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REVISION OF SOME CAMBRIAN AND ORDOVICIAN INARTICULATE BRACHIOPODS

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ABSTRACT

Well-preserved specimens freed from matrix by formic acid permit study of internal morphological features, as well as exteriors of shells. Based on such material, ten species of inarticulate brachiopods (all previously described by Walcott) are redescribed in detail for the purpose of reporting variation in many characters. The species are distributed among nine genera (five new) classed in the families Acrotretidae, Siphonotretidae, and Obolidae. Biometric data are recorded both numerically and graphically, thus adding precision to descriptive differentiation.

INTRODUCTION

Significant advances in understanding and knowledge of fossil inarticulate brachiopods have been closely correlated with improvements in techniques available for their preparation. This relationship is particularly apparent if attention is confined to the smaller species like many of the acrotretaceans, whose maximum dimension is commonly less than 3 millimeters.

The oldest comprehensive account of Cambrian inarticulates is included in Walcott's (1912) *Cambrian Brachiopoda,* a monumental work which brought together virtually all that was then known of the systematics of these brachiopods, including their morphology, stratigraphic and geographic distribution. Like earlier studies, it was based primarily on material that had been exposed whilst splitting open the rock or had been partly freed by natural erosion, and a minimum of subsequent preparation of the specimens was needed. Consequently, information was largely confined to relatively gross features of the shells and the internal structures in particular were poorly known.

Schuchert & Cooper (1932) and Ulrich & Cooper (1938) demonstrated that it was possible to dissect away the matrix mechanically from the interior of a valve so as to expose the internal surface. They worked mainly with Paleozoic articulate brachiopods, which are relatively large in comparison with acrotretaceans. Subsequently, Bell (1941), using the same technique, successfully dissected out the internal surfaces of some small Cambrian inarticulate brachiopods. He was able to show that in detail there is a wide diversity of internal structure, even between forms that are externally rather similar to each other. Mechanical preparation of small, thin-shelled specimens is inevitably time-consuming and requires a high degree of skill even with the most favorable enclosing matrix. It is not suprising, therefore, that relatively few specimens of a given species were dissected and that knowledge of variation of characters within a population was very restricted.

It was Bell's (1948) discovery that free valves of phosphatic-shelled inarticulate brachiopods may be obtained by dissolving limestone in acetic acid that pointed the way to further study of these forms. It is a curious fact that the lithology that had previously been the most difficult to handle became the easiest. Dense limestones that only rarely yield good specimens when the rock is split mechanically can be dissolved in dilute acetic or formic acid and the shells accumulate in the insoluble residue. Under these conditions, internal surfaces are now as easy to obtain free from matrix as external ones and since the specimens are commonly present in some abundance, it is possible to study variation of features within a population. Several studies based on etched material have been made (e.g., PALMER, 1955; COOPER, 1956; IRELAND, 1961; ROWELL & BELL, 1961; WRIGHT, 1963) and although all except the last have been essentially qualitative in their approach, they have revealed an almost unexpected wealth of new forms and the known stratigraphic ranges of several families have been extended greatly.

The advent of acid-etching as a means of recovering inarticulate brachiopods, particularly small forms, has high-lighted the limitations of earlier descriptions of mechanically prepared material. It may be exceedingly difficult to compare specimens obtained by acid treatment with descriptions of the nomenclaturally older taxa, because the finer structures of the latter are largely unknown. Since these structures, like the form of the apical process and the morphology of the posterior margin of both valves among the acrotretids, are now widely used as discriminative characters between genera or ever higher taxa, the problem may be acute. Occasionally the difficulty may arise because of inadequate description of the original material, but more commonly the primary types and original collections fail to provide the degree of detail required. It is apparent that if older names are to be employed in any meaningful fashion, a great deal more must be known about the morphology of the animals for which the names were erected.

The purpose of the present study is to reinvestigate WALCOTT's North American acrotretid species from undeformed specimens prepared by acid treatment of suitable topotype material. Since in many cases there would be considerable difficulty in establishing the exact geographic and stratigraphic position of the type locality, only topotype material collected at the same time as the primary types was used. This material affords the maximum probability of having been collected from the same horizon and locality as the primary types and reduces the possibility of misidentification of the species. It suffers from the obvious limitation of quantity of available specimens. These restrictions on the material reduced the number of acrotretid species that could be considered to 11. Nine of these are still referred to the family, but two are believed to belong to other suprageneric taxa.

That there is a real need for a re-evaluation of some of the older taxa may be demonstrated from the results of the present study. For example, four species that had been assigned to *Linnarssonella* by WALCOTT, author of the genus, have been investigated. Of these four assignments, only that of the type species, *L. girtyi* is considered acceptable. A second species is also an acrotretid, but is better placed in *Acrothyra,* a genus known to WALCOTT. The remaining two species are more distantly related to *L. girtyi,* one seemingly best placed in *Dysoristus,* probably an early siphonotretacean, and the second in a different order, an undoubted lingulacean regarded as belonging to a new genus. It might be considered that the inclusion of a lingulacean within an acrotretacean genus was an act of carelessness on WALCOTT's part, but considering the small size of the specimens, his action is more readily explained as reflecting the inherent limitations of the preparatory techniques available to him.

ACKNOWLEDGMENTS

I am indebted to Dr. G. A. COOPER, for the loan of WALCOTT's topotype material and Dr. A. R. PALMER for etching it and picking the specimens cited in this paper by their U.S. National Museum (USNM) numbers. I am also grateful to Dr. PALMER for providing information on the age of the beds at many of the type localities. The cost of computer time on their IBM 7040 was defrayed by the University of Kansas to the controllers for which I express my thanks.

MORPHOLOGY

GENERAL DISCUSSION

Many aspects of the morphology of inarticulate brachiopods have been discussed recently by WILLIAMS & ROWELL (1965) and it would be superfluous to repeat them here. The excellent state of preservation of the material, however, enables additional comment to be made about modifications of the posterior sector of the pedicle valve of the acrotretid genera. This sector, the pseudointerarea, is typically gently flattened and in some species is divided medially by a narrow triangular groove which BELL termed the intertrough. The intertrough extends from the pedicle foramen to the dorsal surface of the pseudointerarea, becoming progressively broader in a dorsal direction. The functional significance or explanation of the structure is obscure. WALCOTT, knew it as a "false pedicle groove," but as BELL (1941, p. 222) pointed out, its growth is associated in no way with the pedicle opening which lies entirely ventral of the mantle responsible for the secretion of the groove. BELL suggested that it might represent the growth track of an internal pedicle tube, but the groove is now known to be present in genera like *Linnarssonia* which lack such an internal structure. The anomalous behavior of the growth lines across the intertrough of the new genus *Hadrotreta* may provide some information on the mode of growth of the groove. The growth lines are disposed concentrically about the apex of the pedicle valve, but even in the best-preserved specimens these lines cannot be traced across the intertrough (Pl. 1, fig. 12). The intertrough seemingly defines a very narrow sector of the valve in which secretion of at least the outer layers of the shell was disturbed. It can be shown topologically for modern inarticulate brachiopods and inferred for their fossil representatives, that the posteromedian sector of the ventral mantle is developed later than the remainder (WILLIAMS & ROWELL, 1965, p. 51). It is also known that the secretory behavior of this sector of the mantle is variable, even within small, relatively homogeneous stocks like the discinids (*ibid.* 1965, p. 142). In adult *Discina*, for example, the secretion of this part of the mantle is fully integrated with that of the tissue lateral to it and the posterior sector of the valve behind the pedicle opening is not interrupted medially. This may be contrasted with *Discinisca lamellosa* in which the posterior margin of the pedicle valve is not entire (BLOCHMANN, 1900). A narrow median sector of the mantle, disposed posterior to the pedicle, never secretes mineralized shell in this species, although the outer organic periostracum is continuous with that of the shell lateral to it. Consequently it is not unreasonable to assume that the intertrough, at least in *Hadrotreta,* is an expression of secretory abnormality of the later-formed posteromedian sector of the mantle. Secretion of the outer layers of the shell by this region of the mantle margin is not concordant with that of the mantle lateral to it. The functional significance of the structure is difficult to imagine and the possibility that it was essentially functionless cannot be readily dismissed.

In many acrotretid genera the intertrough is not developed and the growth lines are not interrupted in the posteromedian sector of the valve. The secretory activity of this sector of the mantle is thus comparable with that of *Discina.* In the majority of these genera, the growth lines in a broadly triangular, posterior sector of the shell are deflected in a gentle curve, convex dorsally. This region of the valve is commonly either elevated or depressed relative to the shell lateral to it. For this triangular feature of the shell PALMER (1965, p. 768) coined the rather unfortunate term "deltoid pseudointerarea." As PALMER (1955) noted, the dorsal surface of the deltoid pseudointerarea fits into the gently concave median plate of the dorsal pseudointerarea. These structures along the posterior margin of the shell possibly functioned as a simple form of articulation. Unless the two valves were widely separated from each other, the structures would have certainly constrained relative longitudinal and rotational movements between them.

In *Linnarssonella* additional modifications of the brachial propareas and dorsal surface of the deltoid pseudointerarea seemingly produced a more effective form of articulation. The presence of deep grooves in the dorsal propareas was first noted by BELL (1941, p. 235) who also observed that the posterolateral margins of the opposing valve fitted into these like teeth. The fine suite of topotype specimens of *L. girtyi* reveal additional detail of these structures (Pl. 2, figs. 31, 35). The ventral propareas project farther dorsally than the deltoid pseudointerarea. The dorsal surface of the latter structure bears a fine groove that is bounded anteriorly by a transversely disposed ridge. The ridge is continued laterally on the inner surface of the shell and there lies somewhat ventral of the free edge of the propareas (Pl. 2, fig. 31). With the valves together, these free edges of the ventral propareas slot into the grooves on the propareas of the brachial valve, whilst the transverse ridge bears on the triangular dorsal propareas in front of the grooves. By analogy with modern inarticulate brachiopods, it appears probable that the dorsal pseudointerarea, like that of the pedicle valve, is secreted by the posterior segment of the mantle margin. Its essentially orthocline attitude can only be explained under this hypothesis by anteriorly directed growth of this tissue. If the inference is correct, it follows that although the articulatory mechanism of *Linnarssonella* is broadly similar to that of many articulate brachiopods and they both fulfill a comparable function, none the less they are of different origin, since the teeth and sockets of the Articulata are secreted by infolds of the body wall, not by the mantle margins.

BIOMETRICS

Whenever the acid treatment enabled recovery of more than two or three complete valves of a species from one locality, the verbal description has been supplemented by descriptive statistics. Although the desirability of such statistics is perhaps not universally acknowledged, there can be little doubt that they are capable of expressing more precisely than any words various meristic features of the fossil sample. The case for the routine inclusion of descriptive statistics in systematic work has been eloquently presented by several students of the phylum (e.g. Imbrie 1959, Williams 1962). These authors and an increasing number of other students have used both univariate and bivariate statistics. Such statistics have some advantages over more sophisticated methods for descriptive purposes in that they are easy to calculate and are relatively simple to visualize. They are not however as powerful as multivariate techniques when comparison is made between two assemblages (discussed by Miller & Kahn, 1962, p. 251, and following).

In the present study, only univariate and bivariate statistics have been employed. Bivariate data have been analyzed by the reduced major axis techniques advocated by Kermack & Haldane (1950). In this method, if the growth is isometric or allometry cannot be proven with the available sample, an equation is derived of the form:

$$y = ax + b$$

If allometry is present a curve of the form

$$y = \beta x^{\alpha}$$

better describes the data. This may be expressed logarithmically as

$$\log y = \alpha \log x + \log \beta$$

The allometric form of the equation is given in the table of statistics only if α is significantly different from 1. Logarithms are given to the base e. The following conventional abbreviations have been used in the tables.

$\bar{x}$	=	mean value of x
$\bar{y}$	=	mean value of y
var (x)	=	variance of x
var (y)	=	variance of y
$\overline{\log x}$	=	mean value of natural logarithm of x
$\overline{\log y}$	=	mean value of natural logarithm of y
var (log x)	=	variance of natural logarithm of x
var (log y)	=	variance of natural logarithm of y
r^1	=	correlation coefficient between x and y
r	=	correlation coefficient between natural logarithms of x and y
a	=	growth ratio, slope of line $y = ax + b$
var (a)	=	variance of 'a'
α	=	growth ratio, slope of line $\log y = \alpha \log x + \log \beta$
var (α)	=	variance of α
n	=	number of specimens

SYSTEMATICS

Order ACROTRETIDA Kuhn, 1949

Suborder ACROTRETIDINA Kuhn, 1949

Superfamily ACROTRETACEA Schuchert, 1893

Family ACROTRETIDAE Schuchert, 1893

Subfamily ACROTRETINAE Schuchert, 1893

Genus CANTHYLOTRETA Rowell, n. gen.

Entymology.—Greek, *kanthyle,* swelling, tumor, and Greek, *tretos,* perforated.

Types species.—*Acrotreta marjumensis* WALCOTT, 1908.

Diagnosis.—Medium-sized for family, ornament of fine growth lines; biconvex, pedicle valve apsacline to procline when adult, deltoid pseudointerarea broadly triangular, well developed; external foramen small, circular, immediately posterior of beak. Brachial valve convex, beak lacking nodes.

Ventral interior with subtriangular apical process, extending anteriorly from thickened apex of valve and lying ventral of internal pedicle opening, process posteriorly almost parallel-sided but expanding anteriorly between diverging *vascula lateralia,* commonly bearing spatulate depression anteromedially, anterior margin of process abrupt; apical pits small, adjacent to internal pedicle opening.

Dorsal interior with moderately well-developed, triangular anacline propareas separated by depressed median plate; high triangular median septum continued posteriorly as low ridge, broadening to buttress median plate.

Age.—Middle Cambrian, ?Late Cambrian.

Discussion.—In its external features *Canthylotreta* resembles several other acrotretid genera. Its profile and outline are reminiscent of *Linnarssonia,* although the normally well-developed intertrough of the latter genus serves to distinguish the two. Internally there are marked differences, the apical process of *Canthylotreta* is much more subdued than that of *Linnarssonia* and there is no tendency for it to form a high conspicuous boss bounding a deep apical cavity into which the internal pedicle foramen opens. There are also equally strong differences between the two genera in the brachial valve, for the dorsal propareas of *Linnarssonia* are either completely absent or almost linear, whereas those of *Canthylotreta* are relatively broad and prominent features of the brachial interior.

The structure of the dorsal pseudointerarea of the new genus is very similar to that of *Apsotreta* and the similarities extend to other features of the shell. Indeed, the brachial valves may be readily separated only by the presence of a pair of small nodes on the protegulum of *Apsotreta,* for in *Canthylotreta* this region of the valve is smooth. The gross form of the pedicle valves of the two genera is similar, but no *Apsotreta* is known to have the solid apical process characteristic of *Canthylotreta* and there are differences in the relationship of the internal pedicle foramen to the process. In the former genus, the pedicle traverses the thickened apex of the valve and emerges into the interior of the shell through a foramen within the apical process, but in *Canthylotreta,* although the initial course of the pedicle is similar, the relatively large internal foramen lies entirely dorsal of the apical process. Because of the many gaps in our knowledge of Cambrian acrotretids it is premature to try to erect any comprehensive phylogenetic hypothesis. In many cases the stratigraphic range of taxa, even at the generic level, is inadequately known and there is an associated dearth of information on the variation of internal structures. *Apsotreta* is an Upper Cambrian genus, at present unknown earlier than the Dresbachian, but both phenetic and stratigraphic considerations, in so far as they are known, suggest that it is at least plausible that *Canthylotreta,* appearing in the Middle Cambrian, is closely related to the ancestral stock of *Apsotreta.*

CANTHYLOTRETA MARJUMENSIS (Walcott)

Acrotreta marjumensis WALCOTT, 1908, p. 94, pl. 9, fig. 2, 2a; WALCOTT, 1912, p. 693, pl. 78, fig. 2, 2b-d.

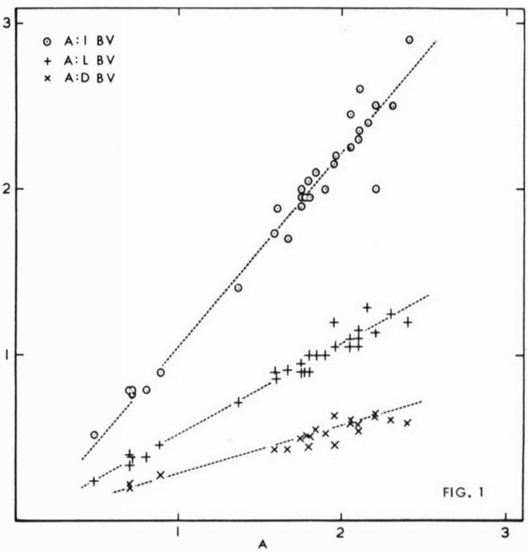
Acrotreta ophirensis descendens WALCOTT, 1908, p. 95, pl. 9, fig. 1, 1a; WALCOTT, 1912, p. 698, pl. 78, fig. 1, 1a-c.

