomytilus oviformis [Conrad, 1841] from the New York Hamilton [Middle Devonian]), but are not preserved well enough to show cardinal teeth. In fact, preservation of the anterior hinge and its delicate cardinal teeth is a rare occurrence in most species of this form group. Hall's (1883) suite of Mytilarca chemungensis (Conrad) contained only one specimen that preserved cardinal teeth and they were partially destroyed. It is obvious that more careful examination and gathering of better preserved material is necessary before precise generic subdivision can be made in this group. Pojeta has assigned 38 species to Mytilarca, mainly on the basis of shell outline or prosopon. Most Silurian and Devonian ambonychiids with a terminal beak and without radial prosopon have been assigned here.

Distribution

The genus, as currently conceived, is represented by species from Lower Silurian through Upper Devonian strata in

North America and northern Europe. Several species from the Swedish Ordovician (Isberg, 1934) may be assigned here (Pojeta, 1966). The greatest number of described species come from the northeastern United States and adjacent Canada.

"Mytilarca" foerstei Clarke and Ruedemann

Pl. 7, fig. 4, 5

1852 non Myalina mytiliformis Hall p. 100, Pl. 30, fig. 1a-d

1895 Mytilarca mytiliformis Foerste, p. 559, Pl. 37, fig. 1a-e

1903a Mytilarca foerstei Clarke and Ruedemann, p. 49 [pro Mytilarca mytiliformis Foerste, 1895, non Mytilarca mytiliformis (Hall), 1852]

1966 Mytilarca foerstei Clarke and Ruedemann, Pojeta, p. 188, Pl. 37, fig. 20

Type specimen

The type of Foerste's (1895, p. 559, Pl. 37, fig. 11a-c) species (=Mytilarca foerstei Clarke and Ruedemann, 1903a new name) is a single specimen, a left valve, from the upper ferruginous zone of the Brassfield Formation, in Todd Fork Creek, near Wilmington, Ohio (USNM 88537).

Diagnosis

This species contains extremely convex (gibbous) mytilarcids with a prominent straight umbonal ridge extending from a large blunt beak to the posterior-lateral margin. The straight, short hinge is about half the shell length.

Description

Medium size for the genus (greatest valve dimension, oblique height, is 34mm), this species is still known only from a single well preserved left valve preserving some of the shell. It is an inequilateral, very robust (inflated) shell. The prosogyrous beak is broad and blunt, extending slightly above the dorsal hinge. The shell has a general tear-drop shape with the beak at the apex. The dorsal hinge line is relatively long (14mm, which is approximately one-half the greatest length of the shell). The valve margin is gently curved along the posterio-lateral margin of the shell. A prominent umbonal ridge extends from the beak to the postero-lateral margin along the greatest length of the shell (Pl. 7, fig. 5). An antero-lateral view of the valve shows a uniformly convex profile from the beak to the posterior commissure (Pl. 7, fig. 4). The shell exterior is marked by numerous, fine, uniformly spaced comarginal growth varices (Pl. 7, fig. 5). Since the only known specimen is adherent to a slab of limestone and only the external surface is exposed, no details of the internal morphology are known.

Discussion

Foerste (1895, p. 559), following Ulrich's advice, placed a new species from the "Ohio Clinton" (Brassfield Formation) in the genus *Mytilarca*. His species was called "*Mytilarca mytiliformis* sp. nov." In the description of this species, Foerste included a quotation from a letter by

Ulrich. In referring Foerste's specimen to *Mytilarca*, Ulrich (*in* Foerste, 1895, p. 560) commented that "Hall's *Ambonychia aphara* [*sic pro aphaea*] and *Ambonychia acutirostra* [both Niagaran of Indiana] are regarded as congeneric, likewise his [Hall's] *Myalina mytiliformis* [Clinton (Middle Silurian) of New York]. All four of these species are closely related but it cannot be said that any two are identical." Despite this statement, Foerste (1895) proposed the trivial name *Mytiliformis* for his new species, a clear homonym of Hall's Silurian species. The way *Mytilarca* is currently conceived, there seems to be no reason to question Ulrich's analysis of the congeneric nature of these species. The necessary new name for *Mytilarca mytiliformis* Foerste (1895) was proposed by Clarke and Ruedemann (1903a p. 49) as "*Mytilarca*" *foerstei*. "*Mytilarca*" *foerstei* may be satisfactorily distinguished from *Mytilarca mytiliformis* by the greater convexity of "*M.*" *foerstei* (Pl. 7, fig. 4). *M. mytiliformis* has a low profile (Pl. 7, fig. 7) and a dorsal hinge length about two-thirds the length of the shell (compared to half in "*M.*" *foerstei*) (Pl. 7, fig. 8).

The lack of knowledge of internal features in this species makes generic placement questionable. However, as Pojeta (1966, p. 186) pointed out, internal features are relatively rare on specimens of most species assigned to *Mytilarca*.

Distribution

The holotype and only specimen of this species is from the ferruginous zone of the Brassfield Formation (upper 5 feet) at Todd Fork Creek, 2 miles northwest of Wilmington, Ohio.

Figured Specimens

M. mytiliformis AMNH 1611; "M." foerstei, USNM 88537

Superfamily PTERIACEA Gray

Family PTERINEIDAE Miller

Diagnosis

Pteriaform shells (usually prosocline with an anterior ear and posterior wing) with opisthodetic duplivincular ligament and left valve generally more convex than right.

Discussion

As Pojeta (1971, p. 19) pointed out, Paleozoic pteriaceans (mostly Pterineidae) have not been studied in detail and are poorly known. Although preservation of pteriaceans is generally less than ideal, external features may often be well preserved. Details of internal morphology, however, are conspicuously lacking in most of the published accounts of species and genera assigned here. The lack of definitive morphologic traits has led, in part, to considerable confusion in the taxonomy of this group. Newell and LaRocque (1969, p. 298-302) present rather long synonymies for some genera and indicate that authors often create taxa (particularly genera) on the basis of rather superficial traits such as "slight variation in obliquity, [shell] form, dentition [taxa apparently have been erected for virtually identical forms with the teeth in various states of preservation]" and minor differences in prosopon.

Williams (1890) attempted to subdivide the genus Pterinea. Although he erected a number of new genera, it is the general view today that his taxa can be accommodated within pre-existing genera, and this supposed revision seems to have enhanced nomenclatorial turmoil rather than ease it (see McLearn 1924, p. 113, for additional comments). No attempt is made here to evaluate and revise the systematics of the family, as that would entail an entirely separate study. The Brassfield specimens were assigned to the most plausible taxa according to current standards (essentially the taxa considered valid by Newell and LaRocque, 1969).

Genus Actinopteria Hall, 1884

1826 non Pterinea Goldfuss, p. 133

1883 Actinoptera Hall, p. 3

1884 Actinopteria Hall, Hall p. xii

1889 Actinopteria Hall, Miller, p. 459

1889 Pterinea Goldfuss, Miller, p. 505 (partim)

1908 [?]Tolmaia Willimas, p. 85

1908 [?]Actinopterella Williams, p. 87

1915 Actinopteria Hall, Bassler, p. 16

1915 Pterinea Goldfuss, Bassler, p. 1058 (partim)

1924 Pterinea Goldfuss, McLearn, p. 113 (partim)

1962 Actinopteria Hall, McAlester, p. 26

1966 Leiopteria (Actinopteria) Hall, Babin, p. 158

1969 Ptychopteria (Actinopteria) Hall, Newell and LaRocque, p. 302

Type species

Avicula decussata Hall (1843, p. 203) is the type species as subsequently designated by Bassler (1915, p. 16). This species is represented by the type suite of approximately one dozen specimens (AMNH 4665/1-4665/4) collected from the Hamilton Group (Middle Devonian) in the vicinity of Livingston County, New York.

Diagnosis

Strongly prosocline Pterineidae with lobose ear and well developed posterior wing. Inequilateral and inequivalved pteriaceans, with the left valve more convex than the right. Surface sculpture consists of a reticulate pattern of prominent radial ribs and evenly spaced comarginal growth varices, commonly unequally developed on the two valves.

Description

Species in this genus are medium to large sized (20 to 50mm), with the shell strongly prosocline and the large blunt beaks extending slightly above the hinge line. Each valve consists of a subtriangular central body portion, an anterior lobose auricle (ear) and a larger posterior wing, with a distinctly different topography and sometimes different prosopon from the shell body.

The teeth, although rarely preserved, are typically pterineoid with one to three cardinals just anterior to the beak and one or two long posterior lateral teeth along the internal dorsal margin of the wing.

Musculature is rarely preserved on specimens assignable here. Some individuals do show a relatively large posterior adductor scar on the postero-dorsal flank of the body. For many years this genus was supposed to be monomyarian, but there is a smaller and often obscure anterior adductor scar on the ear near the beak (see Pl. 7, fig. 12). A small lobe on the antero-dorsal edge of the posterior adductor scar represents the posterior retractor, while the anterior retractor is obscure, but may be confluent with the adductor. Additional small (byssal?) muscle scars are sometimes preserved on the anterior flank of the body (see Hall, 1884, Pl. 19, fig. 31). The pallial line is often incomplete anteriorly and vaguely sinupalliate, which is curious, since it is assumed that these, like most or all pteroids, were byssate, the notch at the base of the ear being the emergence site of the byssal strand. The ligament is opisthodetic and of a duplivincular type, occupying long narrow grooves in the dorsal part of the posterior hinge plate.

The prosopon diagnostic of the genus (under present taxonomic philosophy) consists of radial ribs and comarginal growth lines of varying strength and spacing. Either radial or comarginal elements may dominate; cancellation also occurs where the two are equal. The left valve shows better development of all, especially radial, prosopon, while the right valve has weaker and predominantly comarginal prosopon. The left valve is usually thicker shelled and much more commonly preserved.

Discussion

Hall (1884, p. xii) proposed Actinopteria for Avicula decussata Hall (1843) and several other species of Devonian pterineoids. Actinopteria has mainly been used for Devonian species, while similar Silurian species have generally been placed in Pterinea Goldfuss. Pterinea, as represented by its type species, P. laevis Goldfuss (from the German Lower Devonian) and as redefined by Williams (1908, p. 84), is a rather orthocline shell with comarginal prosopon only.

Most Ordovician pterineoids may be placed in Pterinea (Pojeta, 1971, p. 19). Radial prosopon is rare or absent in the Ordovician forms, and the shell shapes of most species are similar to Pterinea laevis. Pterinea corrugata James, however, is a Richmondian (Upper Ordovician) species with some morphologic features of Actinopteria. It is prosocline with a broad, blunt ear and a large wing. The shell surface is marked with prominent, raised comarginal varices, that are folded into aligned, ventrally projecting, spine-like crenulations (see Pl. 8, fig. 8, 10, 11, 14). These alignments create a discontinuous radial ornamentation. The absence of continuous radial sculpture. i.e., "ribs," would seem to eliminate the species from Actinopteria under present taxonomic standards. P. corrugata may well be of the lineage that evolved into Actinopteria in the Early Silurian, and might be accommodated in the genus with slight emendation of generic criteria.

Although many authors have correctly applied Actinopteria to various species of pterineoids, others have placed species assignable there in Pterinea (McLearn, 1924, p. 113 and others). Williams, who (1886) had been very critical of James Hall's work (1883, 1885) on the New York state Devonian bivalves and what he thought was too much splitting into species, especially in the pterineids, emended (1908) Pterinea in genotypic terms to include only smooth forms, or those with prosopon, while erecting four new genera to contain species with radial prosopon. Two of these, Actinopterella and Tolmaia (Williams, 1908), are here synonymized with Actinopteria because they are based only on prosoponal features that are currently acceptable within the variation in Actinopteria. All four of these genera (plus eight others) are placed in synonymy with Ptychopteria (the genus to which Actinopteria is assigned as a subgenus), by Newell and LaRocque (1969, p. 32). Actinopteria has also been considered a subgenus of Leiopteria Hall (1883) from the Middle Devonian of New York (Babin, 1966).

These assignments are not realistic because the morphology of A. decussata (type species of Actinopteria) is vastly different from the types of Ptychopteria (P. eugenia) Hall, Upper Devonian, New York) and Leiopteria (L. dekayi Hall, 1883). P. eugenia is an extremely prosocline form with the anterior auricle or ear relatively large and having its dorsal tip pointed and angular rather than blunt and rounded as in _A_. _decussata_. The posterior auricle or wing of _P_. _eugenia_ is also relatively large and separated into two distinct regions by postumbonal furrows (_A_. _decussata_ has only one). While the posterior margin of the wing of _P_. _eugenia_ is linearly continuous with the postero-lateral body of the shell, the wing margin of _A_. _decussata_ is deeply recurved producing a strong posterior re-entrant in the wing region. The wing of _A_. _decussata_ is small relative to the shell body. _L_. _dekayi_ has a much more erect shell with the beak being nearly orthoclinal. The ear and wing have distinct comarginal prosopon, while the shell body is smooth or shows only faint comarginal growth varices. _A_. _decussata_ has distinct comarginal and radial ornament which is continuous from the shell body onto the auricles. The umbo and beak region is high, inflated and narrow in _L_. _dekayi_, but broad low and rounded in _A_. _decussata_.

