Walcott, Charles Doolittle
Classification and
terminology of the Cambrian
Brachiopods

SMITHSONIAN MISCELLANEOUS COLLECTIONS

PART OF VOLUME LIII

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WITH TWO PLATES

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By CHARLES D. WALCOTT

(With Two Plates)

CONTENTS

INTRODUCTION

My study of the Cambrian Brachiopoda has advanced so far that it is decided to publish, in advance of the monograph,[2] a brief outline of the classification, accompanied by (*a*) a schematic diagram of evolution and scheme of classification; (*b*) a note, with a diagram, on the development in Cambrian time; (*c*) a note on the structural characters of the shell, as this profoundly affects the classification; and (*d*) a section on the terminology used in the monograph. The monograph, illustrated by 104 quarto plates and numerous text figures, should be ready for distribution in the year 1909.

SCHEMATIC DIAGRAM OF EVOLUTION

In order to formulate, as far as possible, in a graphic manner a conception of the evolution and lines of descent of the Cambrian Brachiopoda, a schematic diagram (see plate 11) has been prepared for reference. It is necessarily tentative and incomplete, but it will serve to point out my present conceptions of the lines of evolution of the various genera, and it shows clearly the very rapid development of the primitive Atrematous genera in early Cambrian time.

[1] Published by permission of the Director of the U. S. Geological Survey.

[2] Monograph LI, U. S. Geological Survey.

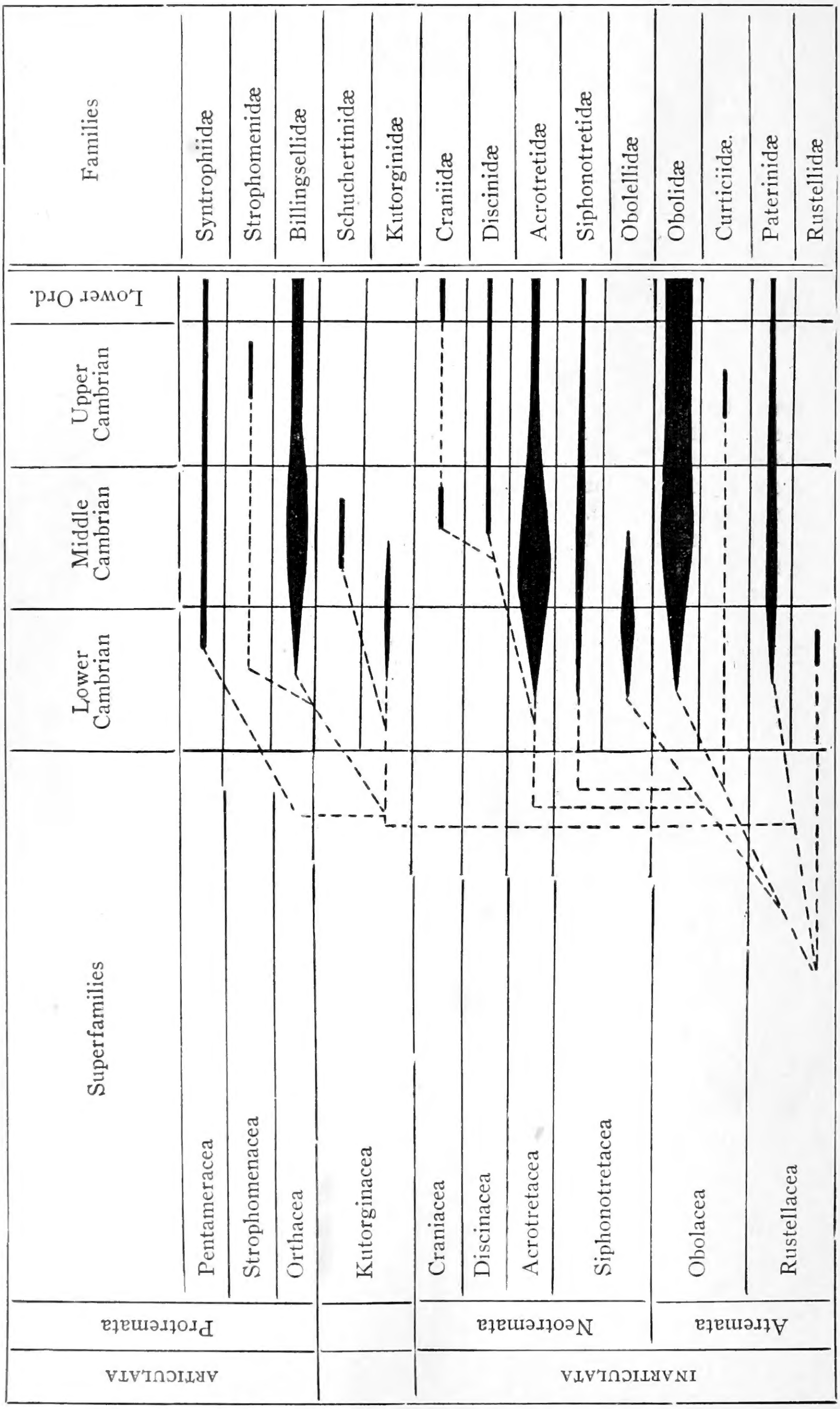
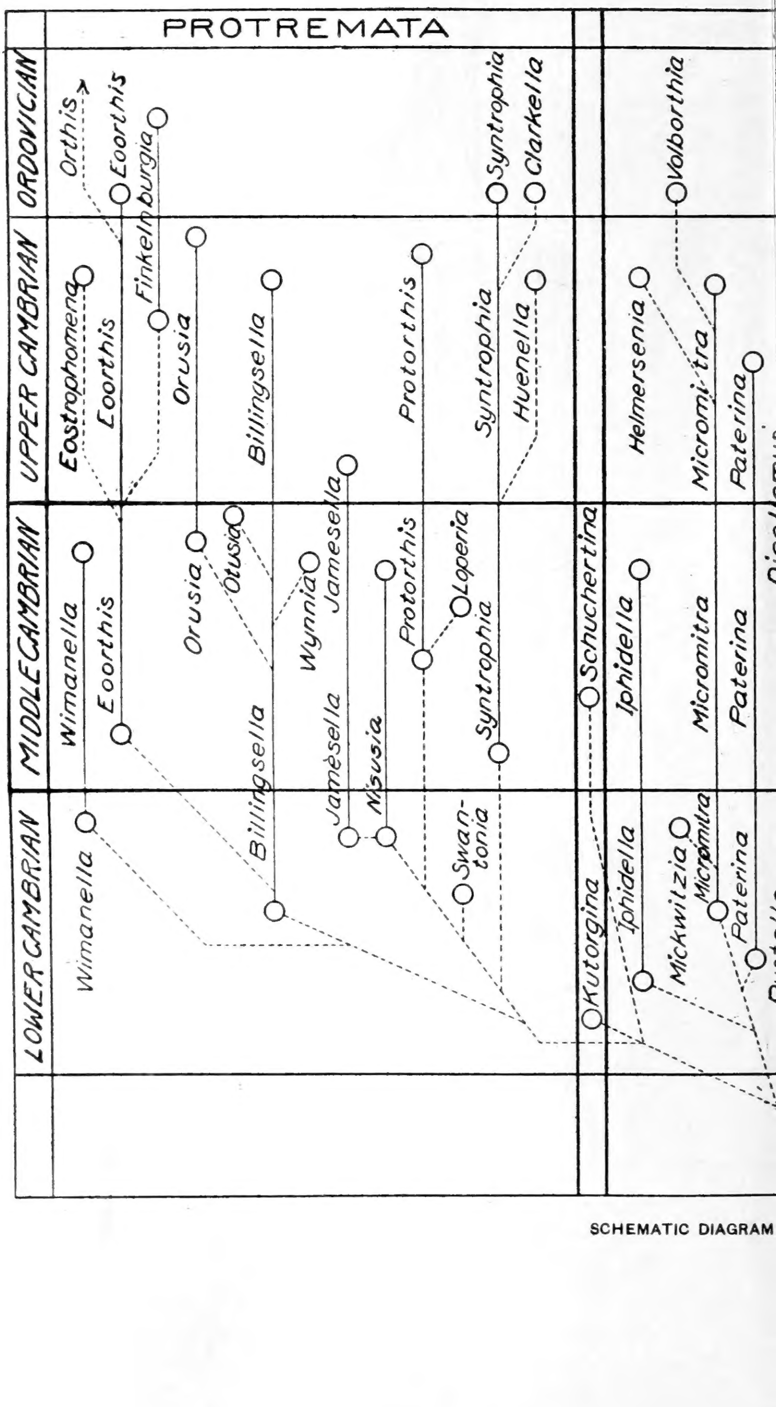
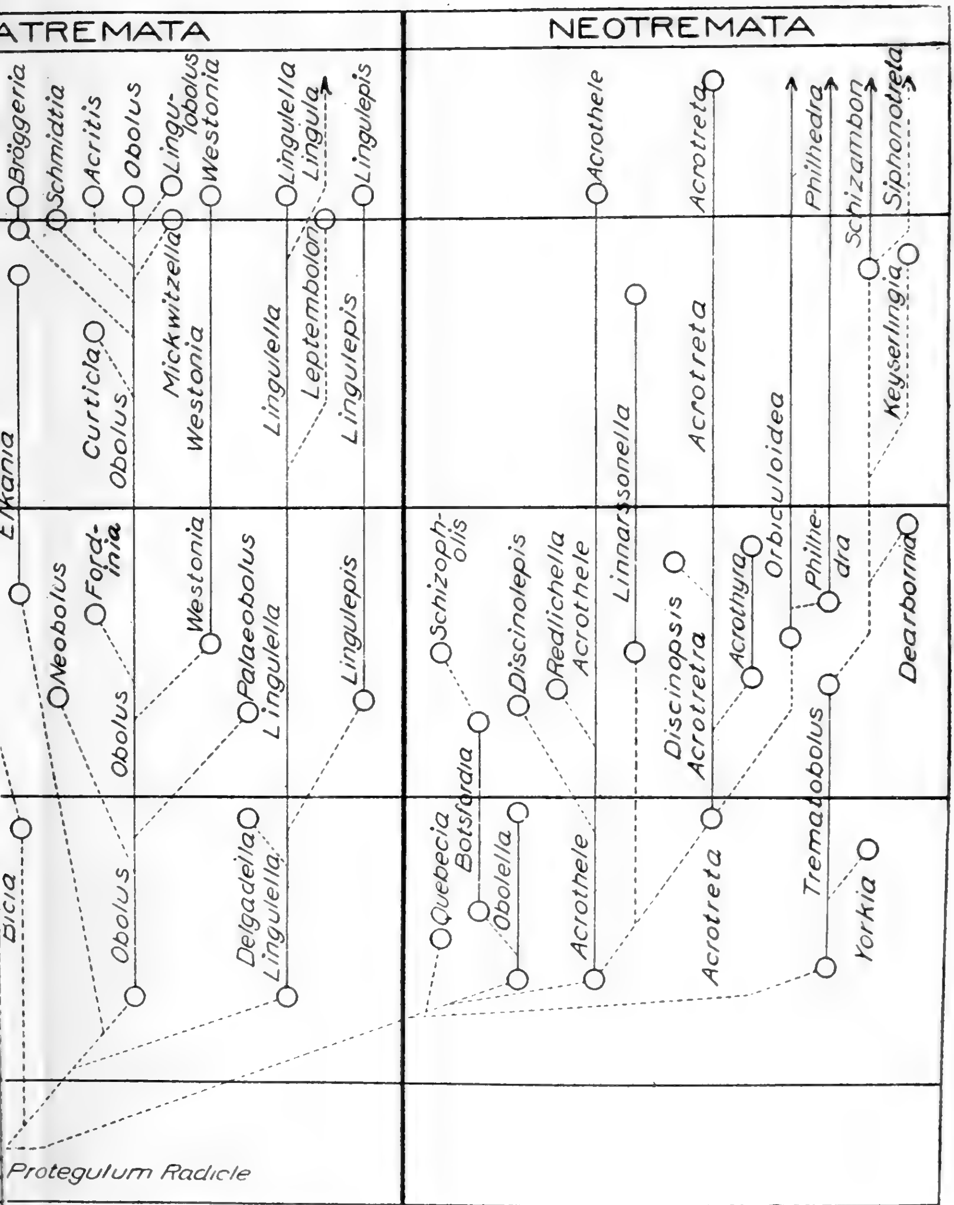