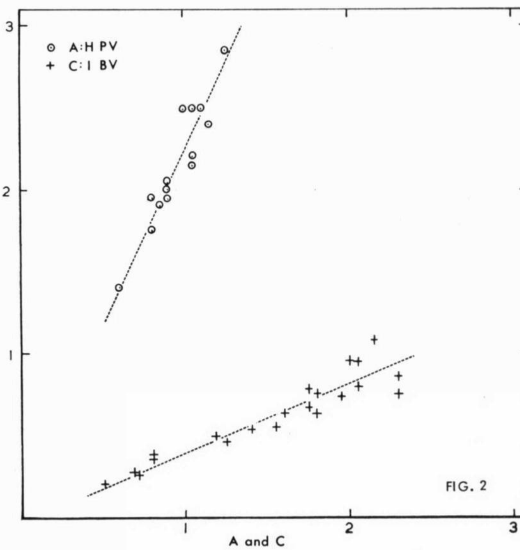
Shell transversely oval in outline, width about 0.1 greater than length; pedicle valve apsacline, in lateral profile anterior slope gently convex, more strongly rounded posteriorly, valve about 3 times as long as high, maximum height occurring at about 0.25 of valve length in front of beak; beak small, slightly incurved, overhanging deltoid pseudointerarea, small foramen immediately behind apex directed posterodorsally; deltoid pseudointerarea broadly triangular, depressed anterior of adjacent shell, angle at apex about 60 degrees. Brachial valve convex in lateral profile, more strongly rounded posteriorly than anteriorly; shallow sulcus arising in front of beak and extending to anterior margin; in anterior profile lateral flanks very gently convex interrupted medianly by sulcus.

Ventral interior with apical region of valve strongly thickened, traversed by subconical passage for pedicle, internal pedicle opening large, facing anterodorsally, lying immediately dorsal of apical process, process extending forward about 0.4 of valve length, typically subtriangular in outline, expanding in width anteriorly; subelliptical cardinal muscle scars on posterolateral flanks of valve, lateral of inner surface of deltoid pseudointerarea; apical pits small, close to and slightly ventral of internal pedicle opening; bacculate *vascula lateralia* bordering apical process posteriorly, divering anterolaterally, separating process from cardinal muscle scars.

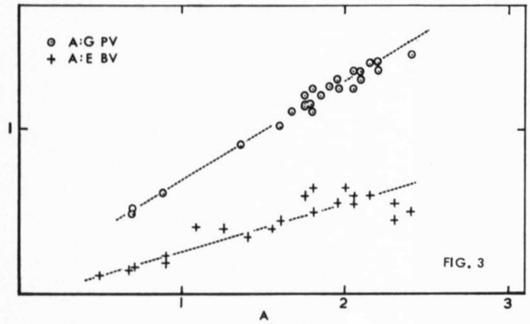
Dorsal propareas separated by strongly developed, depressed median plate extending forward about 0.1 of valve length, propareas anacline; narrow peripheral zone of shell lateral to them flattened, flattened region merging with normal curvature of valve anteriorly; subelliptical cardinal muscle scars diverging anterolaterally from in front of propareas extending forward rather more than 0.3 of valve length, maximum distance between scars slightly less than 0.5 of valve width; anterior muscle scars low elongate swellings either side of median septum, separated from septum by poorly impressed *vascula media*, anterior margin of scars about 0.6 of valve length in front of beak; median septum subtriangular in lateral profile, blade like ventrally, but thickened toward floor of valve, arising about 0.3 of valve length in front of beak, extending forward 0.8 of this distance, posterior slope longer than anterior, maximum height occurring at about 0.7 of valve length; septum continued posteriorly by low ridge of later deposited shell terminating in triangular buttress to median plate of pseudointerarea.

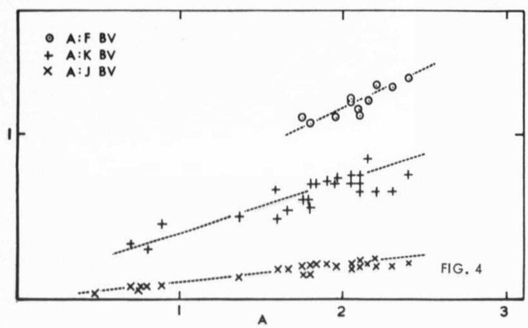
Illustrations.—Figures *1-5*; Plate 1, figures *13-34*; Table 1.——Figs. *1-5*. Scatter diagrams and reduced major axis growth lines for topotype specimens of *Canthylotreta marjumensis*. [Symbols for variables as in Table 1. Variable plotted along abscissa cited first in pair. BV=brachial valve. PV=pedicle valve. All dimensions in millimeters.]——Pl. 1., figs. *13-16*. Lat., post., int., and ext. views of pedicle valve (139500), all ×12.——Pl. 1, fig. *17*. Slightly oblique int. view of brachial valve (139497), ×15.——Pl. 1, fig. *18*.

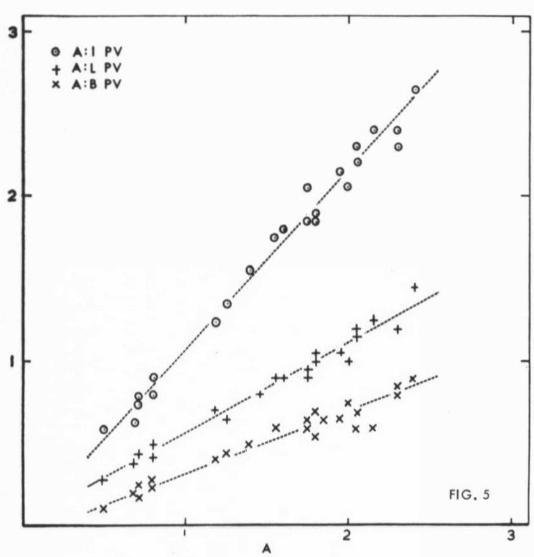




FIGS. 1-2. *Canthylotreta marjumensis* (WALCOTT). Biometric diagrams (see text for descriptions).







FIGS. 3-5. *Canthylotreta marjumensis* (WALCOTT). Biometric diagrams (see text for descriptions).

Ext. view of pedicle valve (139501), ×12.——Pl. 1, figs. *19-20*. Ext. and int. views of brachial valve (139502), both ×12.——Pl. 1, figs. *21-23*. Lat., ext., and int. views of pedicle valve with well-preserved mantle canal impressions (139503), all ×12.——Pl. 1, figs. *24-26*. Lat., post., and dorsal views of complete specimen with both valves together (139504), all ×15.——Pl. 1, figs. *27-29*. Ext., int., and lat. views of brachial valve (139498), all ×15.——Pl. 1, figs. *30-34*. Post., oblique int., lat., ext., and int. views of pedicle valve (in fig. *31* specimen rotated to show large internal pedicle opening) (139499), all ×15. [Specimens 139497-139500 inclusive are topotypes from USNM loc. 11n, late Middle Cambrian, House Range, Utah. Specimens 139501-139504 inclusive are from U.S.N.M. loc. 30n, late Middle Cambrian, House Range, Utah. (Loc. 30n is the type locality of *Acrotreta ophirensis descendens* Walcott).]——Table 1.

Figured Specimens

		USNM	Length (mm.)
Topotype	brachial valve	139497	2.15
Topotype	brachial valve	139498	1.90
Topotype	pedicle valve	139499	1.55
Topotype	pedicle valve	139500	2.10
	pedicle valve	139501	1.95
	brachial valve	138502	2.10
	pedicle valve	139503	2.10
	both valves	139504	1.55

Specimens 139497-139500 from USNM loc. 11n, (upper *Bolaspidella* zone, latest Middle Cambrian—A. R. PALMER, personal communication). "About 3,000 feet (914.4 m.) above the Lower Cambrian and 1,400 feet (426.7 m.) below the Upper Cambrian, in the upper part of the limestones forming 1a of the Marjum Limestone, in the long cliff 2 miles (3.2 km.) southeast of Marjum Pass, House Range, Millard County, Utah" (WALCOTT 1912, p. 693). Specimens 139501-139504 from USNM loc. 30n, "About 3,750 feet (1,143 m.) above the Lower Cambrian and 650 feet (198 m.) below the Upper Cambrian in shaly limestones forming 1c of the Weeks limestone, on the north side of Weeks Canyon, about 4 miles (6.4 km.) south of Marjum Pass, House Range, Millard County, Utah." (WALCOTT 1912, p. 699).

Discussion.—The etched blocks of topotype materials of *Canthylotreta marjumensis* yielded a considerable number of disarticulated valves which allowed determination of some of the growth relationships between various features of the shells (Table 1, text figs. 1-5).

A few specimens of the species preserved details of the mantle canal system which as yet are not well understood. The pedicle valves of the majority of acrotretid species retain impressions of broad bacculate *vascula lateralia* diverging anterolaterally from near the beak. Occasionally the course of relatively slender branches from them may be discerned, as in *Hadrotreta primaaea* (Pl. 1, fig. 11). A few species, notably those referred to *Conotreta,* are characterized by impressions of pinnate *vascula lateralia,* the principal canals dividing into several subequal branches near the ventral apex. In some pedicle valves of *Canthylotreta marjumensis,* however, impressions of two to three pairs of smaller vascular trunks occur medially between those of the main *vascula lateralia* and seemingly are not developed as branches from them (Pl. 1, fig. 23). These vascular trunks possibly represent primary evaginations of the coelom into the ventral mantle, comparable with those forming the *vascula media* of the brachial valve, but they are as yet unknown in any other acrotretid genus (Williams & Rowell, 1965, p. 134).

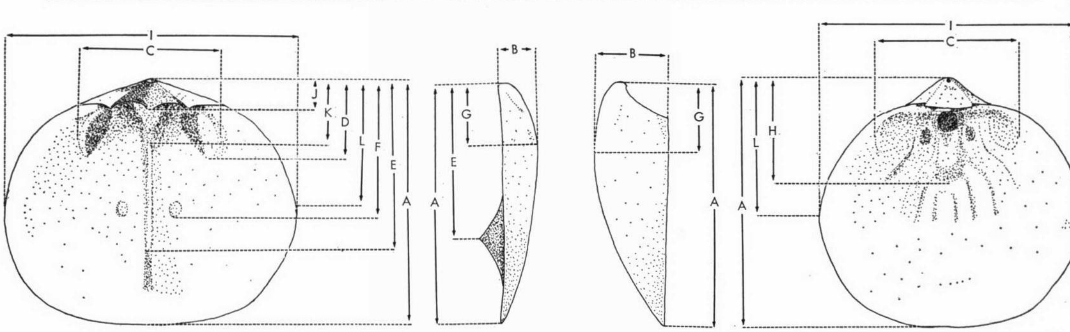
The complement of muscles scars is typical for the family, but as in all acrotretid species the

TABLE 1

CANTHYLOTRETA MARJUMENSIS

Statistics for sample of topotype specimens of Acrotreta marjumensis - upper case letters, not primed (A - L)
Statistics for sample of topotype specimens of Acrotreta ohirensis descendens - upper case letters, primed (A' - L')
Bivariate statistics for allometric growth given only when α differs significantly from 1 (P = 0.05)

Variable x	Variable y	$\bar{x}$	var(x)	$\bar{y}$	var(y)	r'	a	var(a)	$\overline{\log(x)}$	var(log x)	$\overline{\log(y)}$	var(log y)	r	α	var(α)	n	valve
A	I	1.54	0.359	1.66	0.424	0.992	1.0868	0.00085								23	pedicle
A'	I'	1.92	0.107	2.06	0.139	0.966	1.1410	0.00281								33	pedicle
A	L	1.58	0.342	0.88	0.104	0.985	0.5511	0.00046								22	pedicle
A'	L'	1.92	0.107	1.11	0.049	0.913	0.6814	0.00251								33	pedicle
A	B	1.54	0.359	0.53	0.053	0.965	0.3828	0.00048								23	pedicle
A'	B'	1.92	0.107	0.65	0.020	0.813	0.4321	0.00204								33	pedicle
A	G	1.53	0.373	0.42	0.032	0.893	0.2917	0.00086	0.354	0.1472	-0.953	0.1664	0.900	1.0631	0.01068	22	pedicle
A'	G'	1.92	0.107	0.51	0.015	0.756	0.3767	0.00196	0.636	0.0287	-0.694	0.0556	0.759	1.3915	0.02645	33	pedicle
A	H	1.54	0.324	0.63	0.059	0.934	0.4269	0.00122								21	pedicle
A'	H'	1.92	0.107	0.84	0.026	0.916	0.4921	0.00126								33	pedicle
A	I	1.68	0.295	1.86	0.405	0.981	1.1706	0.00182								30	brachial
A'	I'	1.77	0.126	1.98	0.165	0.979	1.1453	0.00104								55	brachial
A	L	1.68	0.295	0.90	0.090	0.984	0.5508	0.00035								30	brachial
A'	L'	1.76	0.124	0.95	0.045	0.906	0.6011	0.00118								57	brachial
A	K	1.76	0.223	0.62	0.018	0.885	0.2868	0.00069	0.529	0.0698	-0.509	0.0475	0.886	0.8253	0.00564	28	brachial
A'	K'	1.75	0.119	0.59	0.012	0.869	0.3233	0.00046	0.543	0.0380	-0.544	0.0350	0.869	0.9605	0.00402	58	brachial
A	E	1.78	0.199	1.15	0.070	0.989	0.5948	0.00034	0.547	0.0608	0.116	0.0516	0.988	0.9212	0.00088	25	brachial
A'	E'	1.77	0.109	1.14	0.042	0.894	0.6220	0.00152	0.554	0.0344	0.118	0.0319	0.895	0.9637	0.00360	53	brachial
A	F	2.08	0.038	1.19	0.008	0.880	0.4705	0.00553								11	brachial
A'	F'	1.77	0.088	1.04	0.029	0.938	0.5685	0.00107								38	brachial
A	D	1.81	0.207	0.52	0.018	0.918	0.2944	0.00062	0.560	0.0614	-0.690	0.0647	0.911	1.0262	0.00743	24	brachial
A'	D'	1.78	0.104	0.49	0.011	0.884	0.3220	0.00045	0.560	0.0324	-0.743	0.0448	0.886	1.1760	0.00582	53	brachial
A	J	1.68	0.295	0.17	0.003	0.937	0.1062	0.00005	0.469	0.0994	-1.820	0.1078	0.940	1.0415	0.00449	30	brachial
A'	J'	1.76	0.121	0.17	0.002	0.759	0.1302	0.00013	0.548	0.0383	-1.788	0.0663	0.766	1.3160	0.01256	59	brachial
C	I	0.95	0.027	2.14	0.131	0.940	2.2235	0.04454								15	brachial
C'	I'	0.93	0.028	2.07	0.132	0.864	2.1688	0.03961								32	brachial



Diagrammatic representation of measurements

A = maximum length of valve B = maximum height of valve C = width between lateral margins of cardinal muscle scars D = length of valve to front of cardinal muscle scars E = length of valve to point of maximum height of median septum F = length of valve to front of anterior muscle scars G = length of valve to point of maximum height H = length of valve to front of apical process I = maximum width of valve J = length of median plate K = length of valve to point of origin of median septum L = length of valve to line of maximum width of valve numbers of muscles involved is problematic. There is no reliable evidence that the muscles responsible for the cardinal scars are composite and it appears very probable that a single, stout pair produced these relatively large, posteriorly located scars. The disposition of the muscles associated with the remaining two pairs of scars is more obscure. The simplest interpretation relates them to a single pair of muscles extending obliquely through the body cavity from the so-called apical pits of the pedicle valve to the anterior scars of the brachial valve. The notoriously delicate nature of muscle scars of modern inarticulate brachiopods, coupled with the known existence of muscles that are "attached" to the shell only at one end, inevitably reduces confidence in the veracity of such an assertion.

The genus is at present known only by its type species, but it is possible that the Upper Cambrian *Acrotreta idahoensis* may belong to it. This species is unknown from etched material and conceivably it should be referred to *Apsotreta,* although the form of the brachial valve figure by WALCOTT (1912, pl. 65, fig. 1f), particularly the flattened peripheral region, suggests provisional assignment to the new genus. WALCOTT (1908, p. 94) noted the resemblance between this species and *C. marjumensis* and also compared the latter with *"Acrotreta" neboensis,* noting that they differed in *"A." neboensis* possessing a more elevated pedicle valve bearing a narrow intertrough. The available etched topotype material of *"A." neboensis* from the Middle Cambrian of Mount Nebo Canyon, Utah, is poorly preserved, but the species appears to belong to *Prototreta.*

Curiously enough *"Acrotreta" ophirensis descendens* WALCOTT, the species showing the greatest resemblance to *Canthylotreta marjumensis,* was erected on the page following the original description of *Acrotreta marjumensis* (WALCOTT, 1908, p. 95) and figures of the two species were adjacent to each other on Plate 9, yet in the description of neither species did WALCOTT compare one with the other. Etching blocks of limestone from the type locality of *A. ophirensis descendens* (USNM loc. 30n) produced considerable numbers of well-preserved disarticulated valves and a few complete shells. Visual comparison of topotype samples of the two species suggested that the only difference between them lay in the relative position of the maximum width of the pedicle valve, this region tending to occur slightly nearer the beak in some species of *C. marjumensis* than in *A. orphirensis descendens,* all other features appeared virtually identical. This subjective assessment is substantiated by a comparison of the statistics (Table 1). With exception of the position of the maximum width of the pedicle valve, all of the bivariate statistics failed to show a significant difference ($P=0.05$) between any of the pairs of growth ratios or initial growth indices when subjected to "t" tests. As is well known, the making of such a test implies assumptions about the distribution of the variables concerned, but since the various pairs of statistics all fall within the range expected in a "t" distribution, the errors involved in making the assumptions are seemingly small. The "t" value obtained in comparing the pair of growth ratios for length against length of the valve to the line of maximum width suggests that *C. marjumensis* and *A. ophirensis descendens* are significantly different in these features ($0.05>P>0.02$). The difference between them however, even if significant, is not very large and the two nominal taxa are here regarded as synonyms. It is perhaps superfluous to add that *A. ophirensis descendens,* although erected as a variety of *"Acrotreta" ophirensis (Linnarssonia ophirensis)* bears little resemblance to it other than gross external form, both being biconvex.