The other two genera of Williams (1908) do not easily fit in _Actinopteria_ as conceived herein. No judgment has been made regarding the other eight genera listed by Newell and LaRocque (1969, p. 302).

Distribution

Actinopteria is found in Upper Ordovician?, Lower Silurian through Upper Devonian strata mainly in Europe and North America. Clarke (1899, 1913) reported the occurrence of species of this genus in the Paraná Devonian in Brazil. Newell and LaRocque (1969) report the genus as ranging into the Early Permian of New South Wales. However, the greatest number of individuals and species come from Silurian and especially Devonian strata of the eastern United States and adjacent Canada.

<u>Actinopteria brisa</u> (Hall)

Pl. 7, fig. 10-12; Pl. 8, fig. 3-7, 9, 12, 13

1861 [?] <u>Pterinea striaecosta</u> McChesney, p. 88, Pl. 9, fig. 4 (Plates published 1865)

1865 <u>Pterinea brisa</u> Hall, p. 384, Pl. 14, fig. 1 [a preprint of the 1868 paper]

1868 <u>Pterinea brisa</u> Hall, Hall p. 384, Pl. 14, fig. 1

1879 <u>non Pterinea brisa</u> Hall, Hall, p. 173 Pl. 27, fig. 7-9

1882 <u>non Pterinea brisa</u> Hall, Hall, p. 316, Pl. 27, fig. 24-25 and Pl. 28, fig. 7-9.

1885 <u>Pterinea brisa</u> Hall, Foerste, p. 91, Pl. 13, fig. 14a,b

1889 <u>Pterinea brisa</u> Hall, Miller, p. 505 [listed as a synonym of <u>P. striaecosta</u>]

1889 <u>non Pterinea brisa</u> Hall, Lesley, p. 808

1895 <u>Pterinea brisa</u> Hall, Foerste, p. 557, Pl. 25, fig. 14a,b and Pl. 27, fig. 30

1909 <u>Pterinea brisa</u> Hall, Foerste, p. 65, Pl. 4, fig. 61

1915 <u>Pterinea brisa</u> Hall, Bassler, p. 1059 (<u>partim</u>)

<u>Type specimen</u>

Hall figured a single specimen along with his original description of the species (Hall, 1865, p. 337, Pl. 14, fig. 1) from the Niagaran Limestone (Middle Silurian) at Bridgeport, Illinois (according to museum label). This specimen is one of two in Hall's original suite (AMNH 1950/2). Neither Hall (1865) nor any subsequent author designated a particular specimen as the type. The specimen originally figured by Hall (1865, Pl. 14, fig. 1) is herein designated the lectotype. It is a partially exfoliated left valve and the smaller of the two in the type suite. The lectotype and lectoparatype are figured herein (Pl. 7, figs. 12 and 11, respectively).

Diagnosis

Actinopteria with a large, broad, anteriorly blunt ear that comprises up to a quarter of the shell's dorsal length in adults. The dorsal length is about 1.3 to 1.5 times the height, but virtually equal to the oblique (umbonal) height. Surface sculpture consists of radial ribs and comarginal varices of nearly equal strength and spacing on the body giving a cancellate prosopon over the body of the shell; comarginal sculpture is more prominent on the ear and wing.

Description

All of the morphologic traits described herein are based on features of the left valve. Of approximately fifty specimens examined, all were left valves and no evidence remained of the right valve. Probably this is because the right valve was thin, delicate, and hence not preserved.

Individuals of this species are small to medium size for the genus (dorsal length from 5 to 15mm). The shell is inequilateral, strongly prosocline and presumably inequivalved (based on other members of the genus). There is a strong umbone with blunt, rounded beak that extends barely above the dorsal hinge line. The relative size of the ear increases during growth, from about 15% of the hinge length in juveniles to 25% in adults. The wing is prominent, being differentiated from the body along about 60% of the hinge length. It extends posteriorly about the same distance as the posteriormost part of the shell body. The wing forms nearly an isosceles triangle, with its posterior edge slightly recurved producing a re-entrant in the shell margin. The main umbonal body of the shell is broadly pear-shaped and moderately inflated, with gently curved ventral and lateral margins.

Internal features of A. brisa are known from a single specimen, the holotype. No cardinal teeth are observable, but the impression of a single long lateral tooth occurs on the dorsal margin of the wing (Pl. 7, fig. 12). Should the anterior teeth prove to be absent, no doubt the generic assignment would need reconsideration. Even so, the single posterior tooth raises doubts. However, lack of dental evidence in most other species of this form group leaves no option other than the present assignment based essentially on external features. Certainly re-evaluation of this form group is necessary to establish a reliable basis for taxonomy. Musculature is represented on the mold (Pl. 7, fig. 12) by anterior and posterior adductor, pedal-byssal retractor and pallial line scars. The rather large subcircular posterior adductor is located in the postero-dorsal quarter of the valve across the area where the body and the wing meet. A vague, postero-ventrally oriented and slightly sinuate, pallial line extends from the posterior adductor to a much smaller anterior adductor. Bordered anteriorly by a small curved septum (not known in A. decussata) the anterior adductor scar appears fused to an equal-sized pedal-byssal retractor scar. A small lobate projection on the dorsal edge of the posterior adductor presumably represents the posterior pedal-byssal retractor muscle scar.

The cancellate prosopon consists of elevated radial ribs and comarginal elevated varices of nearly equal magnitude and spacing. The radial ribs emanate from the beak and increase in number by intercalation of new ribs at various intervals from the beak to the commissure. The varices are comarginal and of the same magnitude as the ribs on the body, but slightly stronger on the ear and wing.

Discussion

James Hall (1865, p. 337) originally proposed the species Pterinea brisa for a partially exfoliated specimen from the Niagaran Group of Bridgeport, Illinois. He later described several specimens from the "Niagaran Group, at Waldron Indiana" as the same species (Hall, 1879, p. 173 and 1882, p. 316). The Waldron specimens (Hall 1879 and 1882) are, however, distinctly different in that the ear is proportionately much smaller (Pl. 7, fig. 6) and the surface sculpture is composed of radial lines that are more closely spaced and slightly weaker than the comarginal ones. Additionally, the comarginal varices often show considerable relief and at the intersection with each of the radii the varices are laterally folded and posteriorly extended into spine-like protuberances (Pl. 7, fig. 10). This spinose prosopon is not found on the Bridgeport types of this species and does not appear to ever have been present in life, nor is it present on the Brassfield material. Brassfield specimens are very close to the Bridgeport, Illinois lectotype in having a broad blunt ear and surface sculpture of radial and comarginal lines of virtually equal magnitude and spacing. These Waldron (Indiana) specimens may still belong to *Actinopteria*, but should be considered a separate species from *A. brisa*.

Foerste (1909, p. 65) describes a specimen as *Pterinea brisa* from the "Waldron beds, at Newsom, Tennessee." He notes in that description that Bridgeport and Waldron specimens of Hall are not conspecific. Foerste's Tennessee specimen is much like the lectotype of *P. brisa* and can easily be assigned to that species. Hall (1865) suggested that *Ambonychia* (*Pterinea*) *striaecosta* McChesney (also from the Niagaran at Bridgeport, Illinois) might be synonymous with his *A. brisa*. McChesney's type material was not located and his illustration is of such a poorly preserved specimens (1865, Pl. 9, fig. 4) that although it may be conspecific with *A.*

brisa it cannot be assigned there with certainty.

Actinopteria brisa (Hall) is probably most closely related to Avicula emacerata Conrad (1842, p. 241, also an Actinopteria) which occurs in Clinton (Lower Silurian) rocks of Oneida and Wayne Counties, New York, and Niagaran (Middle Silurian) rocks at Rochester and Lockport, New York. Avicula emacerata has an ear only slightly shorter than A. brisa and has a bit stronger radial prosopon. Several specimens of A. emacerata figured by Hall (1852) are illustrated herein for comparison with A. brisa (Pl. 7, fig. 9 and Pl. 8, fig. 2.

Distribution

This species occurs in the Niagaran (Middle Silurian) limestones at Bridgeport, Indiana and similar age (Waldron Formation) rocks at Newsom, Tennessee.

Brassfield occurrences are restricted to the general region around Dayton, Ohio. Foerste (1885, 1895) reported finding specimens in the Soldiers' Home Quarry and Huffman's Quarry in Dayton, Brown's Quarry in New Carlisle, Ohio (20 miles northeast of Dayton) and Todd Fork Creek, 2 miles north of Wilmington, Ohio (30 miles southeast of Dayton). Additional specimens collected for this study were found at Todd Fork and the Southwest Portland Cement Company Quarry at Fairborne, Ohio (10 miles east of Dayton). Several layers of strata in the upper 10-15 feet of the section along the northeast wall of this quarry yielded more than 30 whole and broken individuals.

Ontogeny

Fragments and virtually complete valves of 43 individuals from the Brassfield Formation were examined in this study. All of these are left valves, the smallest being 3.9mm in dorsal length and the largest is 21.0mm along the hinge. Twenty-nine valves are from the coarsely crystalline tan limestone in the top 10 feet of the Southwest Portland Cement Company Quarry at Fairborne, Ohio. All of these valves were obtained from a single bed 12 inches thick. Three fragments of valves were collected from other horizons at this quarry. The upper ferruginous zone at Todd Fork Creek, near Wilmington, Ohio, yielded four valves. Foerste (1885) found a single fragmental valve at the Soldiers' Home Quarry at Dayton, Ohio. Seven virtually complete valves are in the Ohio State University collection from Brown's Quarry near New Carlisle, Ohio (OSU 7903).

The anterior length of the hinge varies from about 15 percent of the dorsal length in the smallest specimens (about 4mm in length) to about 25 percent in large individuals (about 20mm in length). Length to height ratios are between 1.2 and 1.5, but most of the valves have a length/height ratio of 1.3 (Text-fig. 19). The number of major comarginal

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Text-fig. 19 --Anterior to posterior length and oblique height to height of Actinopteria brisa (Hall) (all samples).

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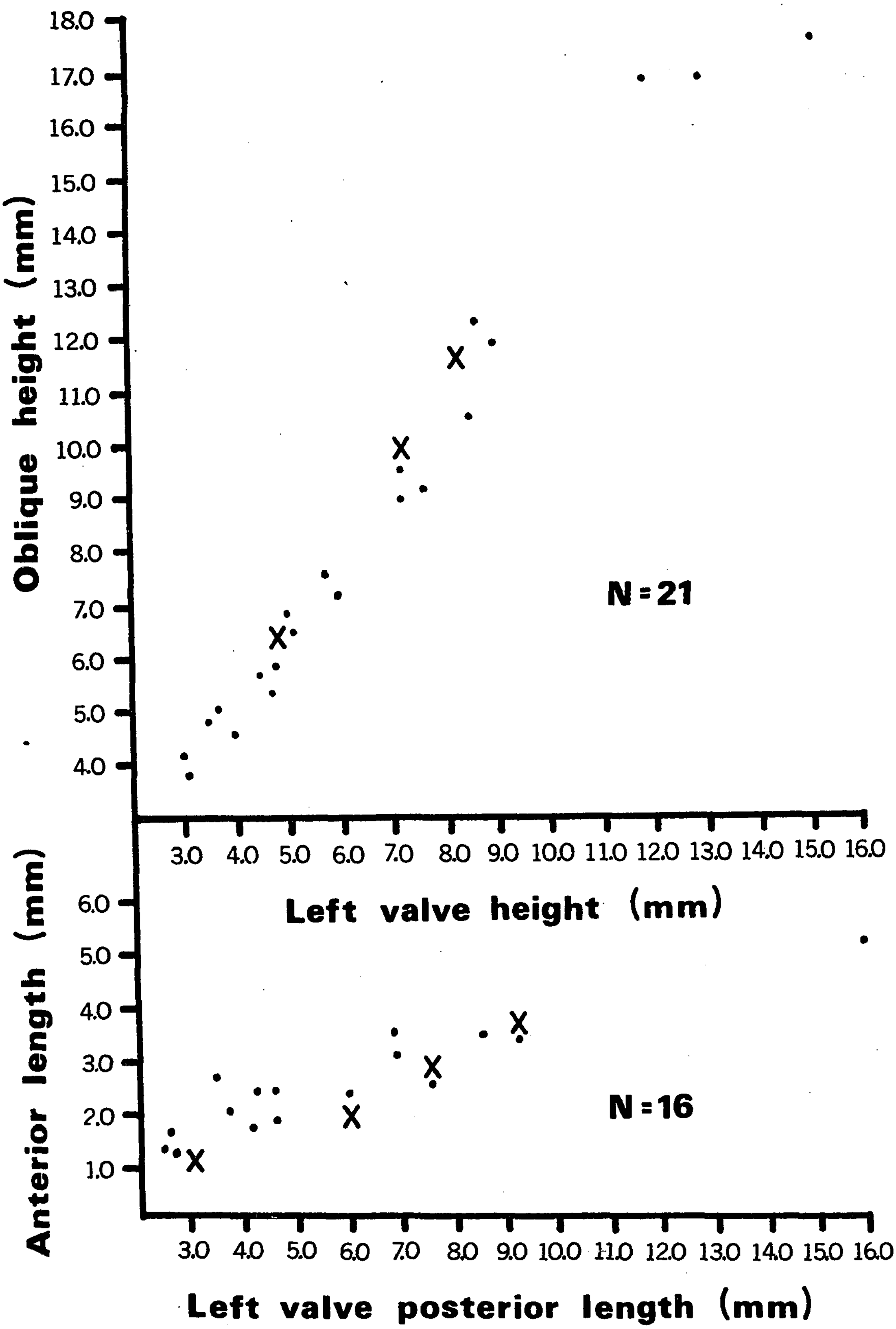
varices in one millemeter was measured on the valve surface at an approximate distance of 3mm ventral to the beak. On larger valves some difficulty was encountered in precisely



Text-fig. 19--Anterior to posterior length and oblique height to height of Actinopteria brisa (Hall) (all samples).

measuring a 3mm distance from the beak, because the beak may have been broken or corroded. The number of comarginal varices within this 1mm distance varied from 4 to 7, with fewer (4 to 5) lines in larger individuals (height exceeding 10mm).