FIG. 1.—Diagram Illustrating Known Distribution of Families in Cambrian Strata.



SCHEMATIC DIAGRAM



EVOLUTION OF CAMBRIAN BRACHIOPODA

DEVELOPMENT IN CAMBRIAN TIME

We do not know of any brachiopoda in strata older than that containing the *Olenellus* or Lower Cambrian fauna. That such existed in pre-Cambrian time seems almost certain when the advanced stage of development of some of the earliest known forms is considered.

In the preceding diagram the known occurrence of the families of brachiopoda in strata of Cambrian age is graphically shown. The diagram is based on the data contained in tables prepared for the monograph giving a summary by families. The Obolidæ, with 7 genera, 9 subgenera, 183 species, and 17 varieties, has the greatest development, and the family continues into the base of the Ordovician with 2 genera, 7 subgenera, and 36 species. The Acrotretidæ has 6 genera, 1 subgenus, 93 species, and 19 varieties, with the greatest development in the Middle Cambrian and with a smaller representation in the Lower Ordovician. The Billingsellidæ, with 9 genera, 2 subgenera, 95 species, and 12 varieties, has a strong development in the upper Middle Cambrian and passes into the Ordovician, where it disappears. The three families mentioned include about 48 per cent of the genera, 80 per cent of the subgenera, 81 per cent of the species, and 81 per cent of the varieties included in the Cambrian brachiopoda. The development of genera of the remaining families containing 3 genera or more is as follows: Paterinidæ, 4; Obolellidæ, 4; Siphonotretidæ, 6; Syntrophiidæ, 3; or 17 genera of the 24 outside of the Obolidæ, Acrotretidæ, and Billingsellidæ, which contain 23 genera. The remaining 7 families include 7 genera.

Of the 46 genera from the Cambrian, 20 occur in the Lower Cambrian, 31 in the Middle Cambrian, and 23 in the Upper Cambrian.