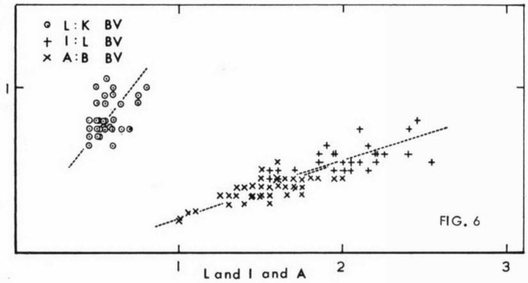
Genus EURYTRETA Rowell, n. gen.

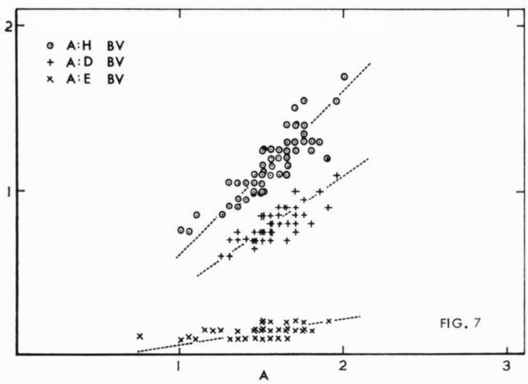
Ethymology.—Greek, *eurys,* broad, wide, and *tretos,* perforated.

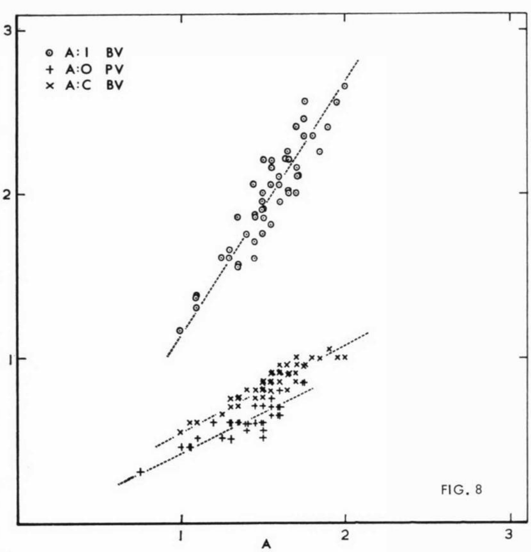
Type species.—*Acrotreta curvata* WALCOTT, 1902.

Diagnosis.—Medium-sized for family, ornament only of fine growth lines, ventribiconvex, pedicle valve approaching subconical with strongly apsacline to catacline pseudointerarea; pseudointerarea externally concave in lateral profile overhung by small but prominent beak; external pedicle foramen small, apical; deltoid pseudointerarea poorly defined, narrowly triangular. Brachial valve with slightly incurved beak, lacking nodes.

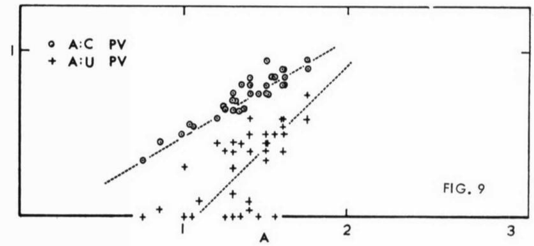
Ventral interior with subtriangular apical process confined to anterior slope of valve, bounded laterally by *vascula lateralia* and not embracing internal pedicle opening, process bearing semicircular depression, curved boundary of depression facing anteriorly; beak not markedly thickened internally and internal pedicle opening consequently small; cardinal muscle scars on conspicuous subelliptical elevations of posterior slope of valve immediately lateral of pseudointerarea. *Vascula lateralia* seemingly bacculate.

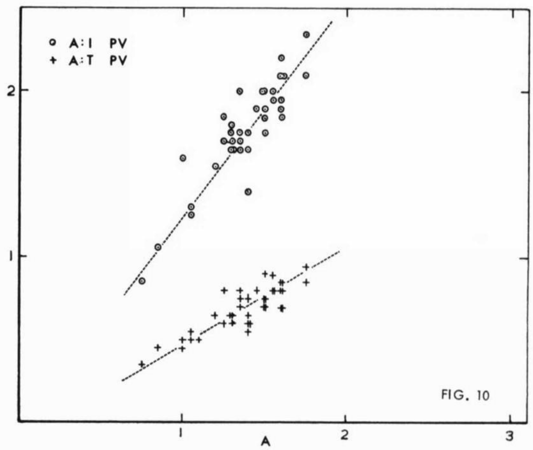






FIGS. 6-8. *Eurytreta curvata* (WALCOTT). Biometric diagrams (see text for descriptions).





FIGS. 9-10. *Eurytreta curvata* (WALCOTT). Biometric diagrams (see text for descriptions).

Propareas of brachial valve well developed, triangular, approximately orthocline, separated by depressed median plate; cardinal muscle scars subelliptical, relatively close together, impressed in conspicuous posteromedian thickening of valve which extends anteriorly to cover posterior end of stout median ridge; anterior muscle scars on low, narrow, elongate elevations near center of valve.

Age.—Early Ordovician.

Discussion.—Although the overall ensemble of characters of *Eurytreta curvata* is strongly suggestive of the Acrotretinae, the species shows no close similarity with any other described form, the internal structure of which is known in any detail. The apical process is not unlike that of the much earlier *Canthylotreta marjumensis*, but the two species differ considerably in many other features, most notably in their deltoid pseudointerareas, position of cardinal muscle scars and thickening of the beak in the latter species. The closest comparison may perhaps be made with *Conotreta*, a genus with first known appearance in North

America in the Middle Ordovician, but which has been recorded from the Tremadocian (Lower Ordovician) of Poland by BEDNARCZYK (1959). In addition to the shared features that characterize the subfamily, the brachial valves of *Conotreta* and *Eurytreta* are similar in their closely spaced cardinal muscle scars which are located on a marked thickening of the valve; they differ in that the median elevation of the shell in *Conotreta* forms a distinct septum rather than a ridge. Rather less resemblance between the pedicle valves of the two genera is seen. The ventral beak of *Conotreta* is strongly thickened internally and the passage for the pedicle expands anteriorly so that the diameter of the internal pedicle opening is many times that of the external foramen. A more marked difference, however, exists in the impressions of the mantle canal system. This system in *Conotreta* is typically pinnate and the canals are commonly strongly impressed in the shell, whereas the more common, bacculate condition, characterizes *Eurytreta.* These differences in the disposition of the mantle canal impressions are probably to be correlated with the difference in outline of the apical process. The process of *Eurytreta* expands anteriorly and is bounded laterally by the posterior unbranched segments of the *vascula lateralia,* but that of *Conotreta* is much narrower and more parallel-sided, and is confined laterally by a pair of median branches of the *vascula lateralia.*

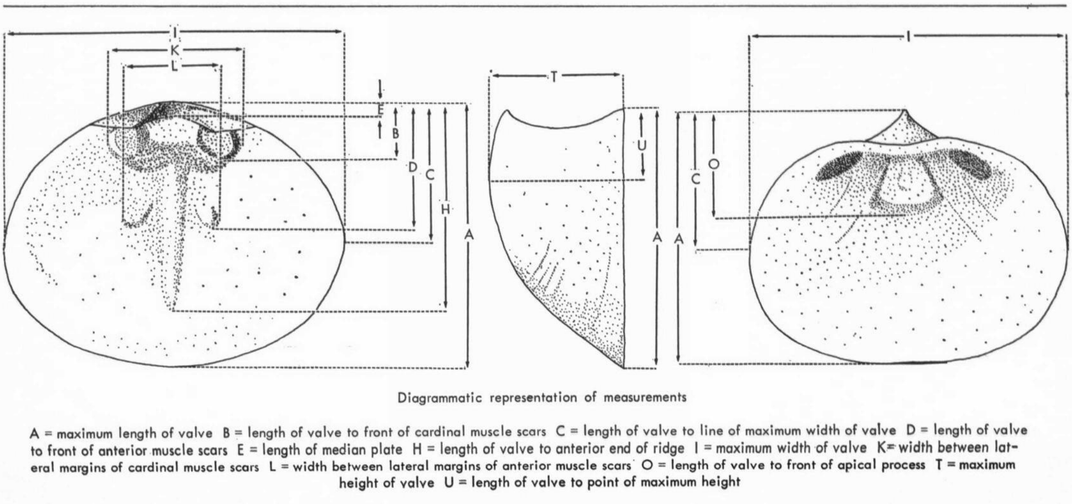
EURYTRETA CURVATA (Walcott)

Acrotreta curvata WALCOTT, 1902, p. 584; WALCOTT, 1912, p. 682, pl. 68, figs. 1, 1a-1n.

Shell transversely oval in outline, maximum width about 0.25 greater than length; pedicle valve strongly apsacline to catacline when adult, young forms may be weakly catacline; in lateral profile valve nearly flat or gently convex for short distance

TABLE 2
EURYTRETA CURVATA
Statistics of sample of topotype specimens
Bivariate statistics for allometric growth given only when α differs significantly from 1 (P = 0.05)

Variable x	Variable y	$\overline{x}$	var(x)	$\overline{y}$	var(y)	r'	a	var(a)	$\overline{\log(x)}$	var(log x)	$\overline{\log(y)}$	var(log y)	r	α	var(α)	n	valve
A	T	1.37	0.054	0.69	0.019	0.864	0.6002	0.00234								41	pedicle
A	I	1.39	0.054	1.76	0.095	0.909	1.3297	0.00904								36	pedicle
A	C	1.38	0.055	0.72	0.020	0.942	0.6027	0.00113	0.303	0.0362	-0.343	0.0476	0.960	1.1465	0.00289	38	pedicle
A	U	1.38	0.055	0.32	0.056	0.664	1.0058	0.01487								40	pedicle
A	O	1.39	0.048	0.61	0.012	0.894	0.5079	0.00136								40	pedicle
A	I	1.54	0.046	1.97	0.109	0.926	1.5507	0.00686	0.421	0.0215	0.661	0.0318	0.936	1.2142	0.00365	52	brachial
A	C	1.54	0.045	0.83	0.013	0.946	0.5423	0.00060								53	brachial
A	B	1.54	0.043	0.39	0.005	0.707	0.3368	0.00105	0.423	0.0205	-0.956	0.0378	0.764	1.3600	0.01427	56	brachial
A	D	1.57	0.023	0.80	0.011	0.794	0.6871	0.00405	0.447	0.0094	-0.233	0.0169	0.799	1.3393	0.01508	45	brachial
A	H	1.54	0.044	1.15	0.045	0.866	1.0060	0.00476	0.423	0.0208	0.123	0.0358	0.878	1.3115	0.00744	55	brachial
A	E	1.54	0.041	0.14	0.001	0.521	0.1720	0.00043	0.425	0.0192	-1.980	0.0624	0.532	1.8020	0.04659	52	brachial
L	K	0.56	0.008	0.81	0.011	0.400	1.2225	0.03691								36	brachial
I	L	2.01	0.078	0.56	0.008	0.576	0.3125	0.00211								33	brachial



Diagrammatic representation of measurements

A = maximum length of valve B = length of valve to front of cardinal muscle scars C = length of valve to line of maximum width of valve D = length of valve to front of anterior muscle scars E = length of median plate H = length of valve to anterior end of ridge I = maximum width of valve K = width between lateral margins of cardinal muscle scars L = width between lateral margins of anterior muscle scars O = length of valve to front of apical process T = maximum height of valve U = length of valve to point of maximum height in front of beak, more strongly rounded anteriorly, maximum height slightly less than 0.5 of valve length occurring about 0.2 of valve length in front of beak; prominent beak incurved over pseudointerarea, which is relatively conspicuous, subtending angle of about 80 degrees at apex; deltoid pseudointerarea narrow, poorly defined. Brachial valve convex in lateral profile, beak slightly incurved; shallow, poorly defined sulcus arising about 0.3 of valve length in front of beak, anterior profile gently convex interrupted medially by sulcus.

Ventral interior with conspicuous cardinal muscle scars raised above adjacent shell on posterior slope of valve, beak of valve not thickened, internal foramen small; apical process lying in front of internal foramen, expanding in width anteriorly, extending forward slightly less than 0.5 of valve length. Brachial valve interior with well-developed pseudointerarea, both propareas and median plate bearing fine growth lines, median plate extending forward about 0.1 of valve length in front of beak; cardinal muscle scars prominent, subelliptical in outline impressed in posteromedian thickening of valve, cardinal scars extending forward about 0.25 of valve length, distance between lateral margins of scars slightly less than 0.5 of valve width; anterior muscle scars on elongate elevations near center of valve, front of scars occurring about mid-length of valve; median ridge low, rounded, obscured posteriorly by later shell material, terminating anteriorly about 0.75 of valve length in front of beak.

Illustrations.—Figures 6-10; Plate 2, figures *8-18*; Table 2.——Figs. *6-10.* Scatter diagrams and reduced major axis growth lines for topotype specimens of *Eurytreta curvata.* [Symbols for variables as in Table 2. Variable plotted along abscissa cited first in pair. BV=brachial valve. PV=pedicle valve. All dimensions in millimeters.] ——Pl. 2, figs. *8-9.* Oblique int. and int. views of pedicle valve (in figure *8* specimen rotated to show apical process) (139506), both ×12.——Pl. 2, figs. *10-11.* Ext. and int. views of brachial valve (139508), both ×15.——Pl. 2, figs. *12-15.* Lat., oblique int., ext., and int. views of pedicle valve (139505), all ×15.——Pl. 2, figs. *16-18.* Ext., lat., and int. views of brachial valve (139507), all ×15. [All specimens are topotypes from USNM loc. 203a, Early Ordovician, Eureka, Nevada.]——Table 2.

Figured Specimens

		USNM	Length (mm.)
Topotype	pedicle valve	139505	1.30
Topotype	pedicle valve	139506	1.75
Topotype	brachial valve	139507	1.51
Topotype	brachial valve	139508	1.30

All specimens from USNM loc. 203a, (basal Ordovician, associated with *Symphysurina*—A. R. PALMER, personal communication). "Limestones at base of Pogonip limestone, in the spur on Hamburg Ridge extending out southwest from Wood Cone, Eureka district, Eureka County, Nevada" (WALCOTT, 1912, p. 683).

Discussion.—Some of the quantitative aspects of the growth of *Eurytreta curvata* are shown in Table 2 and Figs. 6-10.

WALCOTT (1902) compared the species with *Acrotreta idahoensis,* but as has been discussed previously, it is more probable that *A. idahoensis* should be referred to *Canthylotreta.*

HADROTRETA Rowell, n. gen.

Etymology.—Name derived from Greek, *hadros,* large, and Greek, *tretos,* perforated.
Type species.—*Acrotreta primaaea* WALCOTT, 1902.

Diagnosis.—Relatively large for family, with moderately low subconical pedicle valve, apical angle commonly about 90 degrees in lateral profile; pseudointerarea flat to gently concave, catacline to gently procline, divided medially by shallow intertrough; external pedicle foramen small, subelliptical, immediately posterior of apex. Brachial valve gently convex, anteriorly with broad, shallow median sulcus. Shell ornamented by fine growth lines.