There is a primary series of radial ribs which extend from the beak to the ventral margin. New ribs are intercalated at several stages with the secondary ribs arising about 1.5mm from the beak. Another group of ribs (tertiary) are intercalated at about 4mm from the beak. Along the posterior flank of the shell body, the primary ribs become more widely spaced than on the anterior part and intercalation occurs at a more frequent interval as the shell enlarges. This may in part be produced by a differential growth of posterior shell body providing more shell surface for rib formation.

The secondary and tertiary ribs soon become indistinguishable form the primary ones as they grow in size from their originally small diameter. There are fourteen primary ribs on one of the well preserved shells collected from the Portland Cement Quarry (UCGM 42655). There are 10 secondary intercalated ribs and 8 tertiary ribs.

Subclass PALAEOHETERODONTA Newell

Order MODIOMORPHOIDA Newell

Superfamily MODIOMORPHACEA Miller

Family MODIOMORPHIDAE Miller

Description

The genera assigned to this family are commonly large

(30mm or more in length), modioliform, ovate or rhomboid in outline with the beak near one end of the shell, but never terminal. These shells are posteriorly elongate and often expanded; the posterior region being much broader and higher than the anterior (which is sometimes reduced and lobate). Most forms are smooth or prosopon consisting of fine varices. At least one genus traditionally assigned here (Pholadomorpha Foerste (1914) from the Cincinnatian [Upper Ordovician]) has divaricate radial prosopon. The adductors are usually anisomyarian with the anterior one smaller and impressed, sometimes bordered by a ridge of callous deposits. The dentition is poorly preserved in most forms, but posterior lateral teeth are seen most often. A few specimens have cardinal teeth (all lack anterior laterals), while some are thought to be edentulous. Poor preservation is responsible for the lack of diagnostic dental information in many species; and, in fact, most morphologic features of species traditionally assigned here are not commonly preserved with the quality necessary for competent systematics. As a result, this family and especially the genus Modiolopsis (Hall, 1847) has become a receptacle for poor material, probably of several different familial taxa, with a modioliform shape and usually with comarginal prosopon. Unfortunately, it seems that traditional assignments and philosophy will have to be maintained until new taxobases and better preserved material are available for taxonomic revision.

Genus *Modiolopsis* Hall, 1847

1847 *Modiolopsis* Hall, p. 157

1851 *Modiolopsis* Hall, M'Coy, p. 265

1860 *Modiolopsis* Hall, Hall, p. 148

1889 *Modiolopsis* Hall, Miller, p. 489

1894 *Modiolopsis* Hall, Ulrich, p. 502

1909 *Modiolopsis* Hall, Grabau and Shimer, p. 511

1915 *Modiolopsis* Hall, Bassler, p. 812

1920 *Modiolopsis* Hall, Stewart, p. 34

1924 *Modiolopsis* Hall, Ulrich, p. 187

1924 *Modiodesma* Ulrich, p. 183

1956 *Modiolopsis* Hall, Wilson, p. 65

1969 *Modiolopsis* Hall, LaRocque and Newell, p. 397

1971 *Modiolopsis* Hall, Pojeta, p. 20

Type species

Cypricardites (*Pterinea*) *modiolaris* Conrad (1838, p. 118) from the "Pulaski beds" (Upper Ordovician), near Rome, New York, is the type species of *Modiolopsis* by original designation of Hall (1847, p. 157). The holotype of the type species is figured by Hall (1847, Pl. 81, fig. 1a), Ulrich (1924, Pl. 32, fig. 1) and Pojeta (1971, Pl. 15, fig. 1-3). It is in the collections of the New York State Museum(NYSM 2758).

Diagnosis

Modioliform, edentulous(?) Modiomorphidae with a low rounded beak (within the anterior one-fifth of the shell) and a long posterior region that is higher than the anterior region of the shell. The prosopon consists of uniform, fine comarginal varices.

Description

These are medium to large shells (30-70mm in length) for the family with an ovoid shell that is equivalved but inequilateral, with the beaks at the anterior one-fifth of the shell. The outline is generally modioliform with the valve height being greater at the posterior end than at the beak. The margins are gently rounded with a nearly straight or slightly arched dorsal margin. The valves are somewhat compressed.

The anterior adductor is small and deeply impressed while the posterior one is larger and weakly engraved on the shell. There are several sets of accessory (pedal-byssal) muscle scars, particularly in the posterio-dorsal region near the beaks. The pallial line is entire and integripalliate. The ligament is rarely preserved but is elongate and opisthodetic from available evidence (Pojeta, Pl. 15, fig. 5).

The external surface of the valves is marked by numerous uniformly spaced, comarginal varices.

Discussion

When Hall (1847, p. 157) proposed Modiolopsis, he commented that "this genus, as defined, includes a very natural group of shells found in older Silurian strata [Ordovician, at least in part], some of which have been referred to Cypricardia, Modiola, Pterinea and other genera."

This statement apparently gave some authors wide leeway in assigning species to the genus. Hall's (1847) criteria of modioliform, posteriorly elongate, edentulous shells, with comarginal prosopon was rather general, allowing for the assignment of a vast variety of probably heterogeneous species to, what has really become, a form genus. Because of lack of dental preservation in many specimens of this group, many species thought to be edentulous were originally assigned here. Pojeta (1971, p. 7) listed 163 Ordovician species as presently assigned to the genus (also see Bassler, 1915, p. 812-821 for listing of species assigned to *Modiolopsis*). Conrad's type of *Cypricardites modiolaris* has fortunately been preserved and appears to be truly edentulous (Pojeta, 1971, Pl. 15, fig. 1-3).

Hall (1847, p. 154) originally designated *Cypricardites (Pterinea) modiolaris* Conrad as the type species of *Modiolopsis*. Ulrich (1924, p. 183), however, tried to make *Cypricardites ovata* Conrad the type species of *Modiolopsis* and created *Modiodesma* for *M. modiolaris*. His logic was that the morphology of *M. modiolaris* did not represent the vast majority of species assigned to *Modiolopsis*, therefore a more representative type species was necessary. This was, of course, invalid and his genus *Modiodesma* is a junior objective synonym of *Modiolopsis*.

Excellent discussions of the genus may be found in Ulrich (1894, p. 502) and Pojeta (1971, p. 20).

It is evident by Pojeta's discussion that the systematics of *Modiolopsis* are far from being resolved and the assignment of Brassfield forms to this genus must be tentative until there is a generic revision of the forms presently assigned to *Modiolopsis*.

Distribution

Species of *Modiolopsis* have been described primarily from Middle Ordovician through Upper Silurian rocks of North America and Europe, although LaRocque and Newell (1969, p. 397) listed the range of *Modiolopsis* as only Middle to Late Ordovician. The distribution, too, as stated above, will be affected by a revision in the taxonomy of the genus.

Modiolopsis[?] *rhomboidea* Hall

Pl. 9, fig. 1, 2, 5

1860 *Modiolopsis*[?] *rhomboidea* Hall, p. 148, fig. 6

1895 *Modiolopsis rhomboidea* Hall, Foerste, p. 560, Pl. 37, fig. 5a

1924 *Modiolopsis rhomboidea* Hall, McLearn, p. 126, Pl. 19, fig. 4

Type specimen

Hall described and illustrated a single specimen (Hall, 1860, p. 148, fig. 6) of this species. This specimen is the smaller one of two on a slab in the American Museum of Natural History collections (AMNH 1644). The specimen figured by Hall (1860, fig. 6) and illustrated herein (Pl. 9, fig. 1) is now designated the lectotype. The slab containing the lectotype is from Upper Silurian beds at Arisaig, Nova Scotia.

Diagnosis

Rhomboid *Modiolopsis* with a small pointed beak and lobate anterior region. The posterior margin slopes steeply from the dorsal to posterior ventral margin.

Description

This species is small (20-25mm in length) for the genus. The shell is compressed with a rhomboidal outline. The small, pointed beak is near the rounded anterior end. The posterior end is only slightly higher than the anterior end. The dorsal margin is slightly convex upward and considerably shorter than the ventral margin. The posterior margin slopes steeply posteriorly toward the venter. A broad, ill-defined umbonal ridge extends posteriorly from the beak, diffusing near the posterior margin.

The material at hand is not well enough preserved to make certain of absence of teeth; however, the lectotype appears to lack posterior laterals (Pl. 9, fig. 1). Scars of the adductors are prominent in the lectotype, with the oval posterior scar being slightly larger. The lectotype preserves a strong integripalliate pallial line connecting the moderately impressed adductors (Pl. 9, fig. 1). A low ridge along part of the dorsal margin of a natural cast (the lectotype), posterior to the beak probably reflects the scar of the pedal-byssal retractor muscles (Pl. 9, fig. 1).

Hall (1860, p. 148) comments that the exterior shell surface is "evenly striated concentrically." However, of the specimens of this species (including the lectotype) examined for this study, none showed any features of the shells' exteriors. The ligament position is also unknown, but may have occupied an opisthodetic position (as in M. modiolaris).

Discussion

This species is not particularly close to the type species of Modiolopsis in general outline. M. rhomboidea has a rhomboidal outline and has the beak farther forward than M. modiolaris. It seems, however, that M. rhomboidea is a Modiolopsis under current generic concepts, but might be split off if the genus were revised.

Foerste (1895, p. 56, Pl. 37, fig. 8a) described and figured a single poorly preserved specimen apparently assignable to this species from the Brassfield. This specimen (USNM 84805) is the only one known from this horizon (Pl. 9, fig. 2, 5).

McLearn (1924, p. 126) cited M. rhomboidea as occurring in the Stonehouse Formation (Upper Silurian) at Arisaig, Nova Scotia, but did not add any new information as he quoted from Hall's original description.

Modiolopsis nais Billings from the Middle Ordovician strata at Paquette Rapids, Quebec, is perhaps the most closely related species of the genus. M. nais is, however, a distinct species, as there is only a poorly developed umbonal ridge in _M. rhomboidea_ while a strong one is present in _M. nais_. The beaks and umbones are much broader and more erect, although still prosocline, in _M. nais_. Other differences could be listed (Wilson, 1956) but the disparity in morphologies is probably enhanced by the state of preservation of _M. rhomboidea_. Specimens of _M. rhomboidea_ are all casts of the interior, while _M. nais_ is represented by articulated specimens. The holotype of _M. nais_ is illustrated by Wilson (1956, Pl. 9, fig. 12, 13).

Figured Specimens

AMNH 1644; USNM 84805

[?]_Modiolopsis subrhomboidea_ Simpson

Pl. 9, fig. 3

1889 _Modiolopsis subrhomboidea_ Simpson, _in_ Lesley, p. 411, fig. Va

1890 _Modiolopsis subrhomboidea_ Simpson p. 450, fig. 17

1895 [?]_Modiolopsis subrhomboidea_ Simpson, Foerste, p. 560, Pl. 37, fig. 7a,b

Type specimen

The lectotype, a left valve, is designated herein as that specimen figured by Simpson (_in_ Leslie, 1889, p. 411), whereabouts unknown, from "McKee's ore bank (Clinton, Middle Silurian) northeast of McKee's house, Ferguson Valley, seven miles northwest of Lewistown, Miffin County, Pennsylvania."

Description

Shells of this species are small for the genus (20 to

25mm in length), oblong, subrhomboidal in shape. The dorsal margin is straight behind the beaks and shorter than the curved ventral margin. The anterior margin is rounded with uniform convexity from the beak to the venter, while the posterior is only slightly curved and slopes anteriorly toward the dorsum (Pl. 9, fig. 3). The posterior height is also somewhat greater than the anterior height. The beak and umbo are broad and blunt, distinctly prosocline, situated at the anterior one-fourth of the shell length. Only a vague hint of an umbonal ridge is present.

Dentition is not preserved on any specimens seen in this study (although general quality of material is poor). The musculature, nearly as poorly known, is represented only as subtle shading in the region of the anterior adductor scar in Simpson's (in Leslie 1889, p. 411, fig. Va) original figure of the lectotype.

The surface of the valves is marked with regularly spaced comarginal varices of growth.