SCHEME OF CLASSIFICATION

In order that we may have a graphic illustration to aid in description, the following table is inserted. The ordinal classification of Beecher [1891], with emendations, is taken as the basis for the orders, while the arrangement of superfamilies is practically that of Schuchert [1897], with such emendations and additions as greater information has rendered necessary. Dr. Charles Schuchert has been most helpful in discussion and criticism of this scheme of classification, and I am also indebted to Mr. E. O. Ulrich for a discussion of the classification of the Protremata. Due acknowledgment will be made in the monograph to many persons who have aided in various ways in making the monograph much more complete and useful than it otherwise would have been.

TABLE OF CLASSIFICATION.

Order	Superfamily	Family	Subfamily	Genera
ATREMATA	Rustellacea	Rustellidæ		Rustella
		Paterinidæ		Mickwitzia Micromitra (Paterina) (Iphidella) Volborthia (?)Helmersenia
	Obolacea	Curticiidæ		Curticia
		Obolidæ	Obolinæ	Obolus (Bröggeria) (Palæobolus) (Fordinia) (Lingulobolus) (Mickwitzella) (Acritis) (Schmidtia) (Westonia) Lingulella (Leptembolon) (Lingulepis) Delgadella
			Elkaniinæ	Elkania
			Neobolinæ	Neobolus
			Biciinæ	Bicia Dicellomus
	Kutorginacea	Kutorginidæ		Kutorgina
		Schuchertinidæ		Schuchertina
NEOTREMATA	Siphonotretacea	Obolellidæ		Obolella (Glyptias) Botsfordia Schizopholis (?)Quebecia
		Siphonotretidæ		Yorkia Dearbornia Trematobolus Schizambon Siphonotreta Keyserlingia
	Acrotretacea	Acrotretidæ	Acrothelinæ	Acrothele (Redlichella) Discinolepis
			Acrotretinæ	Linnarssonella Acrotreta Acrothyra Discinopsis
	Discinacea	Discinidæ		Orbiculoidea
	Craniacea	Craniidæ		Philhedra
PROTREMATA	Orthacea	Billingsellidæ	Nisusiinæ	Nisusia (Jamesella) Protorthis (Loperia)
			Billingsellinæ	Wimanella Billingsella Orusia Otusia Wynnia
			Eoorthinæ	Eoorthis Finkelnburgia
	Strophomenacea	Strophomenidæ	Rafinesquinæ	Eostrophomena
	Pentameracea	Syntrophiidæ		(?)Swantonia Syntrophia Huenella Clarkella

Order ATREMATA Beecher, 1891 (emend)

Primitive inarticulate, corneous or calcareo-phosphatic Brachiopoda with the pedicle emerging more or less freely between the two valves. Growth takes place in general around the anterior and lateral margins. Specialized forms show tendency to develop rudimentary articulation. Delthyrium originally unmodified, in later genera modified by pseudodeltidia and pseudochilidia, or by thickened, striated, and more or less furrowed or even cleft vertical cardinal margins, the ventral cleft in most specialized forms tending to enclose the pedicle and finally restrict it to the ventral valve; when completely so the genera are referred to the order Neotremata.

Superfamily RUSTELLACEA Walcott, new

Primitive, thick-shelled, corneous or calcareo-phosphatic Atremata developing more or less of pseudodeltidia and pseudochilidia.

Family RUSTELLIDÆ Walcott, new

Primitive Rustellacea with the delthyrium small, open, and not much modified by pseudodeltidia or pseudochilidia. Muscle scars and vascular sinuses not well defined in the shell.

Rustella

Family PATERINIDÆ Schuchert, 1893 (emend)

Progressive Rustellacea with the delthyrium more or less closed by pseudodeltidia or pseudochilidia.

Mickwitzia
Micromitra
(*Paterina*)
(*Iphidella*)
Volborthia
(?) *Helmersenia*

Superfamily OBOLACEA Schuchert, 1896 (emend)

Derived (in Rustellacea), progressive, thick-shelled, calcareo-phosphatic or corneous Atremata without pseudodeltidia and pseudochilidia. Rounded or linguloid in outline, more or less lens-shaped and fixed by a short pedicle throughout life to extraneous objects.

Family CURTICIIDÆ Walcott and Schuchert, new

Primitive Obolacea with a high, well-defined delthyrium. Interior characters much as in Obolidæ.

Curticia

Family OBOLIDÆ King, 1846 (emend)

Derived, progressive Obolacea with thickened, striated, vertical cardinal areas traversed by pedicle grooves. Muscles and vascular trunks strongly impressed in the valves.

Subfamily OBOLINÆ Dall, 1870 (emend)

Primitive Obolidæ with the pedicle grooves more or less shallow or deeply rounded, but never tending to form a sheath or to completely restrict the pedicle opening to the ventral valve. The radicle of the Trimerellidæ, by way of the Neobolinæ, appears to be in this subfamily in the thick-shelled Middle Cambrian forms of *Obolus* (s. s.)

Obolus
- (*Bröggeria*)
- (*Palæobolus*)
- (*Fordinia*)
- (*Lingulobolus*)
- (*Mickwitzella*)
- (*Acritis*)
- (*Schmidtia*)
- (*Westonia*)

Lingulella
- (*Leptembolon*)
- (*Lingulepis*)

Delgadella

Subfamily ELKANIINÆ Walcott and Schuchert, new

Divergent Obolidæ with posterior or marginal (not central) platforms, to which are attached the central and outside and middle lateral muscles.

Elkania

Subfamily NEOBOLINÆ Walcott and Schuchert, new

Progressive Obolidæ with posterior platforms, to which were probably attached the central and outside and middle lateral muscles. Subfamily apparently progressive from the Obolinæ to the Trimerellidæ, though the platform is posterior and not subcentral as in the Trimerelloids.

Neobolus

Subfamily BICIINÆ Walcott and Schuchert, new

Progressive Obolidæ with the pedicle restricted to the ventral valve and more or less enclosed by a pedicle tube, and with rudimentary articulation. The transgressing stock from the Atremata to the Neotremata (Obolellidæ).

Bicia

Dicellomus

Superfamily KUTORGINACEA Walcott and Schuchert, new

Progressive, thick-shelled, almost calcareous Atrematous-like shells, tending to be transverse and developing rudimentary articulation, more or less rudimentary cardinal areas, pseudodeltidia, and muscle scars prophetic of the Protremata. Derived out of Rustellacea.

Family KUTORGINIDÆ Schuchert, 1893

Progressive transverse Kutorginacea with rudimentary cardinal areas, great delthyrial opening, rudimentary articulation, and immature pseudodeltidia. Muscle scars prophetic of the Strophomenacea.

Kutorgina

Family SCHUCHERTINIDÆ Walcott, new

Primitive round Kutorginacea with small cardinal areas. Externally like *Obolus,* with an open subtriangular delthyrium which apparently is without a pseudodeltidium. Muscle scars and vascular markings prophetic, through the Billingsellidæ, of the Strophomenacea.

Schuchertina

Order NEOTREMATA Beecher, 1891 (emend)

Derived and specialized inarticulate Brachiopoda (through the Obolidæ of the Atremata), as a rule more phosphatic than calcareous, more or less cone-shaped, with the pedicle emerging during life through a perforation or sheath in the ventral valve, or a triangular, more or less open cleft, or only so in the youngest shelled stage, after which the ventral valve becomes attached by a pedicle to foreign objects. Pedicle cleft in derived forms modified by a listrium. Pseudodeltidia and pseudochilidia as a rule not well developed.