Ventral interior with short, anteriorly directed pedicle tube opening into apical cavity, apical process forming anterior wall of cavity, process

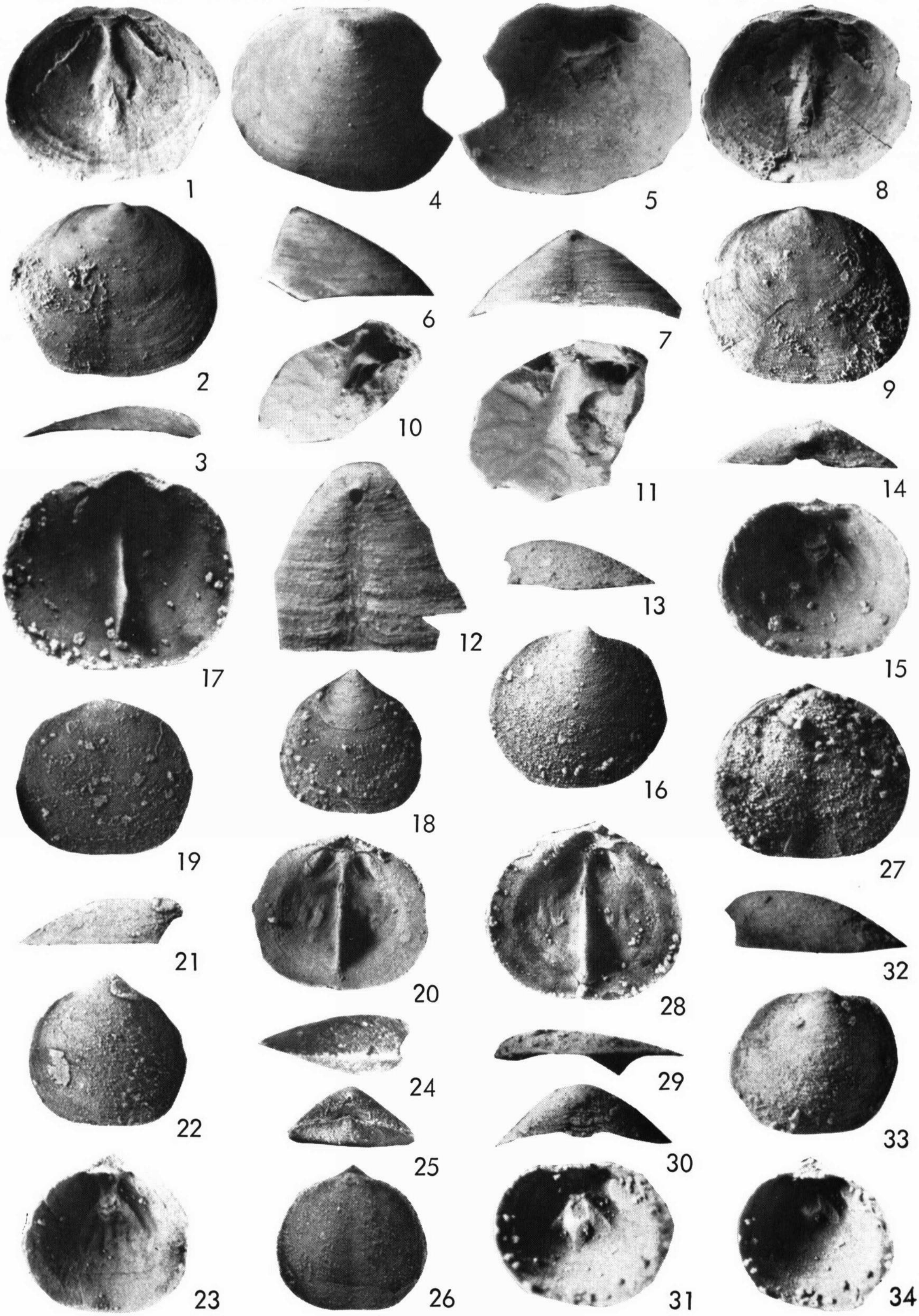
EXPLANATION OF PLATE 1

FIGURES

1-12. Hadrotreta primaaea (WALCOTT), Middle Cambrian, Pioche district, Nevada ....(p. 13)

FIGURES

13-34. Canthylotreta marjumensis (WALCOTT), Middle Cambrian, House Range, Utah ....(p. 5)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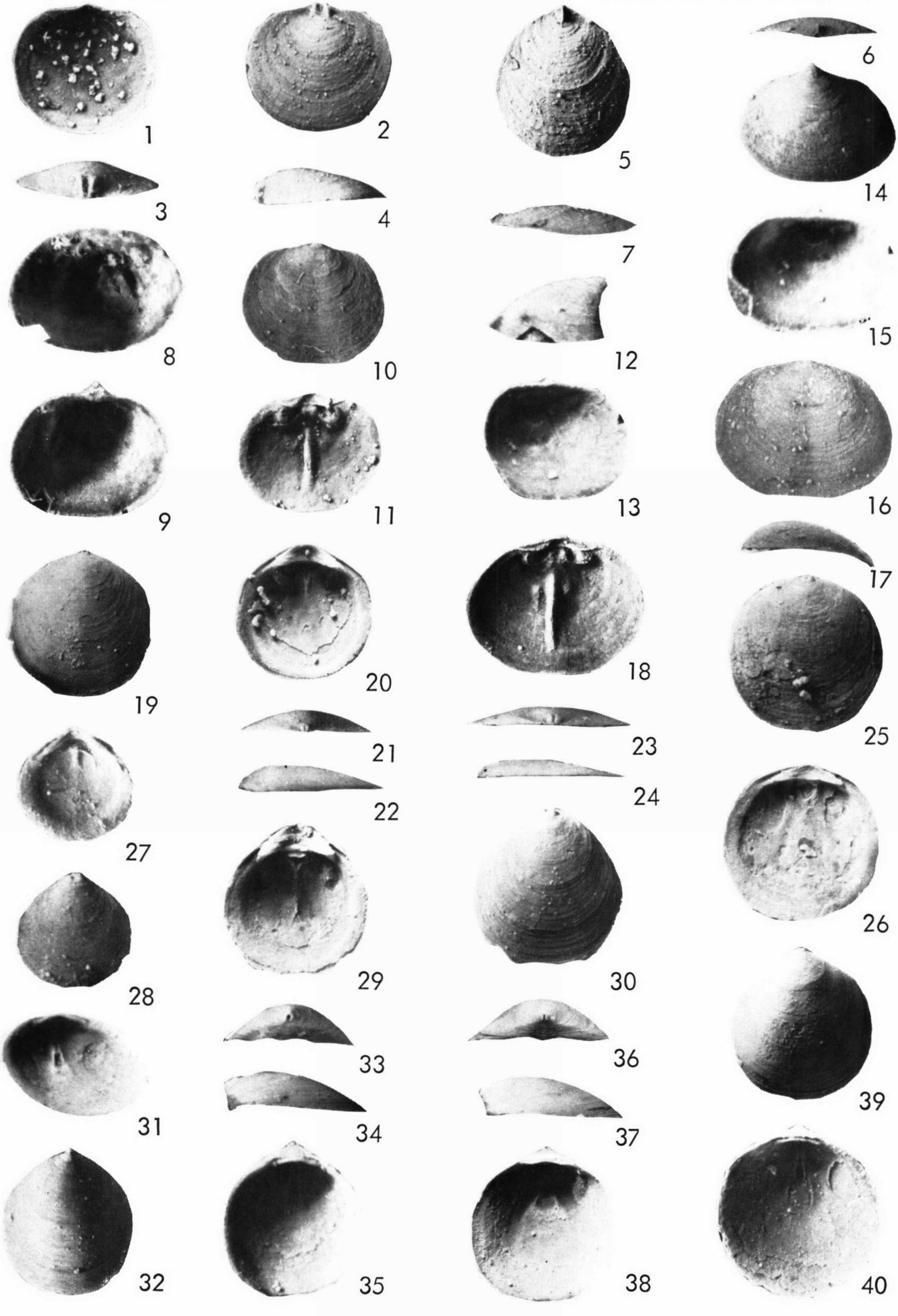
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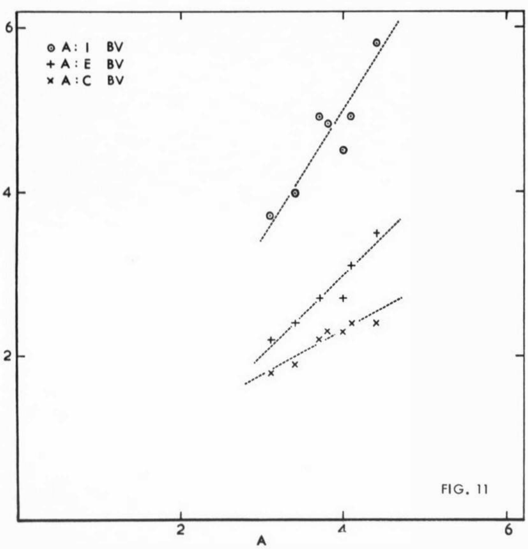


FIG. 11. *Hadrotreta primaaea* (WALCOTT). Biometric diagram (see text for description).

a broadly rounded boss of strongly lamellose shell, entirely anterior of apex of valve, limited laterally by *vascula lateralia;* apical pits on internal surface of pseudointerarea immediately lateral of pedicle tube.

Brachial valve with orthocline to gently anacline, narrowly triangular pseudointerarea, divided by slightly depressed median plate into 2 propareas, median plate buttressed posteriorly by low median ridge; cardinal muscle scars relatively long, laterally placed.

Age.—Middle Cambrian.

Discussion.—The genus occurs in low Middle Cambrian rocks and is one of the oldest acrotretids known from etched material. Late Early Cambrian and early Middle Cambrian inarticulate brachiopod faunas are still poorly known and acid treatment has not routinely been applied to suitable rocks of this age. It is probable that such treatment will reveal additional forms that may be referred to the genus. Currently it is definitely known only from its type species, but the external form of *"Acrotreta" definata* WALCOTT suggests that it may well be assigned to *Hadrotreta.*

Hadrotreta has an unusual combination of characters. Those of the brachial valve lie within the known variation field of the Acrotretinae, although the pseudointerarea is somewhat smaller than one would have anticipated to occur in such a large valve and the majority of the subfamily have a bladelike septum rather than a low ridge. A median ridge however, is known in other Acrotretinae for it characterizes a few species of the Upper Cambrian genus *Angulotreta* and is typical of *Linnarssonella.* The anomalous features of *Hadrotreta* are concentrated in the apical region of the ventral interior. The gross form of the bosslike apical process and its position entirely anterior of the pedicle opening recall that of the type genus of the Linnarssoniinae; but this resemblance may well be a measure of convergence, for the apical process in the new genus is composed of strongly lamellose shell material, a typical acrotretin feature which was first described by BELL (1941) and is now well known in the subfamily. In the rather featureless nature of the apical process, *Hadrotreta* recalls the Ordovician acrotretin *Conotreta* although the 2 genera differ widely in their gross form. The existence of a short, delicate pedicle tube opening into a deep apical cavity is seemingly unique and at present unknown in any other acrotretid.

HADROTRETA PRIMAAEA (Walcott)

Acrotreta gemma WALCOTT, 1886 *(partim)*, p. 98-99, pl. 8, fig. 1, 1a, 1b; WALCOTT, 1891 *(partim)*, p. 608, pl. 67, fig. 5c-5e; WALCOTT, 1899, *(partim)*, p. 449, pl. 62, fig. 2, 2b, 2d.
Acrotreta primaaea WALCOTT, 1902, p. 593.
Acrotreta gemma GRABAU & SHIMER, 1909, p. 199, fig. 243a-c.
Acrotreta primaeva WALCOTT, 1912, p. 700, p. 69, figs. 1, 1a-1f.

Transversely suboval in outline, pedicle valve subconical, between 0.3 and 0.5 as high as long, beak forming highest point of valve; pseudointerarea clearly defined by abrupt flexure of shell from remainder of valve, nearly straight or gently concave in lateral profile, catacline to 20

EXPLANATION OF PLATE 2

FIGURES

1- 7. *Tropidoglossa modesta* (WALCOTT), Upper Cambrian, House Range, Utah ....(p. 32)
8-18. *Eurytreta curvata* (WALCOTT), Lower Ordovician, Eureka district, Nevada ....(p. 11)
19-40. *Linnarssonella girtyi* WALCOTT, Upper Cambrian, near Deadwood, South Dakota ....(p. 17)

TABLE 3

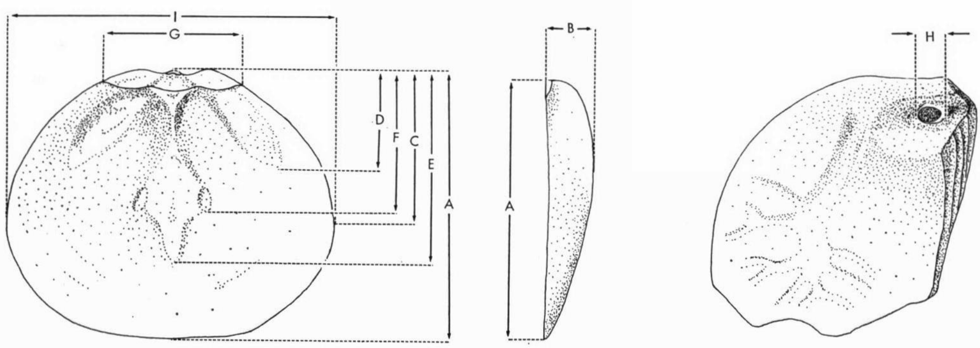
HADROTRETA PRIMAAEA

Statistics of sample of topotype specimens

Bivariate statistics for allometric growth given only when α differs significantly from 1 (P = 0.05)

Variable x	Variable y	$\bar{x}$	var(x)	$\bar{y}$	var(y)	r'	a	var(a)	$\overline{\log(x)}$	var(log x)	$\overline{\log(y)}$	var(log y)	r	α	var(α)	n	valve
A	I	3.78	0.191	4.66	0.469	0.909	1.5662	0.08494	.....	.....	.....	.....	.....	.....	.....	7	brachial
A	C	3.78	0.191	2.19	0.058	0.946	0.5509	0.00637	.....	.....	.....	.....	.....	.....	.....	7	brachial
A	E	3.78	0.230	2.77	0.222	0.956	0.9824	0.02113	.....	.....	.....	.....	.....	.....	.....	6	brachial

Variables	B/A	D/A	F/A	G/I	Variable	H
Mean of ratio	13.4%	33.4%	51.0%	47.4%	Mean	0.227
Var. of ratio	1.2	116.4	25.1	12.0	Var.	0.0006
Valve	brachial	brachial	brachial	brachial	Valve	pedicle
n	5	7	4	5	n	8



Diagrammatic representation of measurements.

A = maximum length of valve B = maximum height of valve C = length of valve to line of maximum width of valve D = length of valve to front of cardinal muscle scars E = length of valve to anterior end of ridge F = length of valve to front of anterior muscle scars G = maximum width of the pseudointerarea H = external diameter of pedicle tube I = maximum width of valve

degrees procline, divided medially by narrow intertrough which extends dorsally from pedicle foramen; foramen immediately posterior of apex, subelliptical, 0.1-0.2 mm. in length. Brachial valve about 0.2 wider than long, maximum width occurring slightly in front of mid-length of valve; convex, maximum height about 0.12 of valve length, gently rounded in lateral and posterior profile, curvature interrupted by broad shallow sulcus arising 1.0-2.0 mm. anterior of beak; beak small, somewhat inflated and projecting above the shell lateral to it, lacking nodes.

Ventral interior with bosslike apical process merging gently with floor of valve anteriorly, posteriorly terminating abruptly at apical cavity, variation in relative length of process not well known, seemingly extending to about 0.25 of valve length; pedicle opening continued internally as pedicle tube, opening into apical cavity, tube typically 0.2 mm. in diameter and 0.3-0.5 mm. in length; cardinal muscle scars subelliptical on posterolateral slopes of valve. Dorsal pseudointerarea short, width slightly less than 0.5 maximum width of valve, buttressed by median ridge extending about 0.75 of valve length anterior of beak; anterior muscle scars small, close to median ridge near center of valve; cardinal muscle scars subelliptical, diverging anterolaterally from in front of propareas, extending forward to about 0.3 of valve length.

Illustrations.—Figure 11; Plate 1, figures *1-12*; Table 3.——Fig. 11. Scatter diagrams and reduced major axis growth lines for topotype specimens of *Hadrotreta primaaea*. [Symbols for variables as in Table 3. Variable plotted along abscissa cited first in pair. BV=brachial valve. All dimensions in millimeters.]——Pl. 1, figs. *1-3*. Int., ext. and lat. views of brachial valve (139483), all ×7.——Pl. 1, figs. *4-7*. Ext., int., lat., and post. views of pedicle valve (139480), all ×10.——Pl. 1, figs. *8-9*. Int. and ext. views of brachial valve (139484), both ×7.——Pl. 1, fig. *10*. Int. view of fragment of pedicle valve, apex of valve to right of photograph, showing lamellose nature of apical process and pedicle tube opening into apical cavity (139482), ×10.——Pl. 1, fig. *11*. Int. view of fragment of pedicle valve, showing branching of mantle canal, same specimen as above (139482), ×15.——Pl. 1, fig. *12*. Fragment of pedicle valve, post. view showing detail of intertrough (139481), ×20. [All specimens are topotypes from USNM loc. 31a, early Middle Cambrian, Pioche, Nevada.]

Figured Specimens

Topotype	damaged pedicle valve	139480	......
Topotype	posterior sector of pedicle valve	139481	......
Topotype	fragment of pedicle valve	139482	......
Topotype	brachial valve	139483	4.0
Topotype	brachial valve	139484	4.0

All specimens from USNM loc. 31a, early Middle Cambrian (*Albertella* zone or older—A. R. Palmer, personal communication), "Limestone and interbedded siliceous shales of the Pioche formation, just above the quartzite on the east side of the anticline, near Pioche, Lincoln County, Nevada." (Walcott, 1912, p. 701).

Discussion.—Several specimens were recovered by etching the small block of topotypic material, but although they included a few perfect or near perfect brachial valves, all the pedicle valves were fragmentary; a situation reflected in the sparsity of biometrics concerned with this valve.