Discussion

The whereabouts of Simpson's specimens is presently unknown. The morphologic data presented herein is based on his description and original figure (Simpson in Lesley, 1889, p. 411, fig. Va). There is some doubt as to whether or not Foerste's specimen (Foerste, 1889, Pl. 37, fig. 7a) is conspecific with those of Simpson. Without seeing Simpson's types, it is difficult to evaluate the species.

Comparison with Simpson's figure indicates that the Brassfield specimen is similar, but the Brassfield preservation is so poor that it is questionable if Foerste's specimen is even a Modiolopsis. This Brassfield specimen was collected by Foerste from the Brassfield at Huffman's quarry near Dayton, Ohio, which unfortunately is inaccessible today.

Other species, similar in general appearance to [?]M. subrhomboidea and the Brassfield specimen (figured herein, Pl. 9, fig. 3) include Modiolopsis rhomboidea and Modiolopsis? dubia Wilson (1956). M. rhomboidea has a shell shape somewhat similar to [?]M. subrhomboidea but is somewhat more angular around its margins and is longer in relation to its height than is [?]M. subrhomboida. The beak is blunter and an umbonal ridge is virtually absent in [?]M. subrhomboidea but present in M. rhomboidea.

Modiolopsis? dubia Wilson (1956, p. 68, Pl. 9, fig. 15) is also near [?]M. subrhomboidea in general outline. M. dubia from the Leray Beds (Middle Ordovician) Glaucester township, Ontario, is shorter than [?]M. subrhomboidea, has a more pointed beak and a strongly developed umbonal ridge. These comparisons are, of course, quite superficial, and without better preserved specimens (especially interiors), [?]M. subrhomboidea occupies very uncertain taxonomic status.

Distribution

The type specimens of [?]M. subrhomboidea are from Clinton Shale (Lower Middle Silurian), seven miles northwest of

Lewistown, Miffin County, Pennsylvania. Foerste's specimen from the Brassfield was collected in the upper shale lenses (upper Brassfield) at Huffman's Quarry near Dayton, Ohio.

Figured Specimen

USNM 84806

Subclass HETERODONTA Newmayr

Order VENEROIDA Adams and Adams

Superfamily CRASSATELLACEA Ferussac

Family CARDINIIDAE Zittel

Description

The Cardiniidae possess cardinal teeth (beneath the beak) and lateral teeth (away from the beak) (Heterodonta) with never more than two cardinal teeth in each valve, and often only one with the other fused to the lateral tooth. There is usually one anterior lamellar tooth and two posterior lamellar (behind and beneath the ligament groove) teeth in each valve. These teeth are often designated by numbers and lower case letters (for cardinals) or upper case letters and Roman numerals (for laterals). This numbering system is supposed to indicate homologies throughout the order (Bernard, 1897 and Chavan, 1969). The type of dentition in members of this family, where there are two cardinal teeth in each valve and 3 laterals (one anterior and two posterior) is called lucinoid dentition. The teeth of the right valve are numbered 3b (larger central tooth), 5 (smaller, more posteriorly located), AIII (anterior lateral), PI and PIII (posterior laterals). The left valve has two nearly equal sized cardinal teeth numbered 2 and 4b (the 2 tooth may be fused to the anterior lateral) and lateral teeth designated AII, PII and PIV (PIV not always present).

The sole presence of 3b and 5 cardinal teeth in the right valve is characteristic of the Cardiniidae, but these teeth in combination with other cardinals may occur in many other heterodonts (i.e., Crassatellacea).

This dentition pattern is not the only characteristic of genera in this superfamily. All forms have distinct comarginal prosopon of rugae or imbricate lamellae. There is also finer textured radial prosopon on many of the forms included here.

Genus *Cypricardinia* Hall, 1859

1859b *Cypricardinia* Hall, p. 226 (*partim*)

1870 *Cypricardinia* Hall, Hall and Whitfield, p. 81

1885 *Cypricardinia* Hall, Hall, p. xlvi

1889 *Cypricardinia* Hall, Miller, p. 475

1889 *Cypricardinia* Hall, Nettleroth, p. 204

1892 *Cypricardinia* Hall, Whidborne, p. 5

1895 *Cypricardinia* Hall, Beushausen, p. 176

1897 *Cypricardinia* Hall, Beushausen, p. 287

1899 *Cypricardinia* Hall, Grabau, p. 268

1959 *Cypricardinia* Hall, Haffer, p. 182

1962 *Cypricardinia* Hall, McAlester, p. 70

1966 *Cypricardinia* Hall, Babin, p. 290

1967 Cypricardinia Hall, Chavan, p. 45

1969 Cypricardinia Hall, Cox and Chavan, p. 579

Type species

The type species is Cypricardinia lamellosa Hall (1859) (non Sanguinolaria [Cypricardinia] lamellosa Goldfuss, 1840, Lower Devonian Germany) = C. halli Beushausen (1897) by subsequent designation of Hall (1885, p. xlvi). The type species is from the "Lower Helderberg Group" (Lower Devonian) of Albany County, New York. The specimen illustrated by Hall (1859, Pl. 49a, fig. 1a-c), here shown on Pl. 7, fig. 11-14 is selected as the lectotype of the type species. It is the smaller of two specimens numbered 2528 in the Hall Collection at the American Museum of Natural History. It is also the specimen figured by Hall (1859). The other specimen in this set is very unlike Hall's figure and probably belongs to another species.

Diagnosis

Posteriorly elongate cardiniids with strong, equidistant, comarginal growth lamellae that in the type species are elevated from the shell surface and curve away from the shell until they stand perpendicular to the valve surface. Some of the posterior lamellae are recurved and directed slightly anteriorly (Pl. 9, fig. 11-13). A shallow ventro-median byssal sulcus is reflected in the course of the lamellae and by a slight indentation in the ventral shell margin.

Description

These are small to medium (5 to 25 mm in length) sized shells with the right valve more convex than the left and possessing a modioliform, trapezoidal, subrectangular or rhomboidal outline with shallow, well-defined byssal sulcus indenting the latero- and ventro-median margins. Shells assigned here are distinctly elongate posteriorly, the beak being within the anterior one-fourth of each valve, sometimes terminal in position. The beaks gently curve inward as well as anteriorly (prosogyrous). A prominent broadly rounded umbonal ridge extends from the beak to the postero-ventral margin. The posterior end of the shell has a greater height than the anterior end, giving the appearance of a slight posterior wing development.

The dentition is lucinoid heterodont with two cardinals in each valve, with moderately well developed anterior and posterior laterals. This is dentition consisting of a larger medially located tooth and a smaller posterior cardinal tooth in the right valve and two nearly equal sized cardinal teeth lateral to the socket of the large right valve tooth, in the left valve. There is one anterior lamellar lateral tooth in each valve and two posterior lamellar lateral teeth in the right valve but only one in the left valve. The information about dentition is based mainly on figures of Beushausen (1895, Pl. 16, fig. 6a,b and 13a,b) for _Sanguinolaria_ [_Cypricardinia_] _lamellosa_ Goldfuss and _C_. _crenistria_ Sandberger, respectively.

The adductor muscles are moderately impressed, producing scars that are subequal, the posterior being slightly larger. When preserved, the pallial line is entire and integripalliate.

The exterior surface is marked by a number of prominent, equidistant, comarginal lamellae or rugae. Between these major lamellae is a variable pattern of prosopon: several species possess smaller scale comarginal, undulose varices while others have radial costellae between the major lamellae; a cancellate or quincunx pattern has been observed in some species and a distinctive zig-zag pattern of lines occurs between the comarginal lamellae in the type species, _C. halli_ Beushausen (_C. lamellosa_ Hall, Pl. 9, fig. 14).

The ligament is opisthodetic, occupying a long, narrow slit which is often deeply excavated.

Discussion

Hall (1859, p. 266) proposed the genus _Cypricardinia_ for "a few species of shells . . . which have the general form of _Cypricardia_." One of the species originally assigned to this genus by Hall, _C. lamellosa_ Hall was later designated as the type species (Hall, 1885). Goldfuss had previously published _Sanguinolaria lamellosa_ (1840, p. 279, Pl. 159, fig. 12), that seemed to Beushausen assignable to _Cypricardinia_ (1895, p. 184). Hall's and Goldfuss' species names thus became homonyms. Beushausen (1897, p. 287) proposed _Cypricardinia halli_ for Hall's thus preoccupied name. This is the proper name for the type species of _Cypricardinia_, on this assumption of this subjective congeneric assignment, that is subject to reappraisal.

The morphology of the interior and especially the dentition as here presented in the description of this genus is gained largely from information presented by Beushausen 1895) and Haffer (1959), pertaining to European specimens, particularly C. crenistria Sandberger and Sanguinolaria [Cypricardinia] lamellosa Goldfuss (Lower Devonian, Germany).

There has been no opportunity to reappraise Beushausen's conclusions, which will depend mainly on securing better American materials than are now available, and on fuller knowledge of the types.

Until cardinal features of the American type species are known, and their correlation with dental features assigned to the genus from European Devonian material demonstrated, Cypricardinia remains somewhat in limbo.

Since internal features are not commonly visible on specimens of Cypricardinia, shell shape (such as length/ height ratio) and outline, along with surface sculpture have been used for recognizing the genus. Posteriorly elongate shells with prominent major growth lamellae and a well defined ventro-median byssal sulcus have been considered diagnostic of the genus.

Bearing in mind the homeomorphic and adaptive nature of these traits in bivalves, such identifications remain problematic, especially for American forms, until better information on shell interior is available.

Species have likewise been separated on the basis of surface sculpture, shell outline and relative proportions of various shell regions (such as anterior length/posterior length, length/height, and anterior height/posterior height ratio differences). Radial prosopon crossing the major lamellae or smaller scale comarginal sculpture is distinctive in many individuals placed in Cypricardinia. The patterns of this type of sculpture have been employed as specific taxobases. Quite probably these external traits will be proven valid specific taxobases here, as elsewhere in Bivalvia, but this is no way resolves the problem of their proper generic assignment to Hall's Cyrpicardinia, or the relevance of Beushausen's (1895) German Devonian internal features to Hall's American-based genus.

It must be borne in mind that the identification of Cypricardinia in the Brassfield, Lower Silurian of Ohio is based wholly on external similarities to the Silurian forms of other Paleozoic species conventionally assigned to this genus.

Distribution

Species assigned to Cypricardinia are most commonly found in Lower Silurian through Devonian strata in Europe, British Isles and North America (particularly eastern United States). Pojeta (1971, p. 25) and Chavan (1966) cited the presumed occurrence of the genus in Ordovician strata; species apparently assigned to the genus have also been found in Carboniferous and Permian beds (see Cox and Chavan, 1969, p.

578 and Meek, 1871, among others). The greatest number of species thus far published occur in Devonian rocks in northeastern United States and the Rheinland of Germany.

"Cypricardinia" undulostriata (Hall)

Pl. 10, fig. 1-9

1852 Modiolopsis undulostriata Hall, p. 254, Pl. 59 fig. 6a,b

1895 Cypricardinia undulostriata (Hall), Foerste, p. 561, Pl. 37, fig. 9a,b

1909 [?]Cyrtodonta undulostriata (Hall), Grabau and Shimer, p. 410 (no figure)

Type specimen

James Hall (1852) described a single specimen of this species from the "Rochester Shale (Lower Silurian) at Lockport, New York." Because Hall had only one specimen (AMNH 1795) it is the holotype by monotypy. That specimen is reillustrated herein (Pl. 7, fig. 7).

Diagnosis

Subrectangular shells with undulating discontinuous comarginal growth varices between the major comarginal lamellae. Each major varix in this species marks the edge of a distinct hiatus in shell growth (Pl. 10, fig. 8). The umbonal ridge is distinct but broad and rounded.

Description

Shells of this species are small to medium size for the "genus" (holotype, Pl. 10, fig. 1, 2, is 11.4mm in length;

largest Brassfield specimen collected (Pl. 10, fig. 6) is 8.9mm in length), inequivalved with right valve more convex than left and quite inequilateral with the beak in the anterior one-fourth of the valve and often nearly terminal (Pl. 10, fig. 8).

The right valve is inflated particularly beneath the prosogyrous beak and umbone (Pl. 10, fig. 3). Relative heights of the elongate posterior and shortened anterior regions are approximately equal (Pl. 10, fig. 1, 8). No specimens of ths species have yet been found that exhibit any of the shell's internal features.

External features are well preserved on the holotype and the specimens collected from the Brassfield Formation. Shells of this species have a subrectangular outline, with the length nearly twice the height. Both valves are inflated with the right valve being more convex. The two left valves collected for this study are both internal molds, and show only the major lamellae as prosopon (Pl. 10, fig. 4). There is a prominent sulcus which obliquely traverses the lateral surface of the valves from the beak, posteriorly to the ventro-median margin. The ventral margin of the shell is slightly indented (Pl. 10, fig. 8).

The external surface of valves of Cypricardinia undulostriata is marked by numerous prominent, comarginal growth lamellae with a relatively uniform spacing (Pl. 10, fig. 1, 4, 6, 8). Between these major lamellae are smaller, undulating and discontinuous growth varices (Pl. 10, fig. 2, 3). There are nine to thirteen of these smaller varices between each of the major growth lamellae.