Superfamily SIPHONOTRETACEA Walcott and Schuchert, new

Primitive, thick-shelled, calcareous or corneous, oboloid Neotremata, with the pedicle passing through a ventral sheath, the aperture of which may remain apical and circular in outline, or it may become elongate through resorption by passing anteriorly through the protegulum and umbo of the shell. A listrium is not developed. Dorsal protegulum marginal.

Family OBOLELLIDÆ Walcott and Schuchert, new

Primitive Siphonotretacea with the pedicle emerging through a small circular perforation in the apex of the ventral valve, posterior to the protegulum. Derived out of the Obolidæ.

Obolella
(*Glyptias*)
Botsfordia
Schizopholis
(?) *Quebecia*

Family SIPHONOTRETIDÆ Kutorga, 1848 (emend)

Progressive Siphonotretacea with the circular or elongate pedicle opening at the apex or passing by resorption anteriorly through the protegulum and the umbo of the shell.

Yorkia
Dearbornia
Trematobolus
Schizambon
Siphonotreta
Keyserlingia

Superfamily ACROTRETACEA Schuchert, 1896 (emend)

Progressive Neotremata with corneous or calcareo-corneous shells. The pedicle opening is a simple, circular, more or less conspicuous perforation through the apex of the ventral valve. Dorsal protegulum marginal.

Family ACROTRETIDÆ Schuchert, 1893

Same characters as superfamily.

Subfamily ACROTHELINÆ Walcott and Schuchert, new

Depressed, large Acrotretidæ.

Acrothele
(*Redlichella*)
Discinolepsis

Subfamily ACROTRETINÆ Walcott and Schuchert, new

Small Acrotretidæ with more or less high ventral valves.

Linnarssonella
Acrotreta
Acrothyra
Discinopsis

Superfamily DISCINACEA Waagen, 1885

Derived Neotremata with phosphatic shells, a listrium modifying the pedicle slit, and without pseudodeltidia and false cardinal areas. Dorsal protegulum usually subcentral.

Family DISCINIDÆ Gray, 1840

Discinacea with an open pedicle notch in early life in the posterior margin of the ventral valve, which is closed posteriorly during neanic growth, leaving a more or less long, narrow slit partially closed by the listrium.

Orbiculoidea

Superfamily CRANIACEA Waagen, 1885

Cemented calcareous specialized Neotremata without pedicle or anal openings at maturity.

Family CRANIIDÆ King, 1846

Craniacea with the pedicle functional probably only during nepionic growth.

Philhedra

Order PROTREMATA Beecher, 1891 (emend)

Progressive (though atrematous Kutorginacea), articulate calcareous Brachiopoda with well-developed cardinal areas. The pedicle opening is restricted to the ventral valve throughout life or during early growth and is often modified and more or less closed by a deltidium. Often there is a chilidum. Brachia unsupported by a calcareous skeleton other than crura.

Superfamily ORTHACEA Walcott and Schuchert, new

Derived, progressive Protemata. Cruralia and rudimentary spondylia (pseudospondylia) free or cemented (through sessility) directly to the valves. Sometimes without deltidia and chilidia. Cardinal process more or less well-developed except in the most primitive genera.

Family BILLINGSELLIDÆ Schuchert, 1893

Primitive Orthacea with an open or more or less closed delthyrium. Cardinal process well developed, rudimentary, or absent. Usually with a clearly defined pseudospondylium, to which the muscles of the ventral valve were attached. Shell structure dense, granular, lamellar, non-fibrous.

Subfamily NISUSIINÆ Walcott and Schuchert, new

Primitive Orthacea with more or less well-developed deltidia and with or without rudimentary chilidia. Spondylia and cruralia rudimentary or small and not supported by septa. Cardinal process rudimentary or absent.

Nisusia

(*Jamesella*)

Protorthis

(*Loperia*)

Subfamily BILLINGSELLINÆ Schuchert, 1893

Primitive Orthacea very much like Nisusiinæ but without true spondylia and cruralia. There is a more or less well-developed cardinal process except in Lower Cambrian forms.

Wimanella
Billingsella
Orusia
Otusia
Wynnia

Subfamily EOORTHINÆ Walcott, new

Derived Orthacea nearly always with large open delthyria; deltidia and chilidia occasionally retained throughout life, but more often only in the younger growth stages. Cardinal process well developed. Shell structure dense, granular, and with punctate lamellæ.

Eoorthis
Finkelnburgia

Superfamily STROPHOMENACEA Schuchert, 1896

Derived, progressive, terminal Protremata, out of Orthacea (Billingsellidæ). Deltidia and chilidia nearly always well developed. Cardinal process always well developed.

Family STROPHOMENIDÆ King, 1846

Subfamily RAFINESQUINÆ Schuchert, 1893

Strophomenoids having generally a convex ventral and a concave or nearly flat dorsal valve.

Eostrophomena

Superfamily PENTAMERACEA Schuchert, 1896 (emend)

Specialized Protremata with well-developed free or supported spondylia and cruralia. Deltidia and chilidia usually absent.

Family SYNTROPHIIDÆ Schuchert, 1896

Primitive Pentameracea with long, straight cardinal areas.

(?) *Swantonia*
Syntrophia
Huenella
Clarkella

STRUCTURE OF THE SHELL

The classification of the Protrematous genera is so profoundly influenced by the structure of the shell that it was decided to include the following notes:

The general structural characters of the shell of the Ordovician and later brachiopoda have been so fully described by authors that it does not appear to be necessary or desirable to repeat them. The student will find a full description given by Messrs. Hall and Clarke in their "Introduction to the Study of the Brachiopoda" [1892, pp. 150–225].

Some of the more important works that contain data on the structure of the shell are Hancock, "On the Organization of the Brachiopoda" [1859, pp. 791–869]; King, "On Some Characters of *Lingula anatina*" [1873, pp. 1–17]; Carpenter, "On the Intimate Structure of the Shells of Brachiopods" [1853, pp. 23–45]; Davidson, "On the Classification of the Brachiopoda" [1853, pp. 41–136]; and Mickwitz, "Ueber die Brachiopodengattung *Obolus*" [1896].

The greater proportion of the Cambrian brachiopoda is largely corneous or chitinous. These brachiopoda are restricted to the inarticulates, but the inarticulates of the Cambrian do not all possess corneous shells. Dr. Mickwitz has shown [1896, pp. 102–142] that the shells of *Obolus* and its subgenera are essentially the same as those of *Lingula* in composition and structure. In both the shells are composed of successive calcareous and corneous lamellæ that vary in thickness and structure. The calcareous lamellæ are prismatic and penetrated by minute tubules; the corneous lamellæ are compact and imperforate.

Messrs. Hall and Clarke, in speaking of the shells of the articulate brachiopoda, say: "Among the articulate genera, under favorable preservation, there may be distinguished three distinct calcareous shell layers: an inner prismatic or fibrous layer, which constitutes the greater portion of the shell; above this is a thin lamellar layer, and the outer surface of the shell is covered by a tenuous epidermal film or periostracum. When the shell is punctate the tubules open on the inner surface in narrow apertures, whence they widen upwards, abruptly expanding in the lamellar layer, at whose upper margin they terminate. They do not pierce the periostracum." [1892, p. 175.]