Walcott's (1902) description of the external form of the species is good, although it has not proved possible to recognize the "irregular concentric striation" that he claimed was superimposed on the regular ornament. This statement appears to be in error, for the irregular ornament is seemingly absent both on the material studied by Walcott and the etched specimens, where its absence could conceivably have been explained by the action of the formic acid on the shell.

The etched specimens have added materially to our knowledge of the internal structure of the species. The apical process was recognized by Walcott, but delicate structures like the pedicle tube were not unnaturally overlooked or not preserved.

The median ridge of the brachial valve is variably developed along its length. The posterior third of the structure is typically narrow and rounded, separating the proximal ends of the anterolaterally diverging *vascula lateralia*; at its extreme posterior end it expands rapidly to form a subtriangular buttress to the median plate of the pseudointerarea. In the center of the valve the ridge may be widened by later shell layers and form a relatively broad, low elevation on the floor of the valve on whose flanks the anterior muscle scars are inserted. In front of these scars the ridge gradually narrows and anteriorly merges with the remainder of the inner surface.

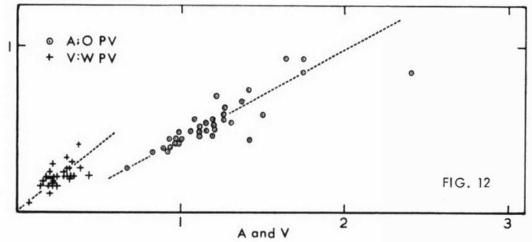
The *vascula lateralia* of both valves are baculate, each valve typically bearing the impressions of a pair of primary mantle canals which lack major dichotomy or bifurcation. One fragmentary pedicle valve of *Hadrotreta primaaea* does fortunately preserve the impressions of the ramifications of the mantle canal system (Pl. 1, fig. 11). The primary canals arise laterally of the apical cavity and are curved, initially diverging anterolaterally but anteriorly converging towards the mid-line of the valve. Anterior of the front of the apical process several fine canal impressions branch off the primary trunk. These branches occur both on sides of the primary canal, subnormally disposed to it, and may themselves branch yet again. The resulting pattern is not unlike that known for the Paleozoic obolids and it is possible that it may be typical of many acrotretids, although rarely impressed.

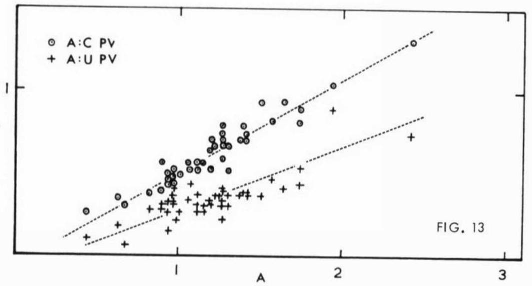
Genus LINNARSSONELLA Walcott, 1902

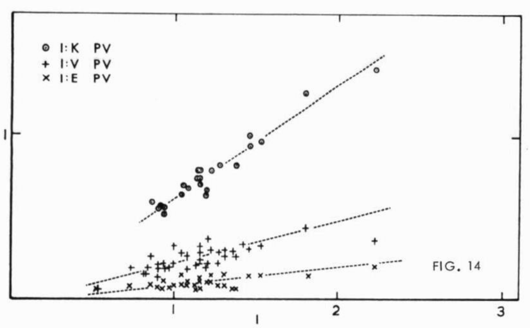
Type species.—*Linnarssonella girtyi* Walcott, 1902 (by original designation).

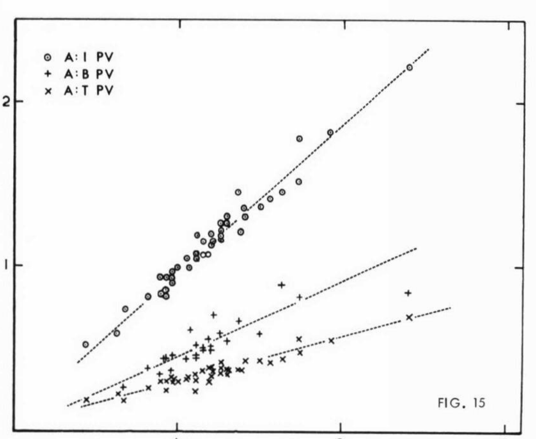
Age.—Late Cambrian.

Discussion.—When the genus was erected (Walcott, 1902, p. 601) four species were attributed to it, *Linnarssonella girtyi, Lingulepis? minuta* Hall & Whitfied, *Linnarssonella tennesseensis* Walcott and *Linnarssonella broadheadi* Walcott. The latter species is a *nomen nudum* and Walcott (1912, p. 666) later indicated that the inclusion of the name was an oversight. The selection of *L. girtyi* as type species was fortunate for the type material of this species is better preserved and reveals more detail of the internal morphology than that of the other two initially included species. Because of this situation, the original generic account was based largely on the morphology of the type species. Indeed, the generic description was only slightly modified in 1912 (Walcott, 1912, p. 665) after Walcott had added four new species to the genus, *Linnarssonella transversa, L. modesta, L. nitens* and *L. urania* (Walcott, 1908, p. 90). Walcott considered the characteristic features of *Linnarssonella*









FIGS. 12-15. *Linnarssonella girtyi* WALCOTT. Biometric diagrams (see text for descriptions).

to include its ventribiconvex profile with incurved beak and apical pedicle foramen overhanging ". . . a slight trace of a pseudodeltidium . . .", the posterolateral location of a pair of well-developed cardinal muscle scars in both valves, together with a pair of much smaller, centrally located scars in the brachial valve; the strong "vascular canals," those of the pedicle valve enclosing "the cast of the pedicle opening" posteriorly. He also observed that the brachial pseudointerarea was well developed and that a narrow median ridge extended to the anterior third of the brachial valve in some shells. BELL (1941, p. 235) added considerably to our knowledge of the genus in the description of his species *L. elongata* from the Upper Cambrian Dry Creek Shale of Montana. Delicate mechanical preparations of specimens of this species revealed the existence of articulatory structures in the posterior regions of both valves. Comparable structures also occur in *L. girtyi* and were illustrated by material referred to this species from the *Elvinia* zone of Texas by BELL & ELLINWOOD (1962, pl. 61, figs. 4, 5, 6). These articulatory structures are probably the most important diagnostic characters of *Linnarssonella* and at present afford a convenient means of differentiating it from species of *Apsotreta.*

When WALCOTT published his monograph in 1912, knowledge of the detailed morphology of many species referred to *Linnarssonella* was meager, and unfortunately there has been little improvement in our understanding of some of these species. It is still not definitely known whether *L. nitens, L. tennesseensis* and *L. minuta* are correctly assigned to the genus. The taxonomic position of the last species is particularly doubtful and probably it is a lingulacean, but until suitable topotype material is available for acid-etching the question cannot be settled. The three remaining species included in the genus by WALCOTT are now known from such etched topotype material and are described subsequently. It is noteworthy that none of these three species is congeneric with *L. girtyi* and indeed only one of them can be referred to the same superfamily.

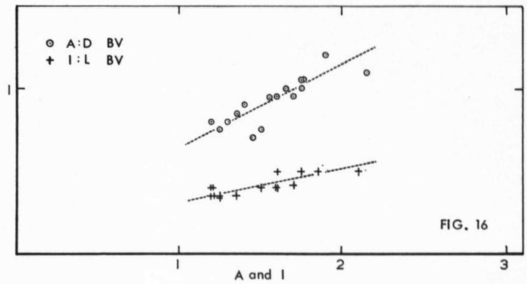
Recently BELL (in BELL & ELLINWOOD, 1962, p. 410) has proposed that his species *Linnarssonella elongata* be regarded as a synonym of *L. girtyi,* for he now considers the former to be merely an elongate morphotype, and has been unable to detect any patterns of geographic or stratigraphic variation in the species complex over a wide area of the United States. He is undoubtedly correct in regarding elongate varieties as common elements of the variation field of many samples of *L. girtyi (s.l.)*, but is perhaps premature in denying areal or chronologic variation patterns. There have been no statistically controlled studies of geographical variation of this species and in so far as invertebrate paleontology is concerned, this subject is still in its infancy. The following description and particularly the statistics, give some idea of the variation of several characters of *L. girtyi* at its type locality. Until we have comparable information from other areas and horizons we are not in a position to assess the significance of the variations that do occur.

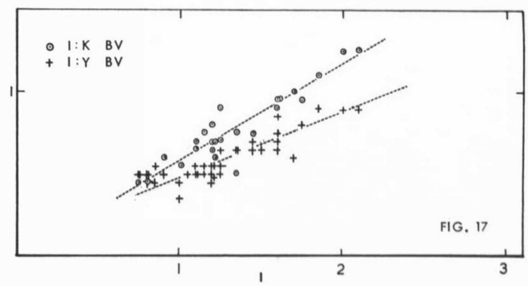
LINNARSSONELLA GIRTYI Walcott

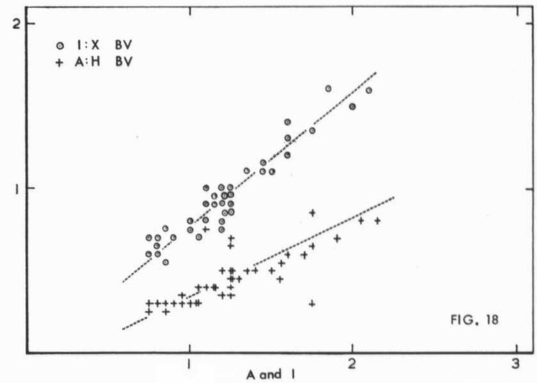
Linnarssonella girtyi WALCOTT, 1902, p. 602; WALCOTT, 1912, p. 666, pl. 79, fig. 1, 1a-1p; BELL & ELLINWOOD, 1962, p. 410, pl. 61, figs. 4-9.

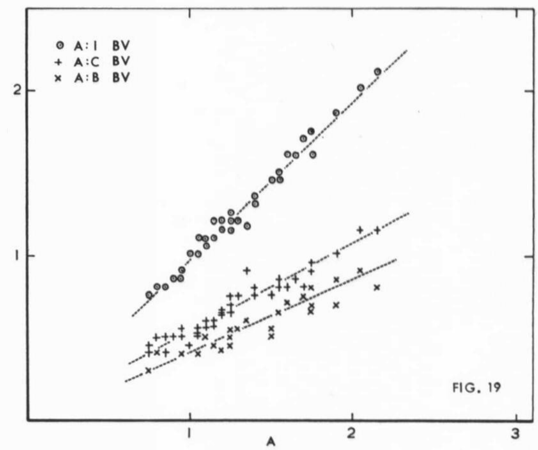
Ventribiconvex shells, subrounded to elongate subtriangular in outline; pedicle valve apsacline, in lateral profile curvature anterior of beak gentle and relatively uniform, maximum height of valve about one third of length, occurring about 0.3 of valve length in front of beak; pedicle foramen minute, circular, opening immediately below small slightly incurved beak; posterior sector of valve forming broadly triangular pseudointerarea, marked off from adjacent shell by change in slope, gently concave in lateral profile, divided into 2 propareas by triangular deltoid pseudointerarea which is flat or externally gently convex and slightly wider than high; valve ornamented by fine, irregularly occurring and frequently impersistent growth lines, becoming well developed and crowded on propareas, and dorsally flexed on deltoid pseudointerarea. Brachial valve typically more rounded than pedicle valve and much lower, in lateral profile gently convex to flat anteriorly, more strongly rounded posteriorly, gently convex in posterior profile; beak small, bearing 2 elongate nodes separated by low groove; ornament as pedicle valve.

Apex of pedicle valve thickened internally, thickening continued anteriorly by low apical process, posteriorly lateral margins of process parallel or very slightly divergent, rarely this section of process consisting of low tube, more commonly dorsal surface of tube absent and process





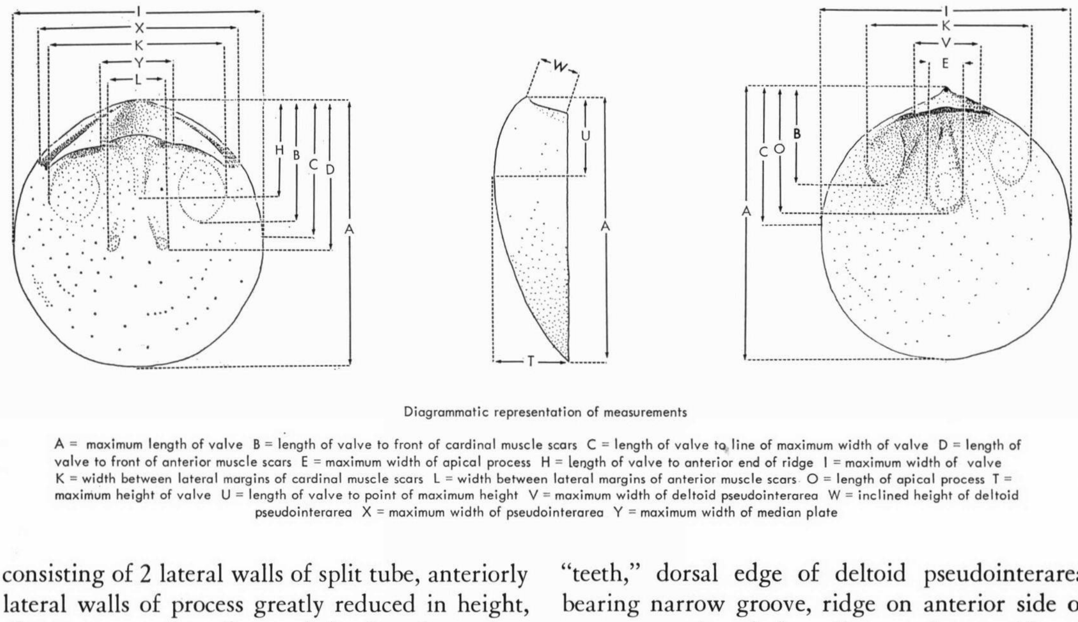




FIGS. 16-19. *Linnarssonella girtyi* WALCOTT. Biometric diagrams (see text for descriptions).

TABLE 4
LINNARSSONELLA GIRTYI
Statistics of sample of topotype specimens
Bivariate statistics for allometric growth given only when α differs significantly from 1 (P = 0.05)

Variable x	Variable y	$\bar{x}$	var(x)	$\bar{y}$	var(y)	r'	a	var(a)	$\overline{\log(x)}$	var(log x)	$\overline{\log(y)}$	var(log y)	r	α	var(α)	n	valve
A	C	1.18	0.112	0.61	0.037	0.955	0.5744	0.00060								50	pedicle
A	I	1.18	0.112	1.13	0.091	0.983	0.8998	0.00057	0.126	0.0808	0.085	0.0685	0.981	0.9209	0.00065	50	pedicle
A	T	1.18	0.112	0.35	0.008	0.940	0.2741	0.00018	0.126	0.0808	-1.074	0.0642	0.915	0.8916	0.00270	50	pedicle
A	U	1.18	0.112	0.34	0.017	0.824	0.3888	0.00101	0.126	0.0808	-1.146	0.1537	0.803	1.3796	0.01406	50	pedicle
A	B	1.21	0.118	0.54	0.024	0.883	0.4485	0.00165								29	pedicle
A	O	1.17	0.100	0.54	0.030	0.940	0.5436	0.00080	0.124	0.0718	-0.670	0.1058	0.931	1.2136	0.00454	45	pedicle
I	K	1.20	0.096	0.76	0.046	0.970	0.6967	0.00124								25	pedicle
I	E	1.12	0.089	0.10	0.001	0.762	0.1199	0.00017	0.082	0.0637	-2.364	0.1165	0.690	1.3520	0.02732	37	pedicle
I	V	1.13	0.086	0.25	0.005	0.770	0.2489	0.00062	0.092	0.0629	-1.448	0.1062	0.800	1.2996	0.01483	43	pedicle
V	W	0.25	0.005	0.21	0.003	0.695	0.8084	0.00824								43	pedicle
A	I	1.29	0.117	1.25	0.110	0.991	0.9664	0.00042								43	brachial
I	L	1.50	0.075	0.41	0.003	0.818	0.2135	0.00108								16	brachial
A	C	1.29	0.117	0.69	0.034	0.961	0.5390	0.00055								43	brachial
A	B	1.36	0.127	0.56	0.025	0.944	0.4450	0.00080								29	brachial
I	K	1.33	0.126	0.78	0.046	0.971	0.6038	0.00084								27	brachial
A	H	1.28	0.122	0.47	0.028	0.761	0.4765	0.00251	0.211	0.0722	-0.820	0.1198	0.779	1.2879	0.01715	40	brachial
A	D	1.53	0.079	0.91	0.021	0.936	0.5088	0.00213								17	brachial
I	X	1.23	0.111	0.95	0.074	0.953	0.8131	0.00165								39	brachial
I	Y	1.25	0.110	0.58	0.018	0.867	0.4020	0.00098	0.189	0.0687	-0.564	0.0454	0.809	0.8130	0.00557	43	brachial



Diagrammatic representation of measurements

A = maximum length of valve B = length of valve to front of cardinal muscle scars C = length of valve to line of maximum width of valve D = length of valve to front of anterior muscle scars E = maximum width of apical process H = length of valve to anterior end of ridge I = maximum width of valve K = width between lateral margins of cardinal muscle scars L = width between lateral margins of anterior muscle scars O = length of apical process T = maximum height of valve U = length of valve to point of maximum height V = maximum width of deltoid pseudointerarea W = inclined height of deltoid pseudointerarea X = maximum width of pseudointerarea Y = maximum width of median plate

consisting of 2 lateral walls of split tube, anteriorly lateral walls of process greatly reduced in height, diverge to enclose low subcircular depression, front of depression near mid-length of valve; cardinal muscle scars oval, on posterolateral flanks of valve, extending forward slightly less than half length of valve, width of muscle field about 0.7 that of valve; apical pits small, close to lateral margins of apical process, about 0.2 of valve length in front of beak; *vascula lateralia* bacculate, diverging anterolaterally, passing between apical process and cardinal muscle scars; dorsal surface of propareas projecting farther dorsally than deltoid pseudointerarea forming pair of elongate "teeth," dorsal edge of deltoid pseudointerarea bearing narrow groove, ridge on anterior side of groove continued laterally on inner side of propareas, ventral of their free edge.