Discussion

Although assignment of this species to Cypricardinia should be considered tentative because of the lack of internal features, the aggregate of external features exhibited by these specimens are consistent with those traditionally used to define the genus (i.e., distinct comarginal lamellae, smaller varices between the lamellae, and shell shape). Because the dentition of the type species of Cypricardinia is unknown, assignment of species to this genus is problematical at this point.

Hall (1852, p. 284) proposed this species as a Modiolopsis, but it was referred to Cypricardinia Foerste (1895, p. 516).

Previous to this study, the species was known from Hall's holotype (a right valve, 11.4mm long and 7.1mm high) and two plesiotypes collected by Foerste (1895, Ol. 37, fig. 9a,b). Of Foerste's specimens only the right valve (USNM 84808) is readily assignable to this species (valve is 6.2mm long and 3.8mm high). The other specimen is a left valve which does not show characteristic prosopon. Although surface sculpture may be affected by the state of preservation in any fossil, this explanation for morphologic differences between Foerste's two specimens seems unrealistic because both occur in similar lithologies and have the same gross preservation of other fossils. It seems more likely that the smooth-surfaced left valve of Foerste (1895, Pl. 37, fig. 9b, USNM 87170) is another species of pelecypod--or perhaps not a pelecypod at all.

The Brassfield strata now yields an addition six specimens referrable to this species (4 right and 2 left valves). Another Brassfield specimen from the Vaupel Collection at Cincinnati (UCGM 42664) is provisionally assigned to this species. With these specimens, greater detail of the shell shape and prosopon has been determined.

The posterior trend of the byssal sinus is seen as a reflection of ontogenetic growth of an individual. The sulcus occupies relatively the same position at any growth stage--ventrally at the shell's mid-length. However, as the valve differentially increases in length, the mid-length point moves posteriorly relative to any prior growth stage. Changes in shell outline and distribution of growth varices during ontogeny seem rather minor, with the posterior elongation being the only apparent change. The number of secondary growth varices is variable, from 9 to 13, but no consistent increase during ontogeny is noted.

"Cypricardinia" undulostriata (Hall) may be related to C. arata Hall from the Waldron Formation in southern Indiana and Illinois (Hall, 1868, 1879, 1882). Although the general shell shape and the distribution of major lamellae are similar in these two species, C. arata lacks the fine, undulose growth varices and a somewhat more inflated shell (Hall, 1882, p. 317). C. arata is found only in Middle Silurian (Niagaran) strata, while "C." undulostriata is apparently restricted to Lower Silurian rocks.

Cypricardinia larocquei McAlester (1962, p. 70) from the Upper Devonian (Chemung), is remarkably similar to "C." undulostriata in its finer prosopon. McAlester's species is more equilateral and less inflated than "C." undulostriata. There is, however, a striking similarity of the surface sculpture in these two species. C. larocquei has the same small-scale, undulose comarginal growth varices that are characteristic of "C." undulostriata. The prosopon of this Devonian form probably represents a homeomorphic occurrence since the various features of shell shape are different from "C." undulostriata.

Distribution

The type specimen was collected from the "Rochester Shale (Clinton Group), near Lockport, New York." The Brassfield occurrences of this species are all in the general area of Dayton, Ohio. Of the two specimens described by Foerste (1895), a questionable representative of this species comes from the "Soldier's Home Quarry," on the grounds of the Veterans Administration Hospital within the Dayton city limits. The other specimen was collected from Brown's Quarry, 2.5 miles west of New Carlisle, Ohio (about 20 miles northeast of Dayton) in approximately the upper ten feet of the Brassfield limestone. All new specimens collected for this study are from the tan colored, coarsely crystalline fossiliferous limestone layers in the upper five feet of the formation, along the east wall of the main pit of the Southwest Portland Cement Company in Fairborn, Ohio (10 miles east of Dayton). The single specimen in the Vaupel collection was collected from the Centerville Shale (lowest Brassfield) at the Centerville Quarry, Centerville, Ohio, about 15 miles south of Dayton, Ohio).

Figured Specimens

C. halli AMNH 2528; "*C.*" *undulostriata* AMNH 1795; UCGM 42662-42665; USNM 84808.

Subclass ANOMALODESMATA Dall

Order PHOLADOMYOIDA Newell

Superfamily PHOLADOMYACEA Gray

Family GRAMMYSIIDAE Miller

Description

The genera assigned here are medium size (20 to 50mm) bivalves usually ovoid or subtriangular in shape, often with the posterior region elongate. These are anisomyarian forms with a hinge plate thickened by callous deposits sometimes having an interlocking fold or rounded protrusion along the hinge, but never discrete teeth. Comarginal ornament is common, but some genera are characterized by radial ornament. Most forms have a well defined lunule and escutcheon, but again homogeneity is lacking when considering genera traditionally assigned here (Ulrich, 1894 and Newell and LaRocque, 1969, especially). Because of poor preservation and lack of definitive morphologic traits (especially interior) in many of these forms the taxonomy of this family is very suspect.

Genus Cuneamya Hall and Whitfield 1875

1844 non Leptodomus M'Coy, p. 66

1847 non Grammysia de Verneuil, p. 696

1851 Leptodomus M'Coy, M'Coy, p. 277 (partim)

1873 [?]Ceromyopsis Meek, p.146

1875 Cuneamya Hall and Whitfield, p. 90

1883 Grammysia (Sphenomya) Hall, Pl. 62, fig. 1-9 (figure only)

1885 Grammysia (Sphenomya) Hall, Hall, p. 383, Pl. 62, fig. 1-9

1894 Cuneamya Hall and Whitfield, Ulrich, p. 620

1920 Cuneamya Hall and Whitfield, Stewart, p. 6

1926 Cuneamya Hall and Whitfield, Ruedemann, p. 6

1956 Cuneamya Hall and Whitfield, Wilson, p. 16

1969 Cuneamya Hall and Whitfield, Newell and LaRocque, p. 820

1971 Cuneamya Hall and Whitfield, Pojeta, p. 24

Type species

Cuneamya miamiensis, which is the type species by original designation of Hall and Whitfield (1875, p. 90), is deposited in the collection of Ohio State University OSU 2999. It is from the "Hudson River Group" (Richmondian) near Waynesville, Ohio.

Diagnosis

This genus is a prosogyrous grammysiid with nearly terminal, strongly incurved umbones with the shell crenulated by regularly spaced comarginal folds (Pl. 10, fig. 10). A broad, rounded posterior umbonal ridge extends from the beaks to the postero-ventral margin of the valves. An oblique, broad, indistinct, medial sulcus is present (Pl. 10, fig. 10).

Description

Species of Cuneamya are of medium size for the family (length 15 to 40mm), equivalved and usually greatly inequilateral. A distinct escutcheon is present posteriorly, and anteriorly a small lunule occurs. Shell outline of various Cuneamya species is subtriangular to subrhomboidal or subcircular. Each valve is inflated, particularly in the umbonal region. There is a wide, rounded umbonal ridge extending from the beaks to the postero-ventral margin, accentuating the prosocline slope of the shell. A broad shallow sulcus, rather indistinct in most species, is present medially on each valve. Some species exhibit an indented ventral margin at the position of this sulcus. This type of indentation has often been interpreted as reflecting a byssate mode of life (Kauffman, 1969, p. 150, Stanley, 1972, p. 193), and if analogy with shell form in some modern bivalves is useful, this indentation may well have served in this function. Several genera of arcoids (including Noetia Gray and Arca Linnè have a similar shell form and are known to have byssal strands projecting from this ventro-medial region (Stanley, 1970). The hinge of Cuneamya is rarely preserved, but is said to be edentulous (Hall and Whitfield, 1875, p. 90, Newell and LaRocque, 1969, p. 819, and others). Musculature is equally poorly known because of poor preservation; although Hall and Whitfield (1875, p. 90) commented that "adductor muscles, at least two are anterior and posterior. Pallial line simple." These "observations" appear to be based on little or no actual data (Ulrich, 1894, p. 621). Other than being external, little is known of the ligament. The external shell surface of each valve is marked by numerous, evenly spaced comarginal crenulations.

Discussion

Hall and Whitfield (1875, p. 90) proposed Cuneamya for a "a group of Silurian [Ordovician, at least in part] Lamellibranchiate shells, which have been variously referred to Leptodomus M'Coy; Grammysia de Verneuil, Sedgwickia M'Coy, etc., but which do not appear to us to possess the true features of any of these groups . . . ." Cuneamya differs from Grammysia in that there are two prominent well defined medial sulci on the shell surface and a tooth-like ridge along the hinge in Grammysia. Cuneamya has only one indistinct sulcus, however the dental comparison of the type species of Cuneamya is problematic with present specimens. Sedwickia is a grammysiid distinct from Cuneamya in having an erect beak, no lateral sulcus and a slight posterior wing or alation. Sphenomya Hall (1883, Pl. 62, fig. 1-9) is apparently a good representative of Cuneamya from Devonian (Hamilton) rocks of New York.

Although numerous new species have been proposed, the initial concept of Cuneamya has been virtually unchanged by subsequent authors (see Ulrich, 1894; Wilson, 1956 and Newell and LaRocque, 1969).

Distribution

Species assignable to this genus are found in Middle Ordovician through Middle Devonian sediments in North America. Members of this genus are most abundant in the eastern United States.

Cuneamya caswelli (Foerste)

Pl. 10, fig. 10, 11

1885 Grammysia caswelli Foerste, p. 92, Pl. 14, fig. 12a,b

1895 Cypricardites caswelli (Foerste), Foerste, p. 561, Pl. 37, fig. 1a-c

1915 Cuneamya caswelli (Foerste), Bassler p. 313

Type specimen

A single specimen (the holotype) was described and figured by Foerste (1885, p. 92, Pl. 14, fig. 12a,b). It was collected from the Brassfield Formation, Soldiers' Home Quarry, Dayton, Ohio.

Diagnosis

Subrhomboidal Cuneamya with the beak one-third of the length of the hinge from the anterior end of the shell, beak is large and blunt; umbo low and broad with an indistinct umbonal ridge, shell crenulations are widely spaced relative to other species and are nearly parallel to the projected hinge axis (along the medial part of the valve).

Description

The holotype is medium sized for the genus (34mm in length). Although Foerste (1895, p. 561) reports finding several specimens of this species subsequent to describing the type, none of these other specimens was located during the research for this study. All information presented about this species is therefore based exclusively upon the holotype. The shell outline is subrhomboidal (Pl. 10, fig. 10) with the umbo projecting above the hinge line. A weakly developed umbonal ridge extends from the prominent, strongly incurved beak posteriorly until it merges with the general shell curvature before reaching the posterior margin. The beak is more centrally placed than in most other species of Cuneamya, being situated one-third of the shell's length from the anterior margin (Pl. 10, fig. 10). The hinge is straight or slightly arched. A distinct subcircular lunule and elongate escutcheon occupy the dorsal margin (Pl. 10, fig. 11). The holotype is a Steinkern, with a small bit of shell material remaining on the posterior flank of the right valve. The right valve side is well preserved, but the left is broken, particularly in the umbonal region. Each valve is inflated giving the articulated mold a very gibbous appearance. Musculature, dentition and ligament are not preserved on the type. There are prominent, equally spaced comarginal rugae marking the shell's exterior.

Discussion

The subequilateral shell outline and a subcentral position of the beak probably led Foerste (1885, p. 92) to place this species in Grammysia. However the lack of two distinct medial sulci in the holotype would prevent that generic assignment. Uncertain about the generic assignment of the species, he later (1895, p. 561) tentatively placed it in Cypricardites. Assignment of Cypricardites cannot be made because of the shell shape, position of beak and the distinct shell crenulations of C. caswelli. Bassler (1915, p. 313) felt that the species belonged in Cuneamya and that view is accepted here.

This species differs from other species of Cuneamya especially in the position of the beak and the general subrhomboidal outline. Other previously described species have a nearly terminal beak and a subtriangular shell outline (Ulrich, 1894 and Wilson, 1950).

Distribution

The holotype and only specimen of the species was found in the upper part of the Brassfield Formation at the Soldiers' Home Quarry in Dayton, Ohio.

Figured Specimen

USNM 84809

<u>Species previously assigned to the Brassfield, but of uncertain taxonomic status or not recognized as occurring in the Tri-state Brassfield</u>

Nucula minima Foerste, 1885

This species was collected from the Beavertown marl (Upper Brassfield) at Huffman's Quarry, Ohio.

No specimens assignable here were collected during this investigation and Foerste's type material was never located. Judging from his illustrations which change from 1885 (Pl. 14, fig. 8a-c) to 1895 (Pl. 26, fig. 13a-c), it may be a nuculoid but is unrecognizable without the original specimens.

Tellinomya elliptica Hall, 1852

Foerste (1893) refers a specimen from Todd Fork, Ohio, to Hall's species. No similar specimens were found in this study and the type material was never located. If conspecific with Hall's species from the Clinton Formation (Middle Silurian), near Mohawk Village, New York, the Brassfield form is probably a nuculoid. Hall's species may belong in *Palaeoneilo*, but the type is rather poorly preserved so accurate generic assignment is unlikely. Hall's only specimen, the holotype by monotypy, is reillustrated herein (Pl. 6, fig. 12).