Among the calcareous, inarticulate brachiopoda the shell of the Cambrian genus *Obolella* shows a dense, compact, slightly lamellated structure made up of a granular ground-mass pierced by extremely small tubules or pores. The substance of the shell of *Rustella* and

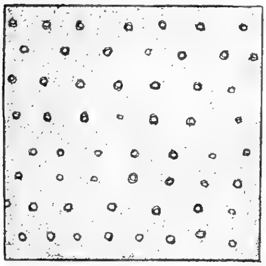
Yorkia is unknown, but from the character of the casts and the fact that the shells of *Micromitra* in the same matrix are preserved, it is probable that it was calcareous. The shells of *Quebecia, Trematobolus,* and *Dearbornia* are also calcareous.

In *Kutorgina* and *Schuchertina,* forms that may be referred to either the Atremata or the Protremata, the shells appear to be calcareous, compact, and without fibrous structure. Messrs. Hall and Clarke, when speaking [1892, p. 174] of the composition of the shell of fossil linguloids, said: "In the group of fossil linguloids, beginning with *Lingula,* passing through *Lingulops* and *Lingulasma* to *Trimerella* and its allies, there is a regular increase in the relative amount of calcareous matter in the shell, so that the *Trimerellas,* which are large and ponderous shells, seem to have wholly lost their corneous matter."

The predominance of corneous or calcareous shell matter does not appear to be of more than generic importance in the classification of the brachiopoda. It is true that the known articulate genera are all calcareous, but it is equally true that among the inarticulate group calcareous shells occur. Alteration, replacement, and removement of original shell substance have changed the shell of so many species that other characters must be depended upon for classification.

Microscopic Structure of the Cambrian Brachiopoda.—In previous work on the Cambrian Brachiopoda, except in the cases above cited, practically no attention has been paid to their microscopic shell structure. The importance of this feature in the classification of later species suggested the possible value of a microscopic study of the earlier forms, and at my request Mr. R. S. Bassler, of the United States National Museum, prepared thin-sections and also assisted in the preparation of the accompanying illustrations and in the preliminary study of the sections.

The preparation of thin-sections of these early brachiopoda is accompanied with difficulties which, together with the lack of sufficiently extensive collections, have undoubtedly prevented previous study along the same line. Specimens suitable for sectioning, especially of the calcareous forms, are not at all common, and when they do occur they are almost invariably buried in the rock, and are so thin that the parting of the enclosing matrix does not leave sufficient shell substance for the preparation of sections. In the present work the specific identity of a shell was first determined by uncovering about one-half the valve, and the other half, still embedded in the matrix, was then used in making the section. The structural features are often restricted to individual lamellæ, and the right zone for microscopic examination was determined simply by close observation as grinding proceeded. Both vertical and tangential sections were prepared, the former cutting the shell at right angles and the latter cutting the shell in planes more or less parallel to the layers or lamellæ of which it is composed. The most interesting results were obtained from the tangential sections, as the thin shells showed little decided structure in vertical sections.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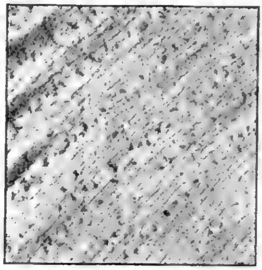
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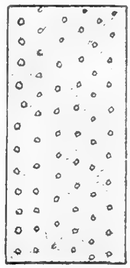
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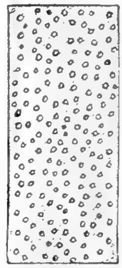
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FIG. 2. *Billingsella plicatella* Walcott [1905, p. 240]. Upper Cambrian, Gallatin Valley, Montana.

Diagrammatic sketch of a small portion of a tangential section, × 200. The granular ground-mass, with small pores and tubules 4 or 5 times their own diameter distant from each other, is also typical of other members of the Billingsellidæ.

FIG. 3. *Dalmanella subequata* (Conrad) [1843, p. 333]. Ordovician (Stones River), St. Paul, Minnesota.

Photograph of a tangential section, × 35, showing the fibrous structure and comparatively large pores.

FIG. 4. *Kutorgina cingulata* (Billings) [1861, p. 8]. Lower Cambrian, Swanton, Vermont.

A small portion of the tangential section figured on Plate 12, fig. 4, × 200. The minute structure of this and the following species is essentially the same as that shown in fig. 1, the only difference being the closer arrangement of the pores.

FIG. 5. *Obolus apollinis* Eichwald [1829, p. 274]. Upper Cambrian Obolus sandstone, Esthonia, Russia.

Small portion of tangential section × 200. The minutely porous granular structure is beautifully shown in this species, in which the pores are arranged more closely than in any other observed.

The general resemblance of the Cambrian eoorthoids to certain Ordovician Protremata is so striking and the lines of descent so suggestive that particular attention was devoted to this group, and the examination brought out the fact that this apparent relationship disappears when the shell structure of the two groups is compared.

Sections of the shells of members of the Billingsellidæ, of which figure 2 is typical, all show a lamellar structure with indications of more or less numerous and scattered, very minute pores or tubules passing without interruption through one lamella. In some sections the spots indicating the tubules are arranged in rows radiating from the beak of the shell to the margins, but no other regular arrangement can be seen. The great mass of the shell is made up of a compact, finely granular base with dark spots and occasional minute crystals of calcite—a ground-mass which, under the microscope, appears very much like that of a fine argillaceous shale.

The Ordovician Protremata have a clearer, more crystalline aspect or color than the Cambrian Billingsellidæ—a difference which probably indicates either a purer lime composition for the former or more probably a higher percentage of calcium phosphate for the latter. In chemical aspect the shells of the Billingsellidæ appear to resemble those of the Atremata and Neotremata more closely than do the Orthidæ. Analyses of the respective shells would be necessary to prove these relations, but to note them is interesting in view of the possible derivation of the Billingsellidæ from the Atremata.

In the Cambrian articulate genera, with the possible exception of *Syntrophia* and *Huenella,* there is an entire absence of the minute, fibrous structure so characteristic of most, if not all, orthoids. But these two representatives of the Pentameracea greatly resemble each other. Thus sections of the shell of *Huenella abnormis* (Walcott) of the Upper Cambrian (see pl. 12, fig. 9) and *Syntrophia lateralis* (Whitfield) of the Lower Ordovician (see pl. 12, fig. 7) show the same radial arrangement of the pores seen in the Billingsellidæ, but the shell structure is fibrous and the rows are coincident in direction with the fibers. Upon closer study this apparent fibrous structure can be resolved into more or less parallel bands or walls of shell substance separating rows of closely arranged, rectangular, pore-like spaces. These spaces may be seen distinctly in thick sections, but when the section is made sufficiently thin to give a clear image under very high power, the pore structure disappears.

Sections of the linguloid genera were also prepared and studied, but the thinness of the shells and their phosphatic character prevented very satisfactory results. The irregular large tubules mentioned by Dr. Mickwitz [1896] are beautifully shown in the sections of *Obolus apollinis* before me. Some of the tubules penetrate several lamellæ of the shell and suggest the tubules of some of the orthoids. (See figures 11 and 12, pl. 12.) The same general structure, with the exception of the larger tubules, appears to be characteristic of all of the corneous shells of the Atremata and Neotremata, and, as far as known to me, all of the Cambrian corneous shells are of this type.

The figures on the accompanying plate, with the exception of figures 11 and 12, are from photographs which have not been retouched. Unfortunately higher magnifications could not be used without a loss of clearness; but, even at the present magnification, these views show a decided difference in structure.