Posterior region of brachial valve thickened, bearing typically orthocline pseudointerarea, width of pseudointerarea about 0.75 maximum width of valve, divided into 2 propareas by depressed, subtriangular median plate, maximum width of plate about 0.6 that of pseudointerarea; propareas narrowly triangular, bounded posterolaterally by deep triangular sockets diverging from beak, outer wall of sockets formed by raised margin of valve; low median ridge commonly extending forward about 0.3 of valve length from thickened region beneath median plate, typically bifurcating at anterior end; cardinal muscle scars posterolaterally located, suboval, extending forward to about 0.4 of valve length in front of beak, width of muscles similar to those of pedicle valve; anterior muscle scars poorly impressed, elongate suboval, front of scars about 0.6 of valve length in front of beak, lying immediately lateral of *vascula media* which are short, diverging anterolaterally from anterior end of median ridge; *vascula lateralia* bacculate, diverging from in front of the beak to pass medianly of cardinal muscle scars.

Illustrations.—Figures 12-19; Plate 2, figures *19-40*; Table 4.——Figs. 12-19. Scatter diagrams and reduced major axis growth lines for topotype specimens of *Linnarssonella girtyi.* [Symbols for variables as in Table 4. Variable plotted along abscissca cited first in pair. PV=pedicle valve. BV=brachial valve. All dimensions in millimeters.]——Pl. 2, figs. *19-22.* Ext., int., post. and lat. views of brachial valve (139509), all ×12. ——Pl. 2, figs. *23-26.* Post., lat., ext., and int. views of brachial valve (139510), all ×15.——Pl. 2, figs. *27-28.* Int. and ext. views of juvenile brachial valve (139512), both ×25.——Pl. 2, figs. *29-30.* Int. and ext. views of brachial valve (139511), both ×15.——Pl. 2, figs. *31-35.* Oblique int., ext., post., lat., and int. views of pedicle valve (in fig. *31* specimen rotated to show detail of posterodorsal margin of valve) (139515), all ×20. ——Pl. 2, figs. *36-39.* Post., lat., int. and ext. views of pedicle valve (139513), all ×10.——Pl. 2, fig. *40.* Int. view of pedicle valve (139514), ×15. [All specimens are topotypes from WALCOTT's loc. 88a, medial Late Cambrian, Deadwood, South Dakota.]

Figured Specimens

		USNM	Length (mm.)
Topotype	brachial valve	139509	1.90
Topotype	brachial valve	139510	1.70
Topotype	brachial valve	139511	1.65
Topotype	brachial valve	139512	0.75
Topotype	pedicle valve	139513	2.45
Topotype	pedicle valve	139514	1.85
Topotype	pedicle valve	139515	1.20

All specimens from USNM loc. 88a, *Elvinia* Zone Upper Cambrian, "Limestone about 100 feet (30.5 m.) above the quartzitic sandstone at the base of the Cambrian, in the northern suburbs of Deadwood," "in the Black Hills, South Dakota" (WALCOTT, 1912, p. 667).

Discussion.—The problem of articulation has been discussed previously (p. 2), but the morphology of the apical process is of some interest. In comparison with that of the majority of the subfamily, this structure is always rather weak in *Linnarssonella girtyi.* Even when most strongly developed it consists only of a low tube adnate to the anterior slope of the valve. The lumen of the tube is seemingly continuous with the external pedicle foramen and presumably it functioned as a pedicle tube, the pedicle emerging into the valve at the anterior end of the tube, its muscles possibly being attached in the depressed region at the extreme anterior end of the apical process. In many specimens, the dorsal cover of the process is absent and it consists only of a split tube. This condition could conceivably be an artifact caused by the acid during preparation of the material, but the regularity of the edges of the tube make it seem more probable that either the dorsal surface was not secreted or alternatively that it was secreted and subsequently resorbed during the lifetime of the animal. In either event, the apical process in this condition is reminiscent of that of some currently undescribed species of *Apsotreta* from the *Dunderbergia* zone of Nevada, a genus which has previously been considered as closely related and probably ancestral to *Linnarssonella* (PALMER, 1955, p. 770; BELL (in BELL & ELLINWOOD) 1962, p. 410).

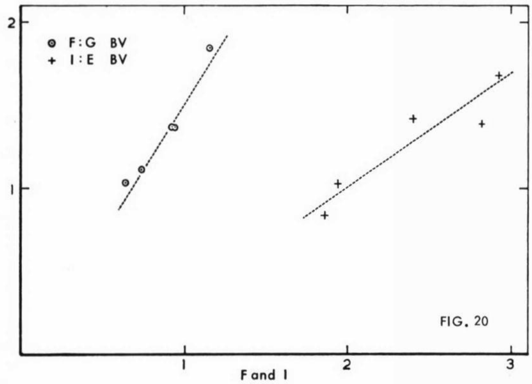
Genus PHYSOTRETA Rowell, n. gen.

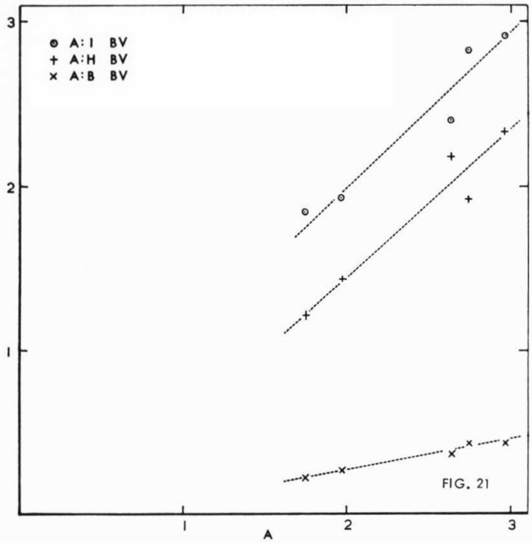
Etymology.—From Greek, *physa,* bubble, and Greek, *tretos,* perforated.

Type species.—*Acrotreta spinosa* WALCOTT, 1905.

Diagnosis.—Pedicle valve strongly convex to low subconical, apex commonly obtuse in lateral profile; pseudointerarea not strongly marked off from lateral slopes of valve, moderately procline in early stages of growth, becoming catacline or more rarely strongly apsacline when adult, divided medianly by flat to gently concave deltoid pseudointerarea; external pedicle foramen small, circular immediately posterior of apex. Brachial valve gently convex, beak moderately incurved, lacking nodes.

Pedicle valve interior with conspicuous apical process of lamellose shell material, plugging apical region of valve and extending from anterior to





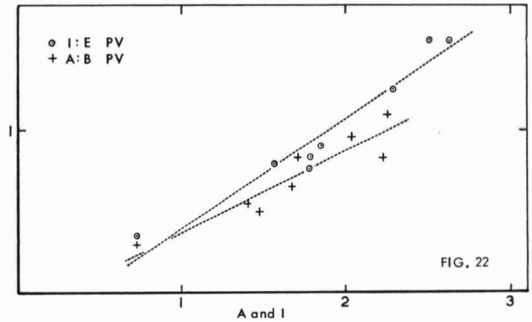
FIGS. 20-21. *Physotreta spinosa* (WALCOTT). Biometric diagrams (see text for descriptions).

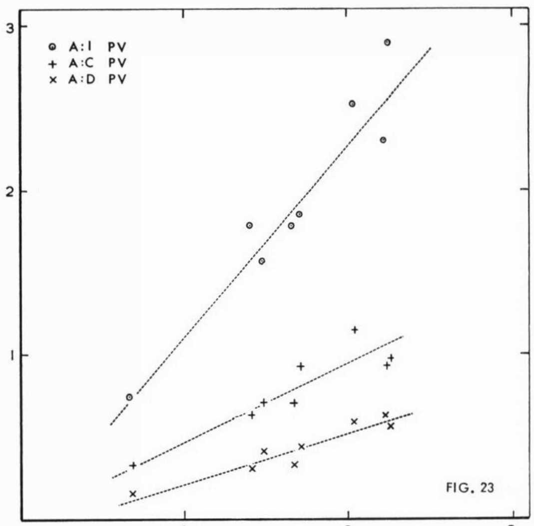
posterior slope; posteriorly, lateral margins of apical process subparallel, but converging anteriorly; pedicle traverses extreme posterior part of apical process, producing circular internal pedicle opening; apical pits small, lateral of pedicle opening and embedded either in apical process or thickened apical region of valve immediately lateral to it.

Brachial valve with well-developed pseudointerarea divided by concave, subtriangular median plate separating two propareas, which are narrowly triangular, curved, anacline laterally, becoming apsacline medially; well-developed subtriangular median septum.

Age.—Late Cambrian.

Discussion.—The internal morphology of the genus, particularly the form of the apical process and the structure of the brachial valve, is typical of the Acrotretinae, although none of the described genera of the subfamily are likely to be confused with it. In gross form, closest comparison can be made with *Apsotreta,* both genera are relatively low for the subfamily and have convex, rather than conical pedicle valves. The posterior sector of this valve, however, is considerably shorter in *Apsotreta* and in adults the beak invariably projects strongly behind the posterior margin, in marked contrast to *Physotreta,* which is only rarely apsacline. These features are associated with consistent differences in the interior of the valves; the apical process is more prominent in *Physotreta* and extends some dis-





FIGS. 22-23. *Physotreta spinosa* (WALCOTT). Biometric diagrams (see text for descriptions).

TABLE 5

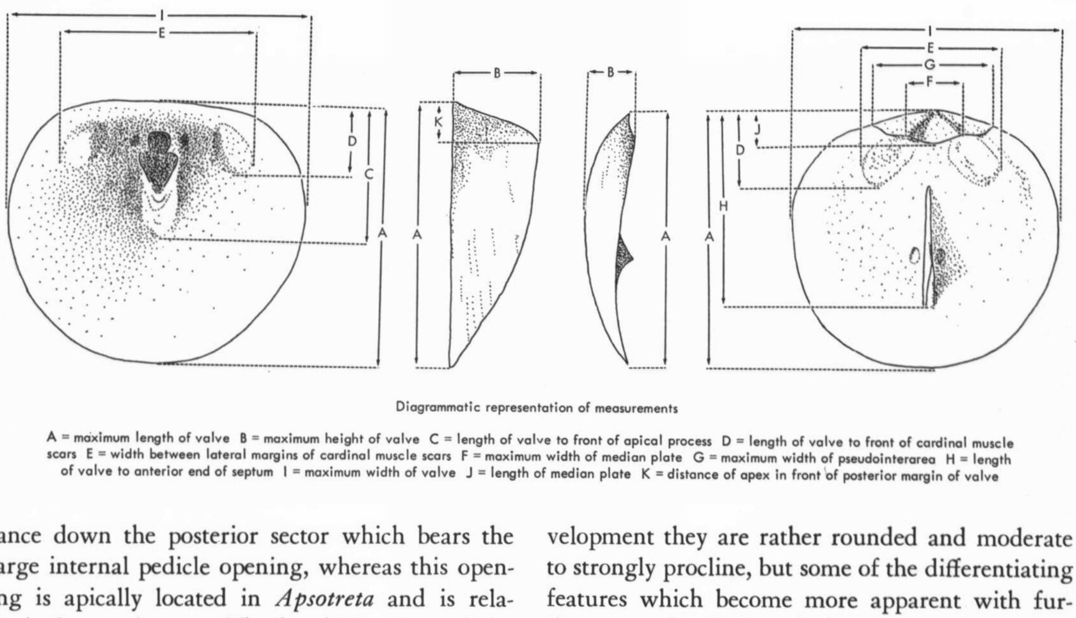
PHYSOTRETA SPINOSA

Statistics of sample of topotype specimens

Bivariate statistics for allometric growth given only when α differs significantly from 1 (P = 0.05)

Variable x	Variable y	$\overline{x}$	var(x)	$\overline{y}$	var(y)	r'	a	var(a)	$\overline{\log(x)}$	var(log x)	$\overline{\log(y)}$	var(log y)	r	α	var(α)	n	valve
A	I	1.68	0.271	1.89	0.366	0.968	1.1578	0.01411	....							8	pedicle
A	B	1.68	0.271	0.73	0.071	0.930	0.5114	0.00588	....							8	pedicle
A	C	1.68	0.271	0.79	0.063	0.903	0.4838	0.00716	....							8	pedicle
A	D	1.68	0.271	0.43	0.027	0.946	0.3157	0.00174	....							8	pedicle
I	E	1.89	0.366	1.01	0.170	0.970	0.6811	0.00463	0.590	0.0973	-0.063	0.1531	0.973	1.2546	0.01387	8	pedicle
A	I	2.41	0.278	2.38	0.243	0.970	0.9357	0.01730	....							5	brachial
A	B	2.41	0.278	0.35	0.011	0.982	0.1962	0.00046	....							5	brachial
A	H	2.41	0.278	1.82	0.227	0.964	0.9032	0.01943	....							5	brachial
I	E	2.38	0.243	1.29	0.116	0.933	0.6912	0.02059	....							5	brachial
F	G	0.87	0.039	1.33	0.101	0.964	1.6032	0.03750	....							5	brachial

Variables	K/A	G/I	J/A	D/A
Mean of ratio	12.0%	55.9%	14.8%	33.6%
Var. of ratio	13.8	32.7	5.1	32.9
Valve	pedicle	brachial	brachial	brachial
n	7	5	5	5



Diagrammatic representation of measurements

A = maximum length of valve B = maximum height of valve C = length of valve to front of apical process D = length of valve to front of cardinal muscle scars E = width between lateral margins of cardinal muscle scars F = maximum width of median plate G = maximum width of pseudointerarea H = length of valve to anterior end of septum I = maximum width of valve J = length of median plate K = distance of apex in front of posterior margin of valve

tance down the posterior sector which bears the large internal pedicle opening, whereas this opening is apically located in *Apsotreta* and is relatively inconspicuous. The brachial valves of the two genera are closely comparable, the most notable differences being in the propareas and form of the protogulum. The propareas of *Apsotreta* are consistently anacline, but in *Physotreta,* although anacline laterally, they are curved and medially are apsacline. This twisting of the propareas is possibly associated with the incurvature of the dorsal beak. The dorsal protegulum of the new genus is essentially smooth, but that of *Apsotreta,* like many Acrotretinae, bears a low groove separating two small elongate nodes.

Pedicle valves of young specimens of *Physotreta* may show a superficial resemblance to those of immature *Ceratreta.* At this stage of development they are rather rounded and moderate to strongly procline, but some of the differentiating features which become more apparent with further growth of the shell are already present, notably the elongate, slitlike, external pedicle foramen of *Ceratreta.*

Amongst described acrotretaceans, only the type species can be referred definitely to the genus. This species was initially described from Upper Cambrian rocks of the Eureka District of Nevada. Preliminary study of a large suite of specimens from the Upper Cambrian of the Great Basin indicates that the type species, or a form very similar to it, occurs over a wide area both to the north and south of Eureka in the upper *Dunderbergia* Zone. A second, currently undescribed species of *Physotreta* also occurs in this region somewhat lower in the same zone.

PHYSOTRETA SPINOSA (Walcott)

Acrotreta spinosa WALCOTT, 1905, p. 302; WALCOTT, 1912, p. 713, pl. 79, figs. 4,4',4", 4a-4g.

Shell ornamented by discontinuous, rather irregular growth lamellae, density in both valves varying between 9 and 14 in 0.5 mm. intervals at distance of 1 mm. in front of beak; lamellae in a few specimens crossed by narrow, discontinuous ribs, producing elongate nodes at their intersection.

Pedicle valve subcircular in outline, about 0.1 wider than long, strongly convex and typically procline-catacline, height of valve slightly less than 0.5 of its length; apex may slightly overhang pseudointerarea, but commonly inconspicuous; pseudointerarea straight or gently concave in lateral profile, valve slightly flattened immediately in front of beak, becoming more strongly rounded anteriorly; deltoid pseudointerarea about 0.7 as wide as high, poorly defined near beak but more strongly marked off posterodorsally. Brachial valve subcircular in outline, maximum width occurring at about mid-length of valve and approximately equal to length; posterolateral margins of valve commonly less strongly rounded than anterior and lateral margins, outline obtusely pointed posteriorly; gently convex in lateral profile, maximum height of valve about 0.14 of its length, in posterior profile valve slightly flattened medianly, but without development of sulcus.