Tellinomya clintonensis Foerste, 1895

In one of his comprehensive reports on the Brassfield fauna, Foerste (1895, p. 563) describes a pelecypod species from the Clinton Limestone, near Mifflintown, Pennsylvania.

No specimens of this species were found in the Brassfield during this study, and although Foerste's type (USNM 88539) is well-preserved, it is omitted from consideration here, since it apparently does not occur in the Brassfield.

APPENDIX

Sample localities

1. Type Brassfield section--exposure on an abandoned cut of the Louisville and Atlantic Railroad between Brassfield and Panola, Madison County, Kentucky

2. Irvine--exposure in creek bed and hillside on north side of secondary road between Panola and Irvine, about 6 miles east of locality 1, Madison County, Kentucky

3. Tollesboro--exposure in roadcut on Kentucky Rt. 10, 2.5 miles east of intersection with Kentucky Rt. 57 in Tollesboro, Lewis County, Kentucky

4. West Union--Road cut and creek on both sides of State Road 41, 2.3 miles north of West Union, Adams County, Ohio. Samples from this locality are prefixed with the letters WU.

5. West Union--Road cut, 0.2 miles north of locality 4, Ohio. Samples from this locality are prefixed with WU-101.

6. Jacksonville--exposure in roadcut on west side of Ohio Rt. 41, south bluff Ohio Brush Creek, 1.4 miles south of Jacksonville, Adams County, Ohio.

7. Louden--natural exposure on the south side of Ohio Rt. 73, 1.6 miles east of Louden, Adams County, where the highway crosses Flat Run, Ohio.

8. Lumberton--abandoned quarry about 1000 feet east of McKay Road 0.2 miles south of where McKay Road crosses Anderson Fork, near Lumberton Clinton County, Ohio.

9. Todd Fork--natural exposures on the northeast bank of

Todd Fork, 200 yards south of where Center Road crosses the creek, about 3.2 miles northwest of Wilmington, Clinton Co., Ohio. Sample numbers from this locality are prefixed by the letters TF.

10. Centreville--Abandoned quarry, 0.3 miles south of Centerville city limits State Road 48, Montgomery County, Ohio. University of Cincinnati collection.

11. Fairborne--Southwest Portland Cement Company Quarry east of city limits of Airborne, Montgomery County, Ohio. Samples from this locality are prefixed with FB.

12. Brown's Quarry--2 miles east of New Carlisle, Green County, Ohio.

13. West Milton-exposure in roadcut on Ohio Rt. 71, 0.25 miles east of West Milton, Miami County, Ohio.

14. Piqua--Aramco Steel Company Quarry, off State Road 1.1 miles west of Piqua, Miami County, Ohio.

15. Sevenmile Creek--natural exposure on Sevenmile Creek about 2 miles south of Eaton, Preble County, Ohio, where Ohio Rt. 127 crosses the creek.

16. Elkhorn Falls--natural exposure in a stream cut of Elkhorn Creek at Elkhorn Falls on the west side of Indiana Rt. 227, 2 miles southeast of Richmond, Wayne County, Indiana.

17. Laurel Indiana--natural exposure in northeast fork of Sains Creek approximately 2.3 miles west of Laurel, Franklin County, Indiana.

18. Wolf Creek--section along a tributary to Wolf Creek, Jennings County, Indiana. Locality 31 of Rexroad (1967).

19. New Point Stone Company Quarry--western part of New Point Stone Company Quarry,Decatur County, Indiana. Locality 26 of Rexroad (1967).

20. Osgood--natural exposures along a small east-west stream approximately 2.3 miles north-northeast of Osgood, Ripley County, Indiana.

21. Cross Plains--east face of quarry wall of the Tri County Stone Company, 4 miles south of Cross Plains, Ripley County, Indiana.

22. Powerhouse Road--exposure in road cut on Indiana Rt. 62, 1.8 miles west of the entrance to Clifty Falls State Park, near Madison, Jefferson County, Indiana.

23. Hanging Rock Hill--natural exposure on north side of Indiana Rt. 7, 1 mile north of Madison, Jefferson County, Indiana.

24. Mt. Pleasant--Road cut on east side of State Road 3.4 miles north of Mt. Pleasant, Oldham County, Kentucky.

25. Crestwood--road cut along south side of State Road 22, 2.1 miles west of Crestwood, Jefferson County, Kentucky.

26. Seatonville--Road cut above abandoned quarry on north side of Seatonville Road on Floyd's Fork Creek about 1.0 mile west of Seatonville, Jefferson County, Kentucky.

27. Mt. Washington--exposure in roadcut on U. S. 31E about 1.3 miles north of Mt. Washington, Bullitt County, on the south bank of Floyds Fork, Kentucky.

28. Ridge Road--natural exposure along Kentucky Rt. 480

about 1 mile west of Section 20, just past intersection with Ridge road where the highway crosses a small creek, Bullitt County, Kentucky.

29. Bardstown--exposure in roadcut on north side of Blue Grass Parkway at the U. s. 31E exit, 0.5 miles west of the Kentucky Rt. 49 overpass, 2 miles south of Bardstown, Nelson County.

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*Unless otherwise stated, all specimens figured are from the Lower Silurian Brassfield Formation in Ohio.

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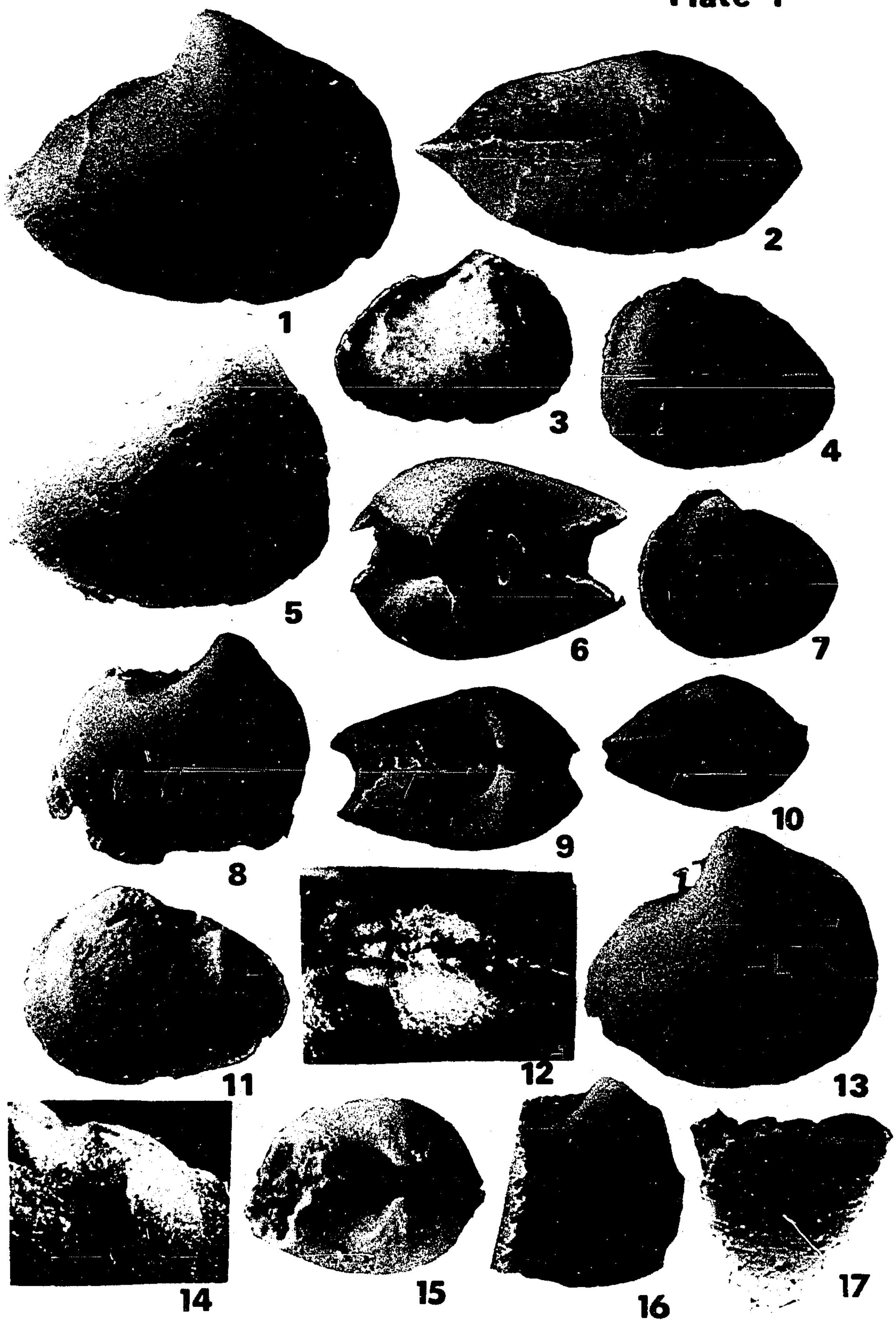

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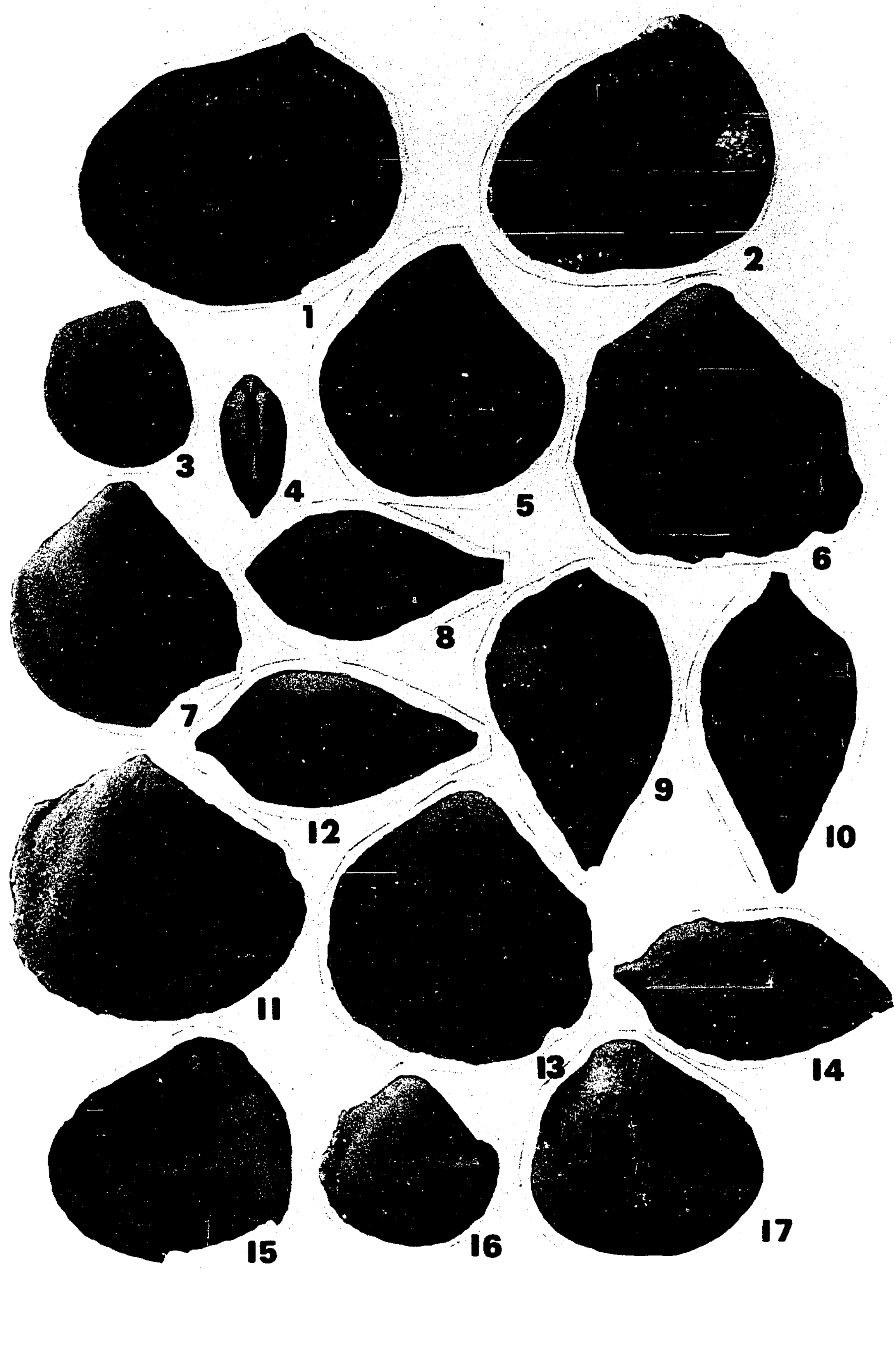