In conclusion, it appears that the Cambrian Billingsellidæ are further removed from the Ordovician and later Protremata than hitherto suspected, the microscopic shell structure in the former being of granular material pierced by small pores and in the latter of fibrous material. On the other hand, the microscopic structure of the Cambrian and later Pentameracea is so similar that an unbroken line of descent is indicated.

TERMINOLOGY RELATING TO THE SHELL

The definitions given in the following pages are largely those of Schuchert [1897, pp. 73–75], with the exception of the muscle scars of the inarticulate brachiopods. For the Atremata and Neotremata the terminology proposed by Professor William King [1873, pp. 5, 6] is adopted, and for the Protremata that used by Messrs. Hall and Clarke [1892, pp. 183–188] and given under the terminology of Schuchert [1897, pp. 73–77]. I agree with Messrs. Hall and Clarke that Professor King's terminology has claims for its adoption, owing to its simplicity. Dr. F. Blochmann has proposed [1900, p. 108] a set of terms for the muscles of the inarticulate brachiopods that has much to commend it. The terminology of Mr. Albany Hancock [1859, p. 800] has been extensively used by authors. The numbers below correspond to the numbers given the terminology of King, Schuchert, and Blochmann.

HANCOCK, 1859

Inarticulates	*Articulates*
1. Anterior occlusors.	1. Anterior occlusors.
2. Posterior occlusors.	2. Posterior occlusors.
3. Divaricator.	3. Accessory divaricators.
4. Central adjustors.	4. } Ventral adjustors.
5. External adjustors.	5. }
6. Posterior adjustors.	6. Dorsal adjustors.
7. Peduncular.	7. Peduncular.

King, 1873	Schuchert, 1897
1. Anterior laterals.	1. Retractors.
2. Centrals.	2. Adductors.
3. Umbonal.	3. Pedicle.
4. Transmedians.	4. Rotators.
5. Outside laterals.	5. Protractors (externals).
6. Middle laterals.	6. Protractors (middles).
	7. Diductors.

Blochmann, 1900

1. Lateralis.
2. Occlusor anterior.
3. Occlusor posterior.
4. Obliquus internus.
5. Obliquus externus.
6. Obliquus medius.

DEFINITIONS

Adductor Muscles.—(See Central muscles.) The term adductor is used for the central muscles of the Protremata.

Anterior Lateral (Retractor) Muscles.—In the Atremata these extend from the outer lateral margins of the visceral area in the ventral valve to its anterior extremity in the dorsal valve and serve to readjust the dorsal shell.

Anterior Region.—That portion of the shell in front of the transverse axis and opposite the pedicle opening.

Apex.—The place of initial shell growth. It may be the most posterior portion of the valve or it may be situated near the transverse axis.

Apical Callosity.—The thickened boss at the inner side of the apex of the ventral valve of *Acrotreta* and other Neotrematous genera through which the pedicle tube or foramen passes.

Area.—See Cardinal area.

Articulate Brachiopoda.—In the orders Protremata and Telotremata the valves articulate by means of teeth and sockets. In some Atremata rudimentary articulation is also developed.

Atremata.—Primitive inarticulate, calcareo-phosphatic or corneous brachiopods with the pedicle emerging more or less freely between the two valves. (For a more detailed description see page 142.)

Brachia.—The fleshy, coiled or spiral, ciliated appendages of brachiopods serving in water circulation and respiration.

Brachiocœle.—All of the anterior half of the valves outside of the anterior portion of the parietal band. (After King.)

CARDINAL AREA.—A more or less well-developed triangular area on each side of the delthyrium, distinctly set off from the general surface of the shell. It is best developed on the ventral valve of articulate brachiopods, but is also present on the dorsal valve, and generally in a rudimentary condition in many inarticulate species. When the area is rudimentary it is often called a false or pseudo-area. The area of some of the inarticulate genera is frequently divided by a line between the delthyrium and the outer margin. In such areas the line is called the flexure line, owing to the slight interruption in the striæ of growth, and the spaces separated by the flexure line are called the inner and outer lateral spaces of the area. (See Deltidium and Foramen.)

CARDINAL EXTREMITIES.—The terminations of the hinge line.

CARDINAL MUSCLE SCAR.—A large scar within which the posterior and anterior lateral and transmedian muscle scars were attached.

CARDINAL PROCESS.—A variously modified apophysis, situated posteriorly at the center of the hinge of the dorsal valve in articulate brachiopoda. To it are attached the diductor muscles, which by their contraction serve to open the valves anteriorly.

CARDINAL SLOPES.—The inclined surfaces extending from the umbonal slopes to the hinge margins.

CENTRAL (ADDUCTOR) MUSCLES.—In the Protremata and Telotremata these muscles have their ventral insertion one on either side of the central axis, between the diductors. In passing to the dorsal valve they divide into four and produce in that shell the two pairs of principal scars known as the anterior and posterior centrals. By contraction these muscles close the shell. In the Neotremata they are the essential muscles, the anterior centrals closing the valves, while the posterior pair serves to open the valves. In the Atremata there is a simple pair of centrals placed near the anterior extremity of the visceral area.

CHILIDIUM.—A dorsal plate, in appearance similar to the deltidium, covering the exterior portion of the cardinal process in many Protremata. Its development does not begin until early neanic or later growth and it is probably secreted by the dorsal mantle lobe. In the Atremata and Neotremata there is a similar plate continuous with the dorsal cardinal region of the shell, and it is named the pseudochilidium.

CRURA.—Processes on the dorsal hinge plate of the Telotremata and some Protremata, to which are attached the fleshy brachia and brachidia. These usually form the inner walls of the dental sockets and may be supported by septal plates.

CRURALIUM.—The dorsal equivalent of the ventral spondylium.

DELTHYRIUM.—The triangular aperture transecting medially the ventral cardinal area, or the posterior surface from the apex to the posterior margin of the ventral valve, through some portion of which the pedicle passes. It has also been termed the *fissure* or *foramen*. The delthyrium may or may not be closed either by a calcareous deltidium or a phosphatic pseudodeltidium.

DELTIDIUM.—A plate more or less continuous with the cardinal margin on the ventral valve covering the delthyrium in Atremata, Neotremata, and Protremata. When present in inarticulate brachiopods it is called the pseudodeltidium, and in the Protremata, where it is always more calcareous, thicker, and more sharply defined, the deltidium and pseudochilidium.

DENTAL PLATES.—Vertical plates supporting the teeth of the ventral valve in articulate brachiopods.

DENTAL SOCKETS.—Excavations in the dorsal cardinal margin of articulate brachiopods in which the teeth of the ventral valve articulate. The inner wall of the socket is elevated and forms the base of the crural plate.

DIDUCTOR MUSCLES.—In the Protremata and Telotremata the principal pair of diductor muscles has the larger end attached to the ventral valve near the anterior edge of the visceral area, while the other end has its insertion on the anterior portion of the cardinal process. By contraction these muscles open the valves.

DORSAL VALVE.—Usually the smaller and imperforate valve and the one to which the brachia are always attached. *Brachial, hæmal, socket,* and *entering* valves are other terms more rarely employed.

EPHEBIC.—Designating the mature shell.

FALSE AREA.—See Cardinal area.