Internally, apical process extending to mid-length of valve, apical pits lying lateral of internal pedicle opening, approximately colinear with its center; ventral cardinal muscle scars large, suboval, on posterolateral surfaces of valve, extending forward about 0.25 of valve length, distance between their outer margins about 0.5 of valve width. Dorsal pseudointerarea relatively large, width typically slightly more than 0.5 that of the valve, propareas separated by abrupt flexure from median plate; free margin of median plate convex anteriorly, extending forward about 0.15 of valve length; median septum slender, subtriangular blade, free margin posterior of apex of septum longer than anterior margin, both concave ventrally in lateral profile; septum arising short distance in front of pseudointerarea but typically buried by later shell material forming broad ridge buttressing median plate, septum terminating some 0.75 of valve length in front of beak; cardinal muscle scars conspicuous, subelliptical, arising immediately in front of median plate and diverging anterolaterally, extending forward about 0.3 of valve length, distance between lateral extremities of scars rather more than 0.5 of valve width; anterior muscle scars small, close to median septum slightly in front of center of valve.

Illustrations.—Figures 20-23; Plate 3, figures *15-35;* Table 5.——Figs. 20-23. Scatter diagrams and reduced major axis growth lines for topotype specimens of *Physotreta spinosa.* [Symbols for variables as in Table 5. Variable plotted along abscissa cited first in pair. BV=brachial valve. PV=pedicle valve. All dimensions in millimeters.]——Pl. 3, figs. *15-18.* Lat., post., ext., and int. views of pedicle valve (139526), all ×15.——Pl. 3, figs. *19-20.* Ext. and lat. views of pedicle valve (139528), both ×15.——Pl. 3, figs. *21-24.* Post., ext., lat., and int. views of juvenile pedicle valve (139525), all ×20.——Pl. 3, fig. *25.* Post. view of pedicle valve (139529), ×15.——Pl. 3, fig. *26.* Post. view of pedicle valve (139530), ×10.——Pl. 3, fig. *27.* Detail of int. pedicle opening, apical pits and apical process of pedicle valve (139527), ×20.——Pl. 3, fig. *28.* Detail of pseudointerarea of brachial valve (139534), ×20.——Pl. 3, figs. *29-31.* Lateral, oblique int. and int. views of brachial valve (in fig. *30* specimen rotated to show shape of median septum) (139533), all ×10.——Pl. 3, figs. *32-33.* Int. and ext. views of brachial valve (139531), both ×15.——Pl. 3, figs. *34-35.* Ext. and int. views of brachial valve (139532), both ×10. [All specimens are topotypes from USNM loc. 61, early Late Cambrian, Eureka District, Nevada.]

Figured Specimens

		USNM	Length (mm.)
Topotype	pedicle valve	139525	0.66
Topotype	pedicle valve	139526	1.74
Topotype	incomplete pedicle valve	139527	......
Topotype	pedicle valve	139528	1.67
Topotype	incomplete pedicle valve	139529	......
Topotype	incomplete pedicle valve	139530	......
Topotype	brachial valve	139531	1.92
Topotype	brachial valve	139532	2.63
Topotype	brachial valve	139533	2.74
Topotype	incomplete brachial valve	139534	......

All specimens from USNM loc. 61, *Dunderbergia* Zone Upper Cambrian, "a little south of Hamburg Mine," "Eureka District, Eureka County, Nevada" (WALCOTT, 1912, p. 713).

Discussion.—The block of topotype material etched produced a considerable number of fragmentary specimens, but relatively few complete valves. The statistics calculated for the species are listed in Table 5 and supplement the diagnosis, but inevitably, because of the relatively small sample size, their value is somewhat restricted.

WALCOTT (1905, p. 302) considered the main character of the species to be "the spinous outer surface." When viewed at low magnifications, some specimens give the impression of being spinose, but at higher powers the "spines" are seen to consist of radially elongate, nodelike thickenings of the growth lamellae, that are associated with very fine discontinuous ribs. True spines are seemingly absent for the nodes are solid and do not appear to be damaged distally. They are not common features of the shells for they occur in only two of the 16 pedicle valves and none of the eight brachial valves examined.

The apical region of the pedicle valve is thickened internally by strongly lamellose shell, material, the median part forming the conspicuous apical process. The posterolateral margins of the apical process are subparallel, elevated above the shell lateral to them and bounded externally by bacculate *vascula lateralia.* Anteriorly, the sides of the process converge and descend to merge with the anterior slope of the valve, the front part of the apical process being subtriangular. In some older specimens with valves strongly thickened posteriorly by later shell material, the anterolateral margins of the apical process may be "buried" and the process may appear to expand anteriorly. The internal pedicle opening lies at the extreme posterior end of the apical process and faces dorsally. Its diameter increases with size of the valve, but invariably is several times that of the external foramen, the passage for the pedicle through the apical region of the shell forming a conical cavity. The central part of the apical process is hollow in all the specimens examined, the space being subtriangular in outline and the shell lamellae projecting into it. In well-preserved valves, this cavity is separated posteriorly from that formed by the dorsally directed migration of the internal pedicle opening by a sheet of shell material (Pl. 3, fig. 27). In many specimens, this delicate piece of shell is destroyed and the two cavities are continuous (Pl. 3, fig. 18). It is not known whether the anterior cavity in the apical process is an artifact produced during the etching by the liberated gas disrupting the thin shell lamellae, or whether it was a cavity whilst the animal was alive. The former seems more probable, for the shell lamellae appear to be broken and one specimen reveals that in life at least the posterior part of this cavity was roofed over by a thin layer of shell.

The apical pits are usually clearly visible, sunk into the thickened shell material lateral of the apical process, only in the youngest specimens is there difficulty in recognizing them. They are invariably close together, symmetrically disposed about the internal pedicle opening and lateral of its center. In young specimens they lie slightly behind the apex of the valve on its posterior slope, but with growth of the shell and subsequent enlargement of the internal pedicle opening they migrate anteriorly. Although in large valves they lie on the posterodorsally inclined slope of the thickened apical region their position may be misleading, because curvature of this surface is not parallel with that of the exterior of the valve, and the apical pits in these specimens are anterior of the apex.

Subfamily LINNARSSONIINAE Rowell, 1965

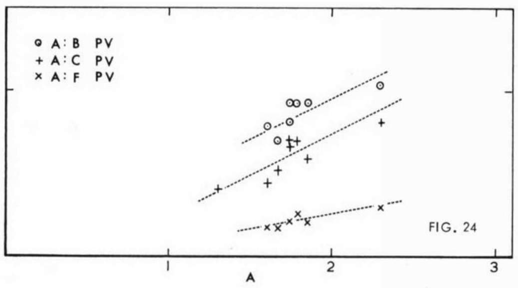
Genus LINNARSSONIA Walcott, 1885

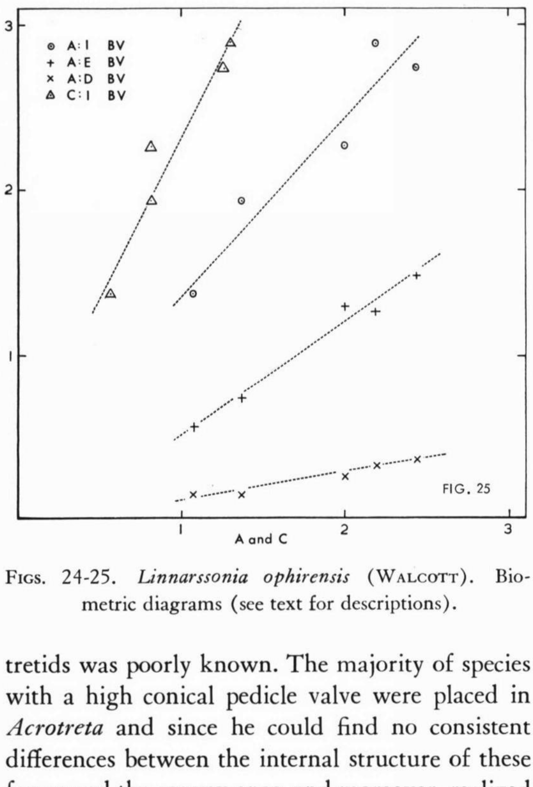
[=*Pegmatreta* BELL, 1941]

Type species.—*Obolella transversa* HARTT in DAWSON 1868, by original designation.

Discussion.—When this genus was first described, WALCOTT clearly recognized many of its characteristic features, although he was under the misapprehension that its shell was calcareous. He noted its convex pedicle valve, eccentric position of the ventral apex and pedicle foramen, and briefly discussed and illustrated the internal features of both valves, drawing attention to the conspicuous cardinal muscle scars and pronounced "triangular shaped projection" (apical process) in front of the pedicle opening. He also commented on the low median ridge and absence of a pseudointerarea in the convex brachial valve.

In 1912, after a much more extensive study of Cambrian brachiopods, WALCOTT had second thoughts about the validity of *Linnarssonia.* At that time, the internal structure of most acro-





FIGS. 24-25. *Linnarssonia ophirensis* (WALCOTT). Biometric diagrams (see text for descriptions).

tretids was poorly known. The majority of species with a high conical pedicle valve were placed in *Acrotreta* and since he could find no consistent differences between the internal structure of these forms and the convex ones, and moreover, realized that complete gradation in external profile existed between the two, WALCOTT considered it necessary to abandon *Linnarssonia* as a valid generic name. He judged that if it were retained at all, it could only be as a subgenus of *Acrotreta* and obviously he was sceptical of the value of the name even in this reduced capacity, for he did not employ it. Having been abandoned by its author, *Linnarssonia* was not used for many years.

In 1941, BELL erected several new acrotretid genera and species. Included in these new taxa was *Pegmatreta* BELL, the type species of which (*Pegmatreta perplexa* BELL) came from the Middle Cambrian Meagher Limestone of Montana. Both the original description of the genus (BELL, 1941, p. 231) and later diagnoses (e.g., ROBINSON, 1964, p. 558) agree almost identically with the original account of *Linnarssonia,* although they are given in more modern technical terminology, of course. Neither of the two type species are known from large suites of etched topotype material and for *L. transversa,* at least, the recovery of such suites will not be possible with present techniques, because the specimens occur in a silty sandstone. In so far as both type species are known, however, little justification is seen for not regarding them as congeneric. They have similar convex to low subconical external form, and internally they show striking similarities in musculature, feeble development of the brachial pseudointerarea, low dorsal median ridge and the dominance of a prominent, boss-like apical process on the anterior slope of the pedicle valve immediately in front of the internal pedicle opening. Consequently, *Pegmatreta* is here regarded as a junior synonym of *Linnarssonia.*

LINNARSSONIA OPHIRENSIS (Walcott)

Acrotreta ophirensis WALCOTT, 1902, p. 591; WALCOTT, 1912, p. 697, pl. 74, fig. 1, 1a-1p.
Acrotreta ophirensis rugosa WALCOTT, 1902, p. 592; WALCOTT, 1912, p. 699, pl. 74, fig. 2, 2a-2e.
?*Pegmatreta rotunda* BELL, 1941, p. 232, pl. 30, figs. 27-31, text fig. 17.
Pegmatreta ophirensis ROBINSON, 1964, p. 558, pl. 91, fig. 1-9.

Diagnosis.—Subcircular to transversely oval in outline, length typically about 0.8 of maximum width; pedicle valve convex to low subconical, catacline to gently procline, maximum height about 0.3 of valve length, occurring at or slightly in front of beak; pseudointerarea flat or gently

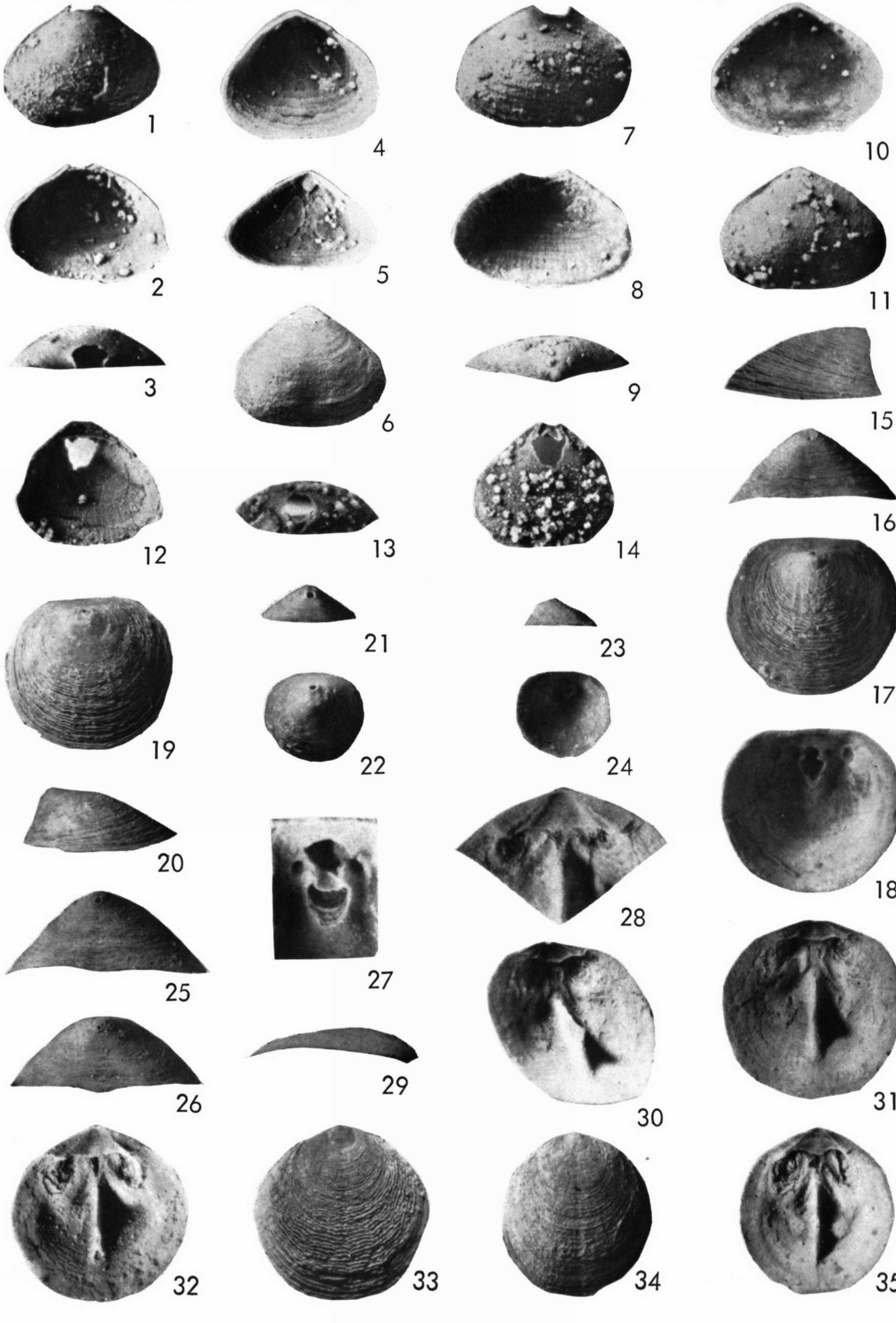
EXPLANATION OF PLATE 3

FIGURES

1-14. *Diorystus transversus* (WALCOTT), Upper Cambrian, House Range, Utah, and Snake Range, Nevada .... (p. 29)