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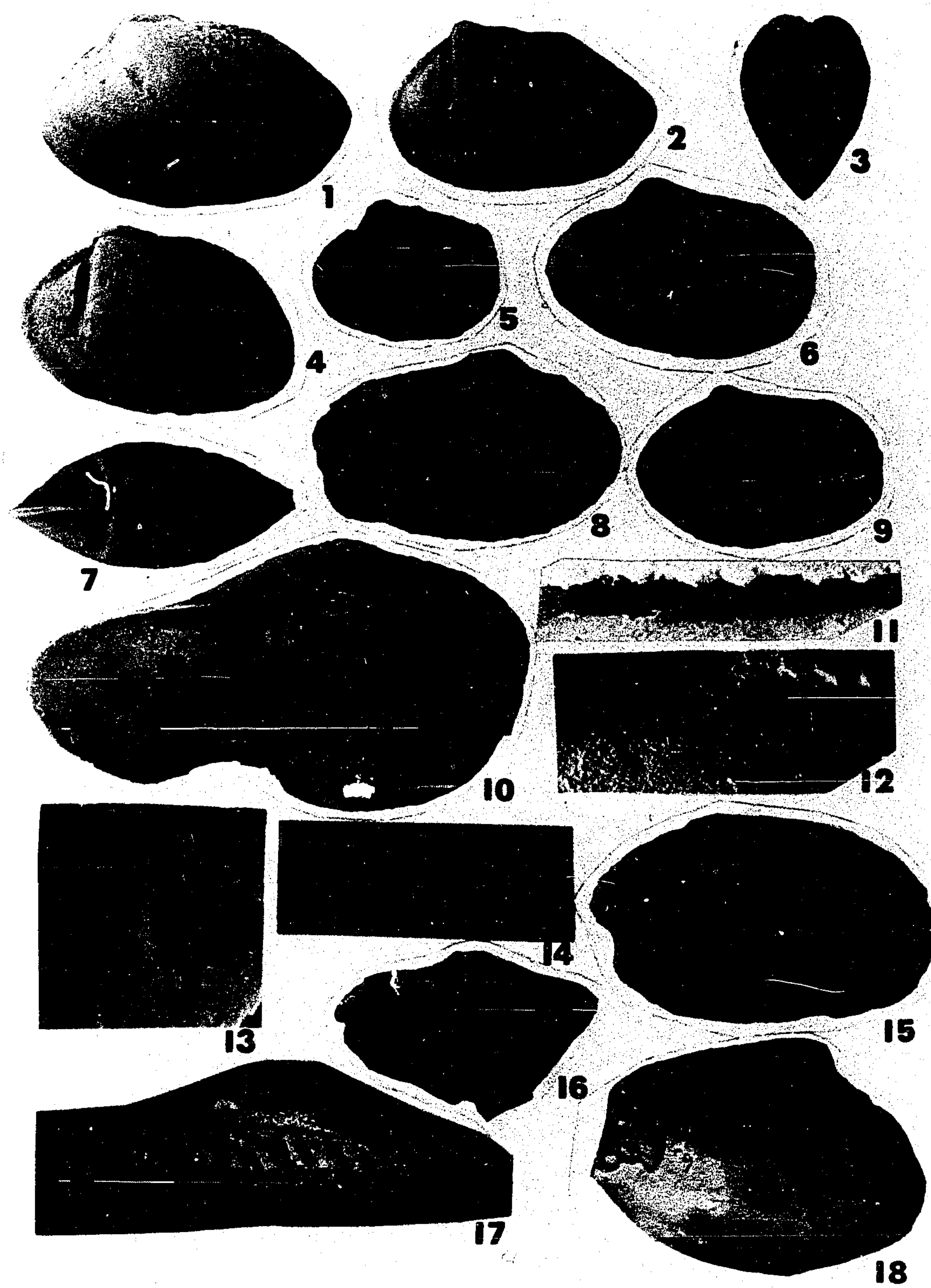

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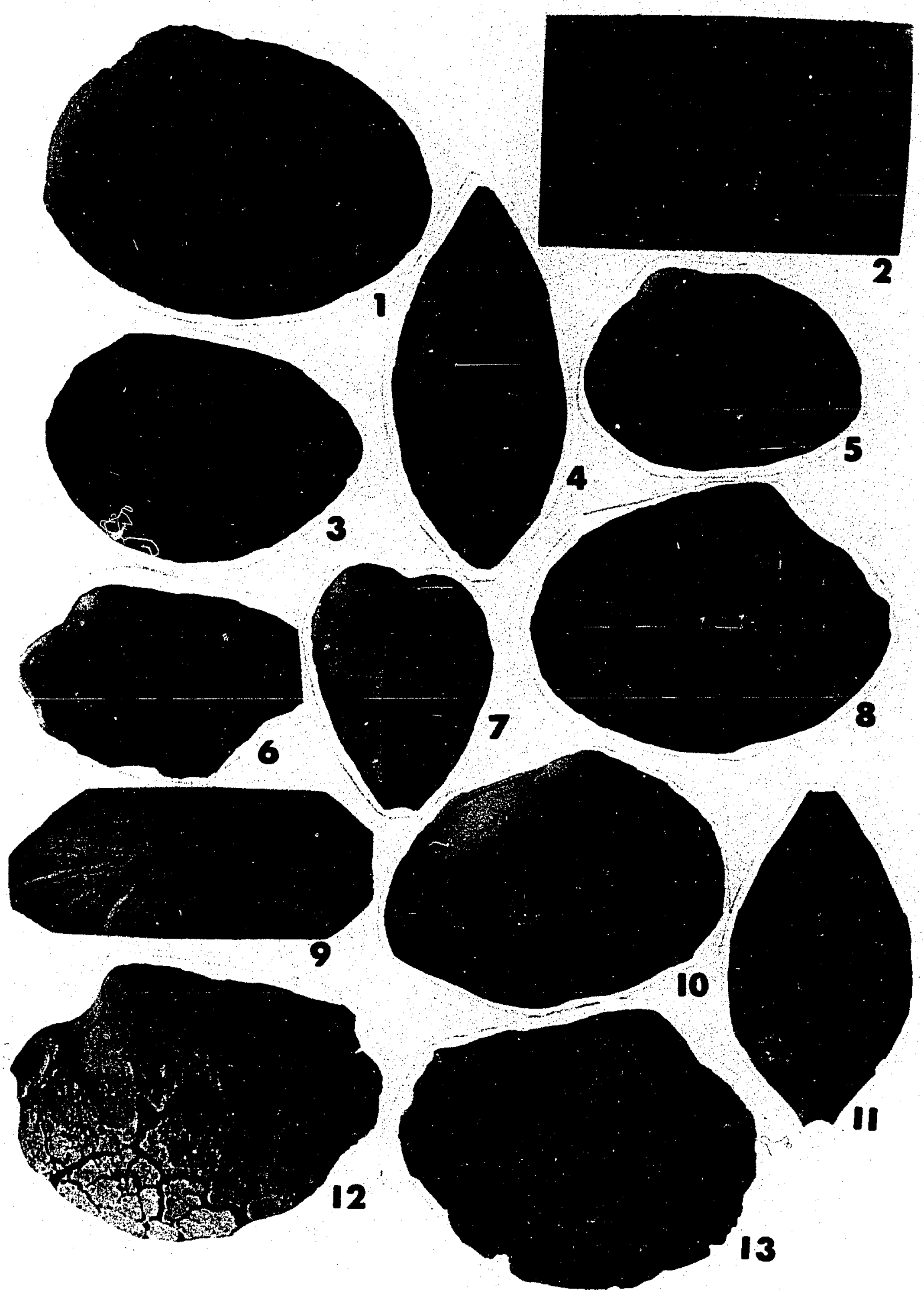

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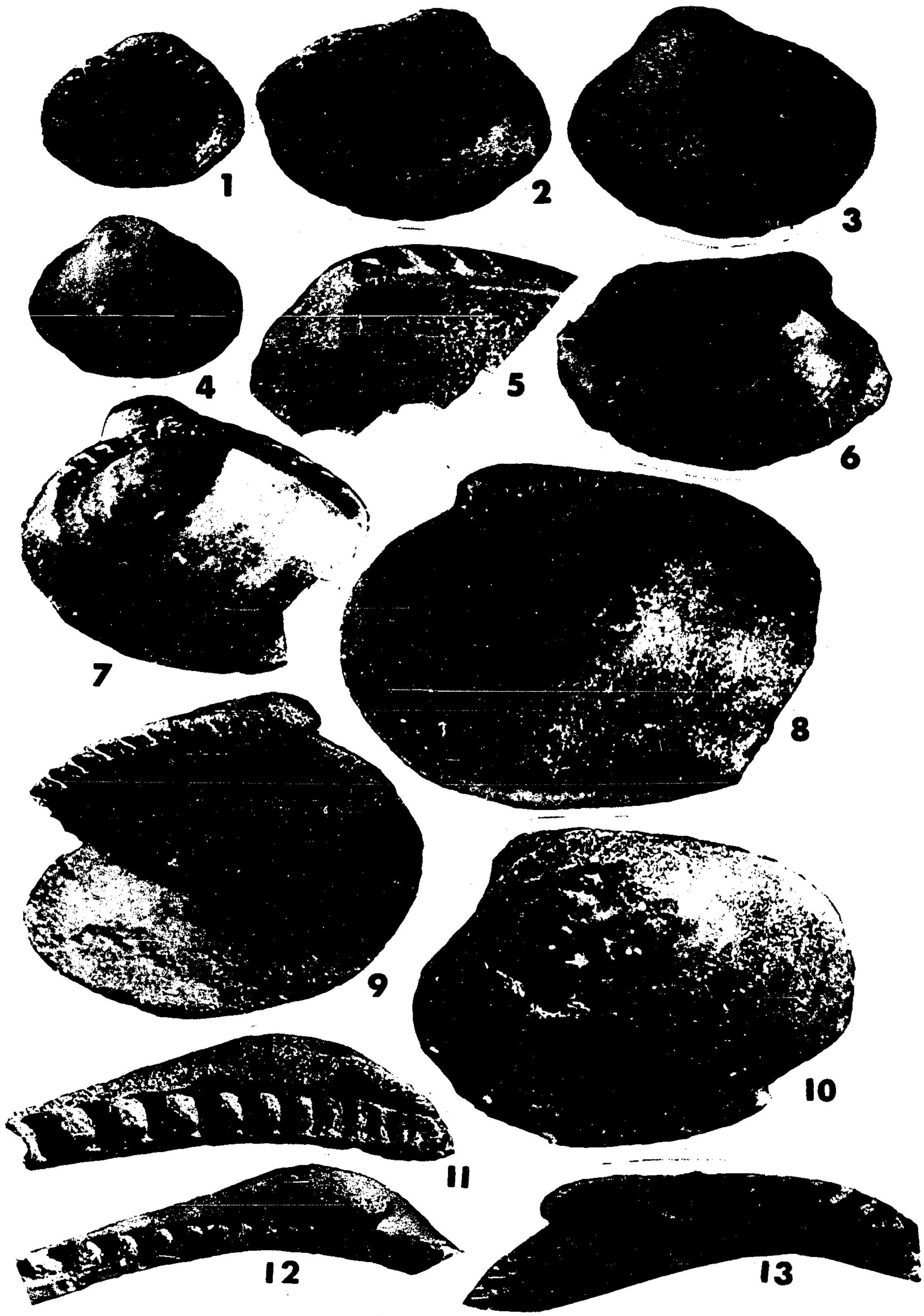

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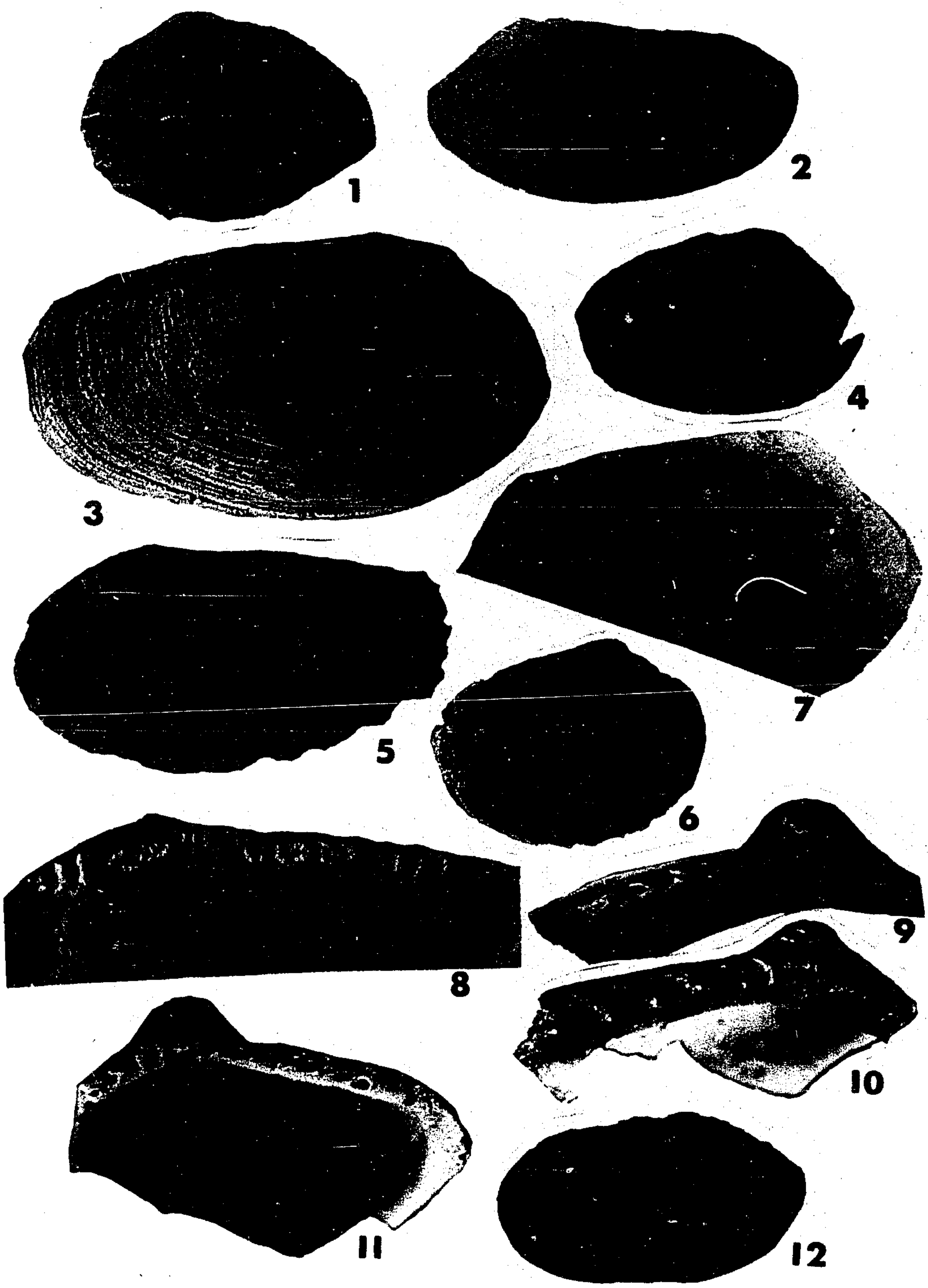