FLEXURE LINE.—See Cardinal area.

FORAMEN.—A small circular passage through the deltidium, either below or at the apex of the ventral valve. Sometimes the foramen encroaches by pedicle abrasion upon the umbo of the ventral valve.

FORAMINAL TUBE.—The pedicle opening through the ventral valve of Neotrematous genera.

GENITAL MARKINGS.—Radial markings or pits within the posterior portion of the visceral space, indicating the position and extent of the genitals.

GERONTIC.—Designating old age. It is indicated in the ontogeny of many species of brachiopods by extreme thickness of the valves, obesity, or by numerous, crowded growth lines near the anterior margin—a condition which sometimes produces truncation and absence of striæ at the margin.

Heart-shaped Cavity.—Central depressed portion of visceral area (Mickwitz).

Hinge Line.—The line along which articulation takes place; also sometimes developed among inarticulate brachiopoda.

Inarticulate Brachiopoda.—In the orders Atremata and Neotremata the valves do not, as a rule, articulate by means of teeth and sockets, as is the case in the articulate orders Protremata and Telotremata.

Lateral Areas.—That portion of the shell on each side of the longitudinal axis.

Listrium.—In some Neotremata a plate closing the progressive track of the pedicle opening or pedicle cleft, posterior to the apex of the ventral valve.

Longitudinal Axis.—A median line through the shell from the beak to the anterior margin.

Median Septum.—An internal vertical plate commonly developed along the longitudinal axis and between the muscles of the ventral valve. Sometimes there is also a dorsal median septum. Lateral septa are rarely developed.

Middle Lateral Muscle Scar.—See Outside lateral.

Neanic.—Designating youthfulness, or the stage in which specific characters begin to develop.

Neotremata.—Circular or oval, more or less cone-shaped, inarticulate calcareo-phosphatic brachiopods with the pedicle opening restricted throughout life to the ventral valve. (For a more detailed description see page 145.)

Nepionic.—Designating the smooth shell stage succeeding the protegulum.

Outside and Middle Lateral (Protractor) Muscles.—In the Obolidæ one pair has the ventral ends fastened at the anterior extremity of the visceral area, extending backward and inserted near the lateral margin of the dorsal valve, outside the transmedians. A second pair originates just behind the centrals of the ventral valve and is inserted posterior to the first pair. These muscles draw the dorsal valve forward.

Parietal Band.—The point of attachment of the muscular wall surrounding the visceral area.

Pedicle.—The flexible muscular organ of the ventral valve by means of which brachiopods may be attached to extraneous objects.

Pedicle Furrow.—The external furrow adjoining the foramen or pedicle opening in certain Neotrematous genera.

PEDICLE GROOVE.—The median groove on the cardinal areas of the valves formed by the pedicle extending through the posterior margin of the valves when they were closed.

PEDICLE MUSCLES.—In the Protremata and Telotremata one pair originates on the ventral valve at points just outside and behind the diductors, and another on the dorsal valve behind the posterior centrals, while the opposite ends of both are attached to the pedicle. Besides these, there is an unpaired muscle lying at the base of the pedicle, attaching it closely to the ventral valve.

PEDICLE OPENING.—See Delthyrium.

PEDICLE TUBE.—See Foraminal tube.

PLATFORM.—An internal median thickening of the shell elevating the muscles. Seen in certain families of the Atremata and more rarely in the Neotremata. (See Spondylium.)

PLEUROCŒLES.—Areas between the parietal band and the outer postero-lateral margins. (After King.)

POSTERIOR REGION.—That portion of the shell back of the transverse axis and toward the beak, or apex.

PROTEGULUM.—The initial shell of brachiopoda. It is smooth and of microscopic size, in outline being semicircular or arcuate and without cardinal areas. Rarely seen in adult shells.

PROTRACTOR MUSCLES.—See Outside and middle lateral muscles.

PROTREMATA.—Articulate, calcareous brachiopods, with the pedicle opening restricted to the ventral valve throughout life or during early growth. Pedicle aperture modified by the deltidium. Brachia unsupported by a calcareous skeleton, but nearly always by a more or less long crura. (For a more detailed description, see page 147.)

PSEUDO-AREA.—See Cardinal area.

PSEUDOCHILIDIUM.—See Chilidium.

PSEUDOCRURALIUM.—Dorsal equivalent of pseudospondylium.

PSEUDODELTIDIUM.—The convex medial portion continuous with the ventral cardinal areas in Atremata and Neotremata. (See Deltidium.)

PSEUDO-PEDICLE GROOVE.—See Pedicle groove.

PSEUDOSPONDYLIUM.—See Spondylium.

RETRACTOR MUSCLES.—See Anterior lateral muscles.

SEPTAL PLATES.—Plates supporting the crural processes; also known as *crural plates*.

SESSILE SPONDYLIUM = Pseudospondylium.

SPLANCHNOCŒLE.—The area within the parietal band. (After King.)

SPONDYLIUM.—A plate in some articulate brachiopoda, mainly the Pentameracea, formed by the union of converging dental plates, to the upper surface of which are attached the adductor, diductor, and pedicle muscles. The spondylium may rest upon the ventral valve or may be supported by a median septum. The spondylium appears to be first indicated in the articulates by a thickening of the shell of the ventral valve beneath the umbonal region so as to form an area upon which all the muscles of the valve have their points of attachment. In *Billingsella* this is beautifully illustrated by *B. exporecta* and *B. plicatella*. In its development the spondylium is foreshadowed in the Atremata by the so-called platform of *Fordinia* and the still more primitive form in *Obolus*. For the purpose of reference, the rudimentary spondylia attached directly to the inner surface of the valve, as in *Billingsella,* may be called pseudospondylia (sessile spondylia, Ulrich), and those free or supported by a septum or septa, spondylia. In the Cambrian Atremata the homologous equivalent has been known as the platform. In *Obolus,* etc., there is sometimes developed in the dorsal valve a plate similar in appearance to the spondylium, but different in origin and known as the cruralium.

TEETH.—Two processes of the ventral valve of articulate brachiopoda, serving for articulation.

TRANSMEDIAN (ROTATOR) MUSCLES.—In Obolacea these are situated posteriorly just in advance of the umbonal muscle, two on one side and one on the other. By their contraction the dorsal valve turns alternately first in one direction and then in the other.

TRANSVERSE AXIS.—A line through the shell from right to left, midway between the beak and anterior region. (See Longitudinal axis.)

TRAPEZOIDAL AREA.—The area on each side of the heart-shaped cavity in *Obolus* in which the outside and middle lateral scars and central muscle scars are attached.

UMBO.—The elevated or prominent portion of the valve anterior to the apex.

UMBONAL CAVITY.—The hollow space in the interior of the shell beneath the umbo.

UMBONAL MUSCLE.—A single muscle situated in the umbonal region of most Atremata. By its contraction the valves are opened anteriorly. In *Obolus* this muscle divides toward the ventral valve.

UMBONAL SLOPES.—The inclined surfaces about the umbo and opposite the cardinal slopes.

VENTRAL VALVE.—Usually the larger valve situated on the ventral side of the animal. Among articulate brachiopoda the valve is usually easily distinguished by the presence of a delthyrium or pedicle opening through which the pedicle is protruded. In many Atrematous genera the ventral valve is not readily distinguished. When the shell is cemented to foreign bodies it is always by the ventral valve. It is usually the larger and deeper of the two valves. *Pedicle, larger, dental, neural,* and *receiving* valves are synonymous terms.