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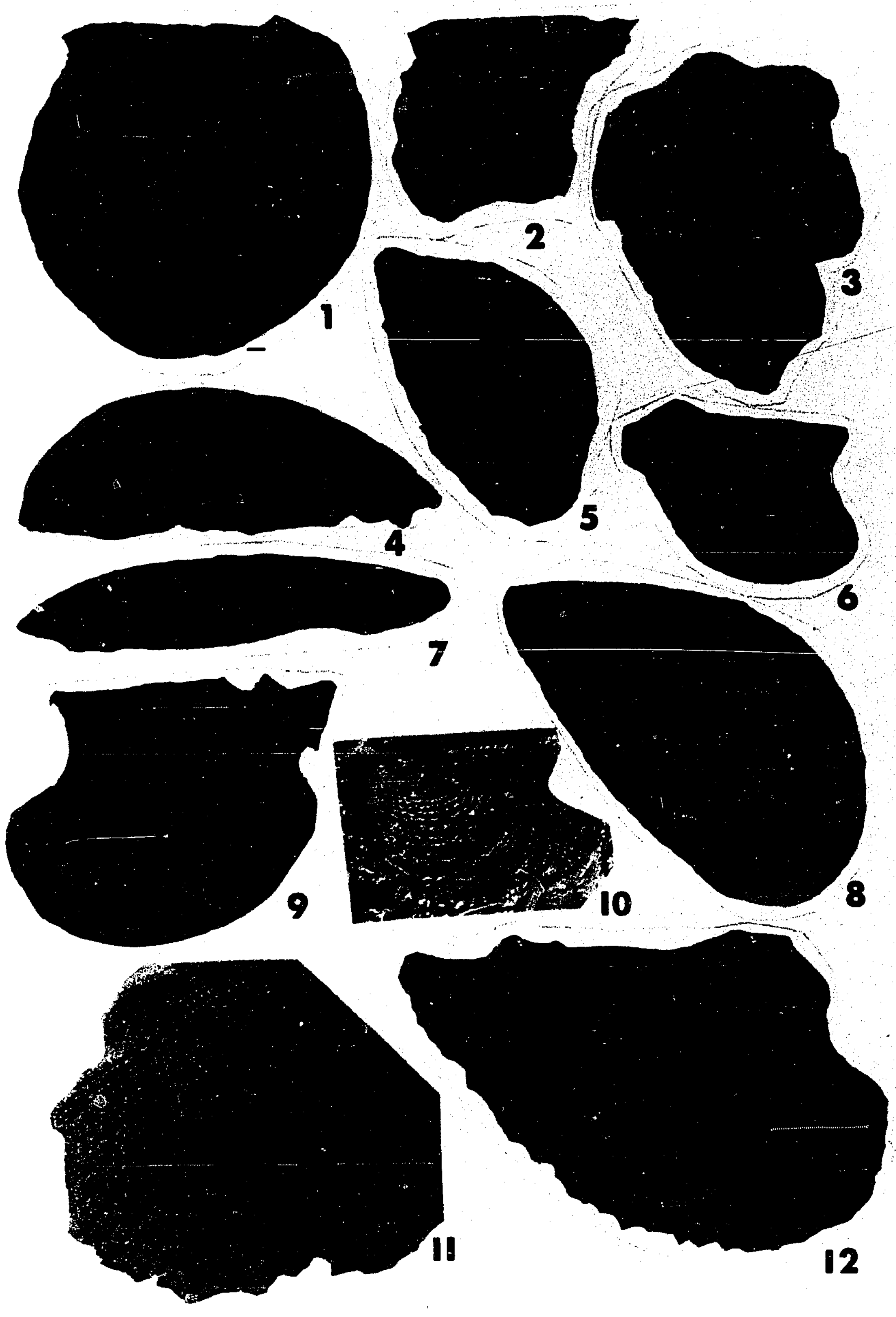

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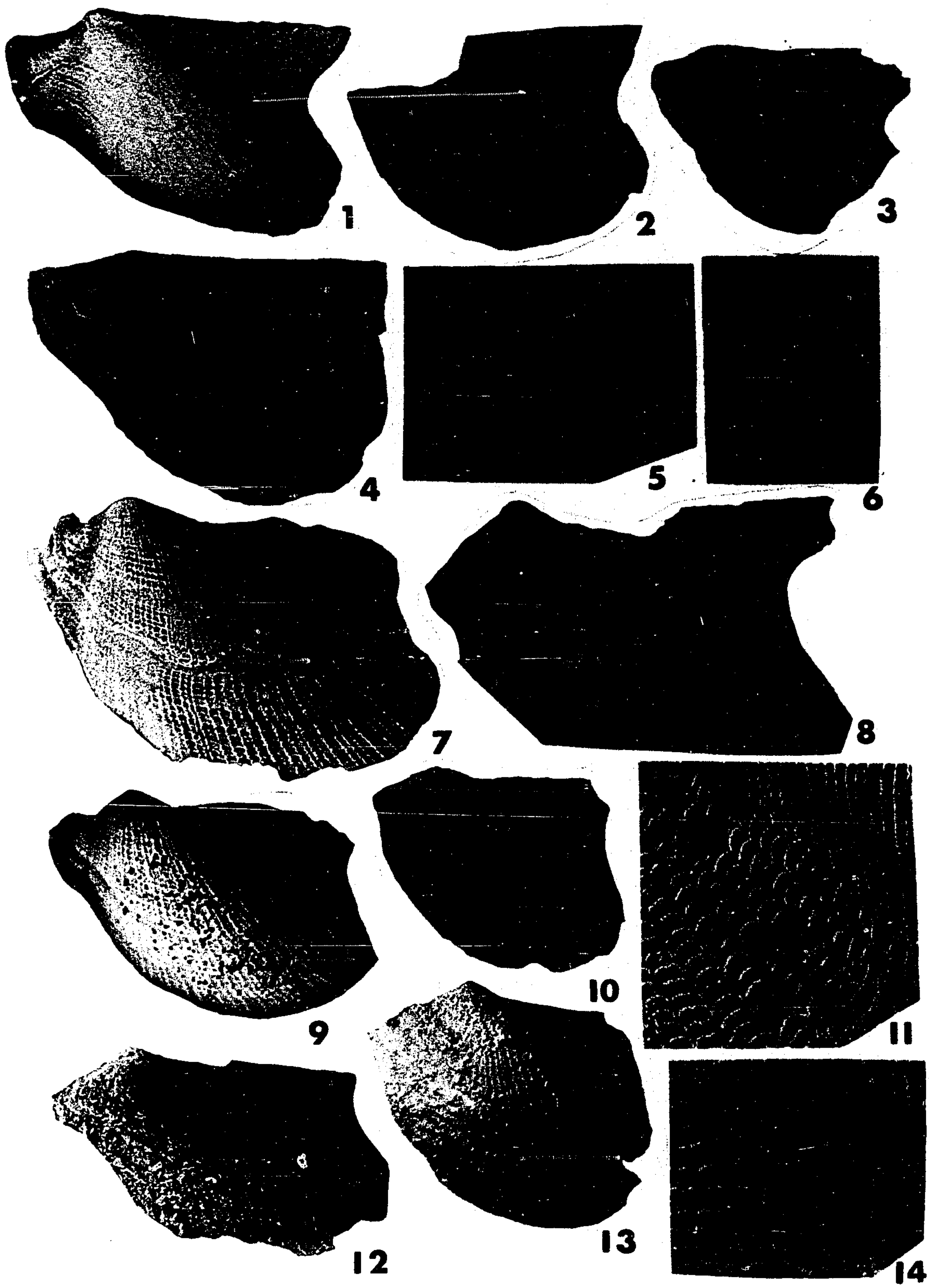

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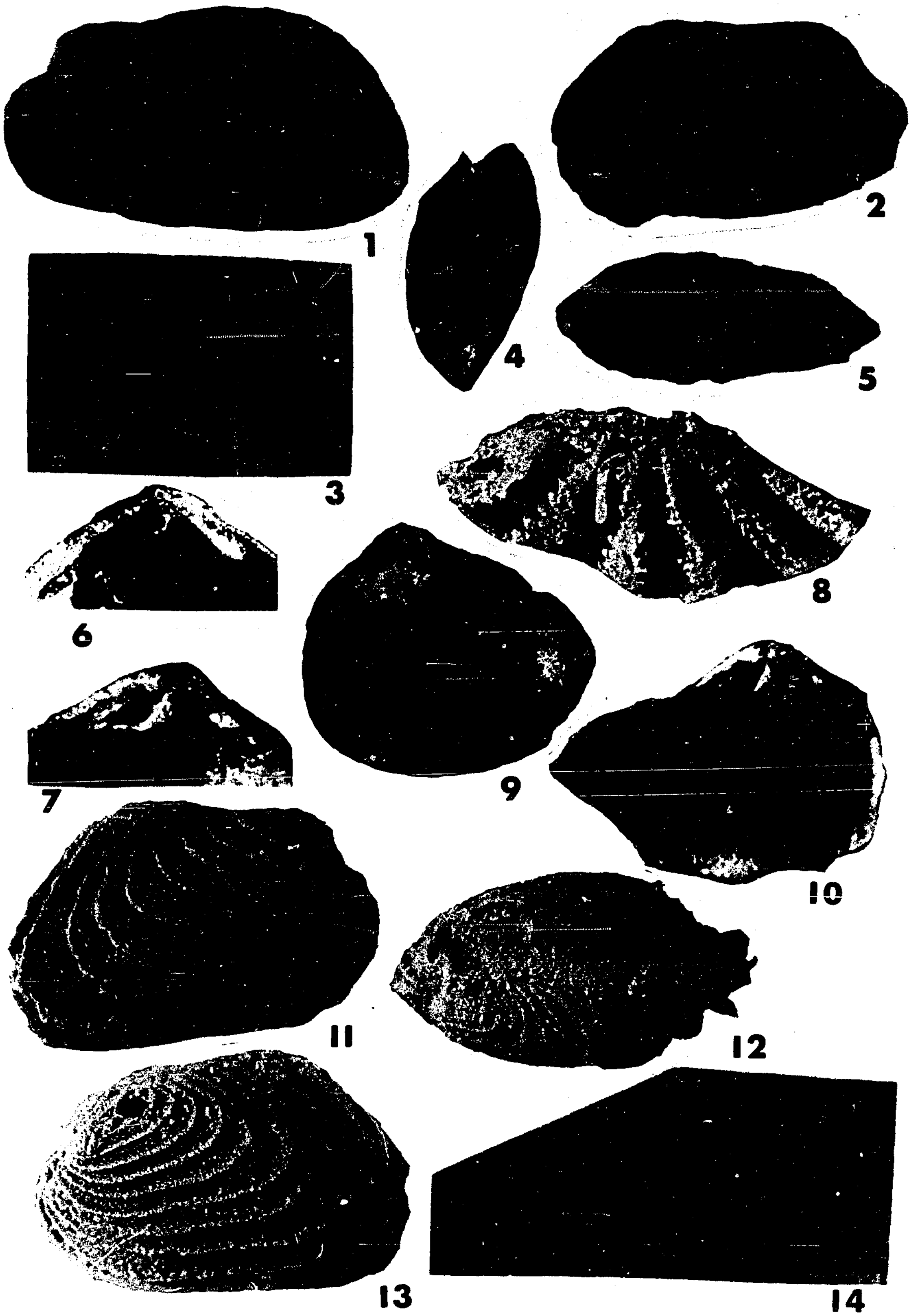

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