VASCULAR (PALLIAL) SINUSES.—Two convergent or divergent primary sinuses of the circulatory system, traversing the mantle and originating in the posterior medial region. They usually have numerous secondary (lateral and peripheral) branches and both often leave impressions in the shell.

VISCERAL AREA.—The posterior region of the interior of the valves between the pallial sinuses; in general, the immediate area of the median muscle tracks.

VISCERAL CAVITY = Visceral area.

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DESCRIPTION OF PLATE 12

Billingsella coloradoensis (Shumard) [1860, p. 627]:

FIG. 1. Photograph of horizontal thin-section enlarged fifty diameters. This shows the characteristic granular ground-mass of the Cambrian Billingsellidæ. Upper Cambrian, Morgan Creek, Burnet County, Texas.

Nisusia festinata (Billings) [1861, p. 10]:

FIG. 2. Photograph of horizontal thin-section enlarged fifty diameters. This section shows a granular ground-mass in which there are faint indications of small pores or tubulæ which may be seen with a high power. Lower Cambrian, 2 miles east of Swanton, Vermont.

Eoorthis remnicha (N. H. Winchell) [1886, p. 317]:

FIG. 3. Photograph of horizontal thin-section enlarged fifty diameters. This section shows the same type of ground-mass as that illustrated by fig. 2. Upper Cambrian, Cold Creek Canyon, Burnet County, Texas.

Kutorgina cingulata (Billings) [1861, p. 8]:

FIG. 4. Photograph of horizontal thin-section showing granular shell substance. There are few slight indications of pores. Lower Cambrian, Swanton, Vermont.

Dalmanella multisecta (Meek) [1873, p. 112]:

FIG. 5. Horizontal thin-section enlarged fifty diameters. This shows the fibrous structure of the shell penetrated by numerous fine tubules. Ordovician Eden formation, Cincinnati, Ohio.

Dalmanella parva (de Verneuil) [1845, p. 188]:

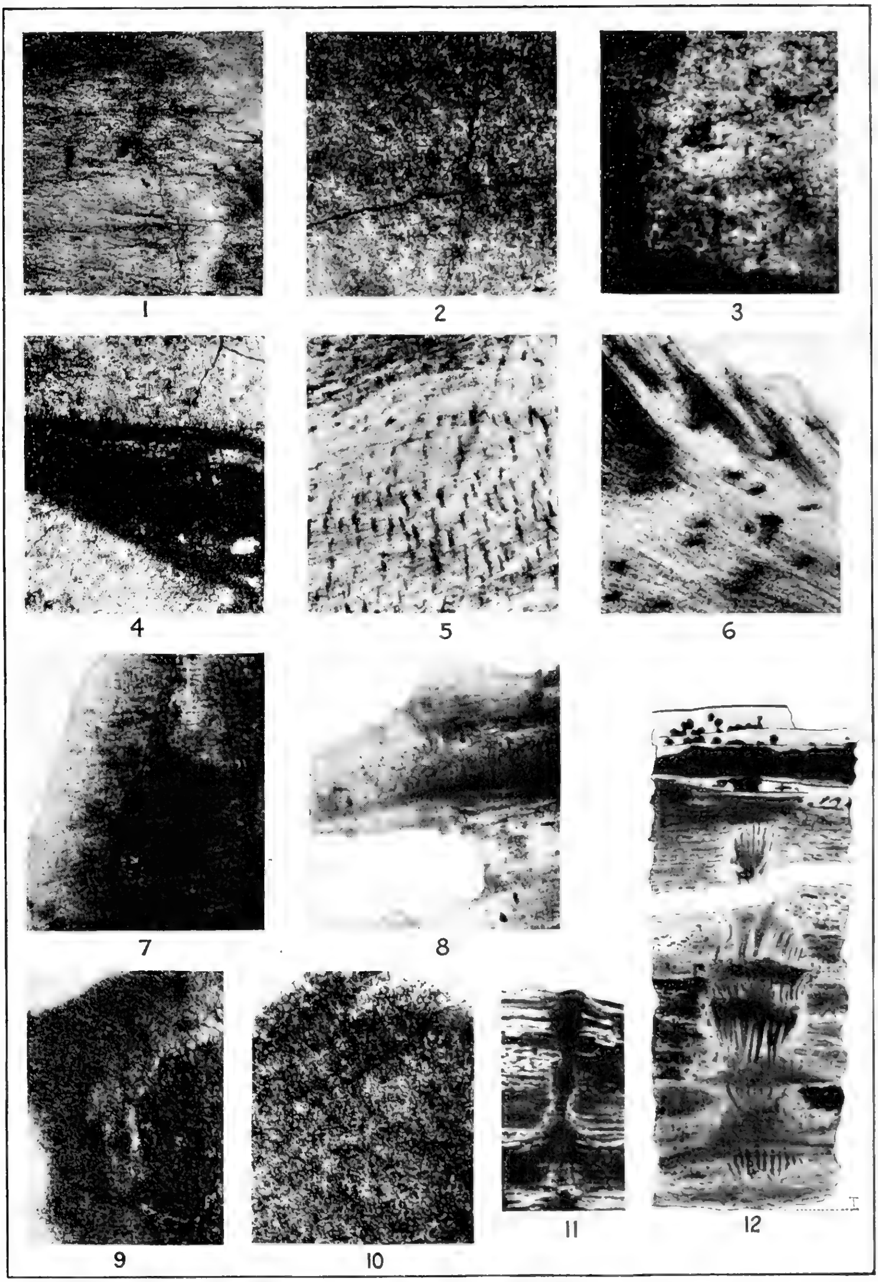
FIG. 6. Horizontal thin-section showing fibrous structure; also section of the tubules that penetrate through the shell. Middle Ordovician of Russia.

Syntrophia lateralis (Whitfield) [1886, p. 303]:

FIG. 7. Horizontal thin-section enlarged fifty diameters, showing the arrangement of the pores in lines that radiate from the apex toward the margin. Lower Ordovician Cassin limestone, Fort Cassin, Vermont.

Plectorthis plicatella (Hall) [1847, p. 122]:

FIG. 8. Horizontal thin-section enlarged fifty diameters. This section shows the fibrous structure so characteristic of the Ordovician orthoids. Ordovician Lorraine shaly limestones, Cincinnati, Ohio.



MICROPHOTOGRAPHS OF ROCK SECTIONS

Huenella abnormis (Walcott) [1905, p. 289]:

FIG. 9. Horizontal thin-section enlarged fifty diameters. The pores in this genus are smaller than in *Syntrophia,* but their arrangement is essentially the same and shows the line effect characteristic of the Pentameracea. Upper Cambrian, Gallatin Valley, Montana.

Obolella crassa (Hall) [1847, p. 290]:

FIG. 10. Horizontal thin-section enlarged fifty diameters. This shows the fine granular ground-mass, with an indication in the upper left side of the section that a surface ornamentation has been cut across. Lower Cambrian, Bic, Canada.

Obolus apollinis Eichwald [1829, p. 274]:

FIGS. 11 and 12. Transverse, vertical thin-section enlarged so to to show the lamellæ and the presence of a large tubule that appears to have more or less imperfectly penetrated through the shell. Upper Cambrian Obolus sandstone, Russia.