FIGURES

15-35. *Physotreta spinosa* (WALCOTT), Upper Cambrian, Eureka district, Nevada .... (p. 22)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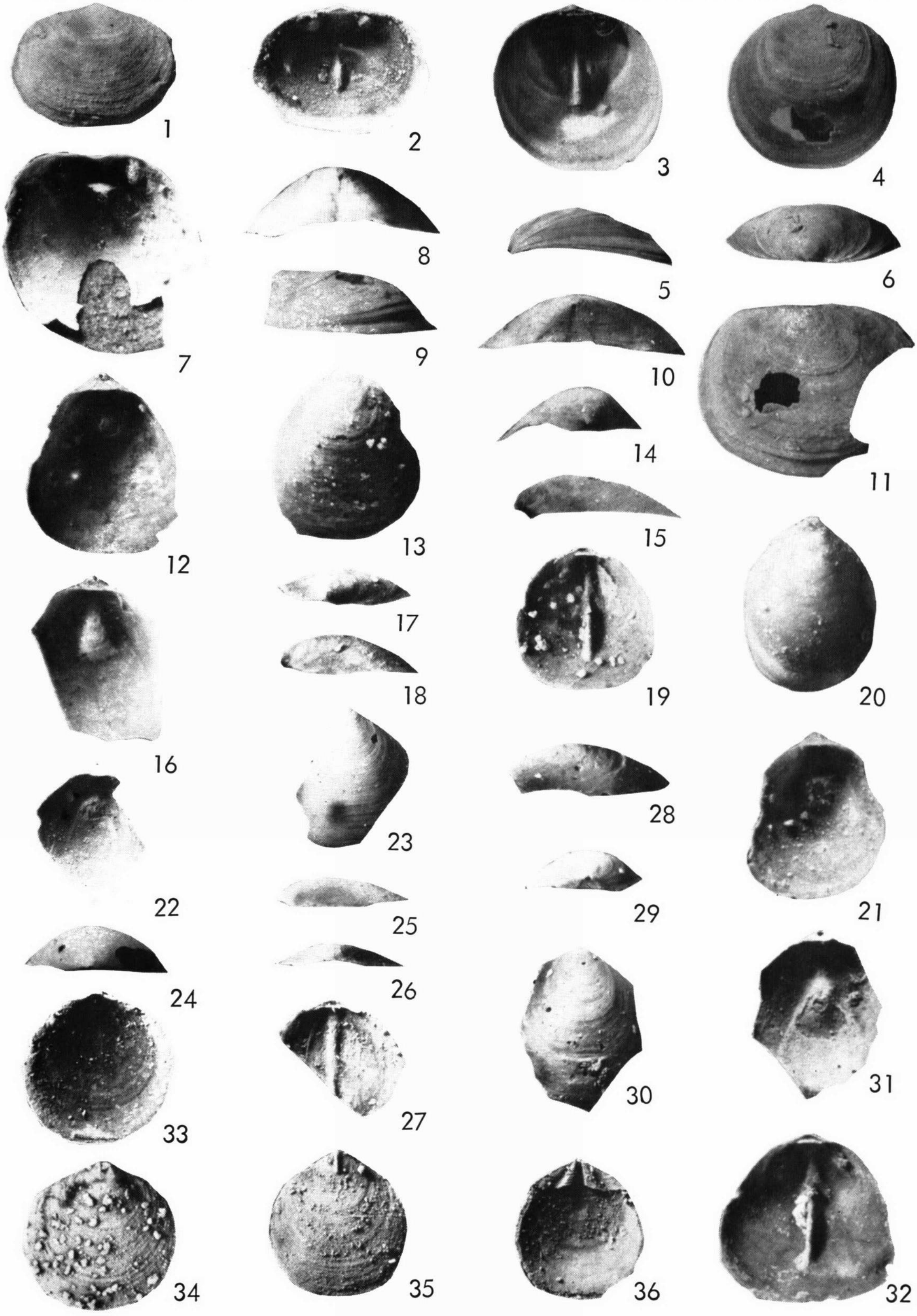
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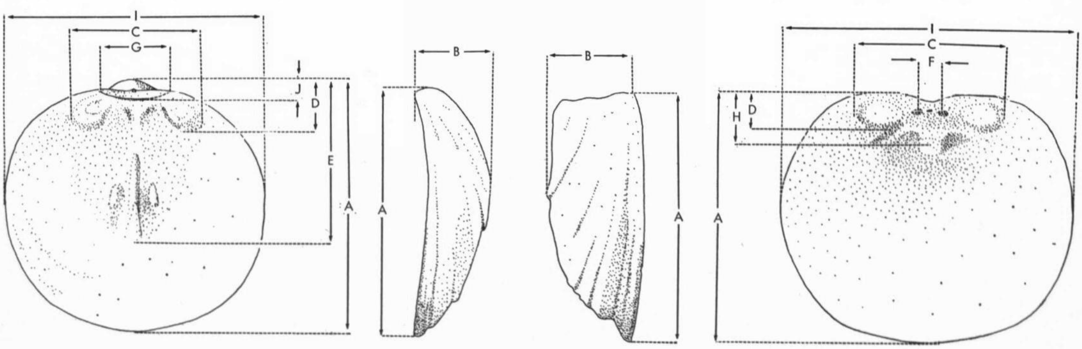
TABLE 6
LINNARSSONIA OPHIRENSIS
Statistics of sample of topotype specimens
Bivariate statistics for allometric growth given only when α differs significantly from 1 (P = 0.05)

Variable x	Variable y	$\bar{x}$	var(x)	$\bar{y}$	var(y)	r'	a	var(a)	$\overline{\log(x)}$	var(log x)	$\overline{\log(y)}$	var(log y)	r	α	var(α)	n	valve
A	I	1.81	0.332	2.24	0.388	0.949	1.0800	0.03896								5	brachial
A	E	1.81	0.332	1.07	0.159	0.988	0.6920	0.00371								5	brachial
A	D	1.81	0.332	0.25	0.010	0.970	0.1778	0.00063								5	brachial
C	I	0.95	0.102	2.24	0.388	0.966	1.9465	0.08539								5	brachial
A	B	1.74	0.080	0.61	0.020	0.860	0.5046	0.01106								8	pedicle
A	C	1.81	0.051	0.87	0.013	0.807	0.5072	0.01794								7	pedicle
A	F	1.81	0.051	0.23	0.002	0.917	0.1862	0.00110								7	pedicle

Variables	B/A	G/I	J/A	D/A	H/A
Mean of ratio	33.1%	16.9%	2.8%	15.4%	20.8%
Var.of ratio	12.5	11.6	0.5	6.5	8.8
Valve	brachial	brachial	brachial	pedicle	pedicle
n	4	4	4	8	8



Diagrammatic representation of measurements

A = maximum length of valve B = maximum height of valve C = width between lateral margins of cardinal muscle scars D = length of valve to front of cardinal muscle scars E = length of valve to anterior end of median ridge F = width between centers of apical pits G = maximum width of pseudointerarea H = length of valve to center of apical boss I = maximum width of valve J = length of median plate

concave, divided by narrow, moderately developed intertrough; external pedicle foramen small, circular, immediately posterior of beak; anterior slope of valve convex in lateral profile. Brachial valve convex, in lateral profile more strongly rounded posteriorly than anteriorly, maximum height about 0.3 of its length, occurring near mid-length of valve; beak lacking nodes, slightly inflated above shell lateral to it. Both valves ornamented by exceedingly fine growth lines and commonly with strong concentric interruptions of profile formed whilst radial growth component temporarily was in abeyance, these being more abundant peripherally.

Ventral interior with subtriangular thickening on anterior slope, bounded laterally by *vascula lateralia,* culminating posteromedially in strong, bosslike apical process with posterior slope descending abruptly to define anterior margin of apical cavity, internal pedicle opening anterodorsally directed in cavity; apical pits close together in cavity, lateral of internal foramen; cardinal muscle scars commonly elevated, on posterior slope of valve, subcircular in outline.

Brachial valve interior with narrow median plate, width typically about 0.2 maximum width of valve and very short anteroposteriorly, propareas obsolescent to absent; median ridge low, buttressing median plate posteriorly, extending forward slightly more than 0.5 of valve length, cardinal muscle scars on elevated callosities, relatively close together, their anterior margins oc-

EXPLANATION OF PLATE 4

FIGURES

1-11. *Linnarssonia ophirensis* (Walcott), Middle Cambrian, Ophir district, Utah ....(p. 24)

12-21, 32. *Acrothyra urania* (Walcott), Middle Cambrian, Wasatch Mountains, Utah ....(p. 27)

FIGURES

22-31. *Acrothyra minor* (Walcott), Middle Cambrian, Malade district, Idaho ....(p. 28)

33-36. *Tropidoglossa modesta* (Walcott), Upper Cambrian, House Range, Utah ....(p. 32) curring at about 0.12 of valve length. Anterior muscle scars elongated, near center of valve, separated by *vascula media* from median ridge.

Illustrations.—Figures 24-25; Plate 4, figures *1-11*; Table 6.——Figs. 24-25. Scatter diagrams and reduced major axis growth lines for topotype specimens of *Linnarssonia ophirensis*. [Symbols for variables as in Table 6. Variable plotted along abscissa cited first in pair. BV=brachial valve. PV=pedicle valve. All dimensions in millimeters.]——Pl. 4, figs. *1-2*. Ext. and int. views of brachial valve (139485), both ×15.——Pl. 4, figs. *3-6*. Int., ext., lat., and oblique post. view of brachial valve (139486), all ×10.——Pl. 4, figs. *7-8*. Oblique int. and post. views of pedicle valve (139487), both ×15.——Pl. 4, figs. *9-11*. Lat., post., and ext. views of pedicle valve (139488), all ×15. [All specimens are topotypes from USNM loc. 3e, late Middle Cambrian, Ophir, Utah.]

Figured Specimens

		USNM	Length (mm.)
Topotype	young brachial valve	139485	1.3
Topotype	brachial valve	139486	2.6
Topotype	distorted pedicle valve	139487	....
Topotype	damaged pedicle valve	139488	1.8

All specimens from USNM loc. 3e, (lower *Bolaspidella* Zone or *Bathyuriscus—Elrathina* Zone, Middle Cambrian —A. R. PALMER, personal communication.) "Limestone less than 400 feet (121.9 m.) above the quartzitic sandstones of the Cambrian, at Ophir, Oquirrh Range, Tooele County, Utah" (WALCOTT, 1912, p. 698).

Discussion.—The available collection of etched topotype material is relatively small and includes a majority of broken or distorted specimens. The collection is sufficiently large, however, to reveal the essential accuracy of WALCOTT's original description and to add to our knowledge of the detail of the internal structures. At present, there seems little justification for recognition of WALCOTT's "variety" *L. ophirensis rugosa,* which shares the same type locality in Utah with *L. ophirensis*. This "variety" reputedly has coarser, rugose growth lines, but there is seemingly a gradation between these forms and those lacking prominent growth halts, and since we know nothing of a significant geographical distribution of this morphotype which might support its recognition as a subspecies, it is better regarded as a synonym of *L. ophirensis*. The species occurs in the *Bolaspidella* Zone in western Utah (ROBINSON, 1964) and if BELL's species *Pegmatreta rotunda* is correctly synonymized with it, it is also present in Montana.

The value of having information on the internal structures of acrotretids based on etched material from their type locality is again emphasized in considering WALCOTT's "variety" *L. ophirensis descendens*. This form is externally somewhat similar to *L. ophirensis* and from the available, mechanically prepared material, WALCOTT considered it to be a descendant, differing only slightly from it. Comparison of etched topotype specimens, however, reveals that in spite of the gross external resemblance there are wide differences in the internal features, differences which affect both valves and which are considered to be sufficiently large to merit the transfer of this so called "variety" to a different subfamily of the Acrotretidae (p. 5).

Genus ACROTHYRA Matthew, 1901

Type species.—*Acrotreta proavia* MATTHEW, 1899, by subsequent designation, WALCOTT, 1912, p. 716.

Discussion.—At its type locality (Dugald Brook, Cape Breton, Nova Scotia) the type species of *Acrothyra* occurs in Middle Cambrian sandy shales. Knowledge of the interior of shells belonging to the genus is largely derived from natural, internal casts of the valves, and since the phosphatic shell is not readily soluble in the natural acids developed as weathering proceeds, the casts are primarily revealed by exfoliation of the shell and are rarely perfect. Consequently, although gross features of the type species are known, there is less certainty about the more delicately impressed detail, with resultant ambiguities in concepts of nominal genus.

As currently interpreted, *Acrothyra* is characterized by its elongate, commonly subtriangular outline and biconvex profile. The pedicle valve is typically apsacline and the external pedicle foramen apical or immediately behind the apex, the pseudointerarea being relatively narrow. Internally, the apical process is an elongate, triangular projection, broadening anteriorly and confined to the anterior slope of the valve. The dorsal interior has a low median ridge that may buttress a narrow median plate posteriorly, the propareas being greatly reduced or absent.

Two species in the present collection may be referred to *Acrothyra*—*Acrothyra minor* WAL-

COTT and *Linnarssonella urania* WALCOTT. Both species are represented by small collections and none of the specimens of *A. minor* are complete valves; both species are present primarily as fragments. As neither species is well known, it seems profitable to briefly describe some of their features, illustrate their internal structure photographically for the first time and to correct a generic assignment.

ACROTHYRA URANIA (Walcott)

Linnarssonella urania (WALCOTT), 1908, p. 92, pl. 9, figs. 9, 9a; WALCOTT, 1912, p. 670, pl. 78, figs. 9, 9a-9c.

Subequally biconvex, typically rounded, subtrigonal in outline, ornamented by fine concentric growth lines; pedicle valve about 3 times as long as high, maximum height occurring about 0.3 of valve length anterior from beak; beak small but prominent, strongly incurved, overhanging apsacline deltoid pseudointerarea, foramen facing dorsally or strongly dorsoposteriorly; posterior sector of valve very short, about 0.1 mm. in inclined length, pseudointerarea poorly developed but posterior slope divided by triangular deltoid pseudointerarea, slightly, but abruptly depressed below level of adjacent shell. Brachial valve with smooth beak, inflated above general level of adjacent shell; very shallow median sulcus; lateral commissure bowed dorsally.

Ventral interior with pedicle aperture widening and curving in its passage through shell, internal foramen facing anteriorly; apical process arising in front of foramen, confined to anterior slope of valve, extending forward between 0.3 and 0.5 of valve length, variation in detail of shape, but basically subtriangular in outline, expanding in width and becoming higher anteriorly, anterior face of process steep, sharply defined, bounded laterally by bacculate *vascula lateralia*; cardinal muscle scars elongate subelliptical on posterolateral flanks of valve, lateral to *vascula lateralia*; apical pits not deeply impressed on lateral flanks of apical process about midway along its length.

Dorsal interior with small, slightly depressed, subtriangular median plate separating narrowly triangular to almost linear propareas; median ridge high in central part of valve extending forward about 0.75 of valve length, highest anteriorly, posteriorly becoming lower and covered by later shell layers associated with lateral margins of *vascula lateralia,* posteriorly buttressing median plate; subelliptical cardinal muscle scars diverging anterolaterally, extending forward about 0.25 of valve length, separated by *vascula lateralia* from median ridge.

Illustrations.—Plate 4, figures *12-21, 32.*——Pl. 4, figs. *12-15.* Int., ext., post., and lat. views of pedicle valve (139490), all ×15.——Pl. 4, fig. *16.* Int. view of damaged pedicle valve (139489), ×20.——Pl. 4, figs. *17-19.* Post., lat. and int. views of brachial valve (139491), all ×15.——Pl. 4, figs. *20-21.* Ext. and int. views of pedicle valve (139492), both ×20.——Pl. 4, fig. *32.* Int. view of brachial valve (139493), ×15. [All specimens are topotypes from USNM loc. 55u, medial Middle Cambrian, Wasatch Mountains, Utah.]

Figured Specimens

		USNM	Length (mm.)
Topotype	damaged pedicle valve	139489	1.35
Topotype	pedicle valve	139490	1.80
Topotype	brachial valve	139491	1.50
Topotype	damaged pedicle valve	139492	1.35
Topotype	brachial valve	139493	1.85

All specimens from USNM loc. 55u (post-*Glossopleura* Middle Cambrian, probably medial Middle Cambrian—A. R. PALMER, personal communication). "0.25 mile (0.4 km.) below the Maxfield mine, in Big Cottonwood Canyon, on the west front of the Wasatch Mountains, southeast of Salt Lake City, Salt Lake County, Utah" (WALCOTT, 1912, p. 671).

Discussion.—Although the external form of this species is not unlike that of *Linnarssonella,* the interior of both valves is greatly different, most notable being the absence of grooved propareas in the brachial valve and the nature of the apical process. The form of this latter structure and the reduced dorsal pseudointerarea are both characteristic of the Linnarssoniinae and the species is seemingly referable to *Acrothyra* as at present understood.

The posterior part of the pedicle valve is not as anomalous as WALCOTT considered it to be, although in view of the small size of the specimens and the techniques available to him, it is hardly surprising that WALCOTT had difficulty in elucidating the structure of this region. The position of the pedicle foramen relative to the beak is quite orthodox for an acrotretid, although its orientation, associated with a strongly incurved apex, is unusual. The structure of the posterior sector of the valve is also not very abnormal, but as WALCOTT correctly predicted, it is reduced in size and, moreover, the propareas are not recognizable, their absence is possibly to be correlated with the extreme narrowness of this sector of the shell.

ACROTHYRA MINOR Walcott, 1905

Acrothyra minor WALCOTT, 1905, p. 303; WALCOTT, 1912, p. 717, text fig. 59, pl. 76, figs. 4, 4a-4b.

Discussion.—In the original account of the species, WALCOTT (1905, p. 303) noted that the material was from "Middle Cambrian. Two miles southeast of Malad City, Idaho." Subsequently, in 1912 (p. 717), he cited two locality numbers from this area (5b, 54s) and restricted the type locality to 5b. In an earlier part of the work listing all the localities, 5b and 54s are equated with each other (p. 168, 204) and in view of the lack of differentiation between the two, material from locality 54s, is here also regarded as topotypic.

The etched material of this species is limited and consists entirely of fragments of both valves. Little can be added to WALCOTT's brief description of the external form, although the specimens add considerably to our knowledge of the major features of the shell interior.

Externally, *A. minor* is very similar to *A. urania,* the brachial valve seeming to be shallower in the former species, but there is inadequate material to establish whether this is a significant difference. The ventral beak of *A. minor* is not strongly incurved and the external foramen faces posteriorly, rather than dorsally, two features, which together with the presence of small but distinct ventral propareas on the present species, readily enable it to be differentiated from *A. urania.*

Previous accounts of the apical process are slightly misleading; the highest part of the process is approximately oval in outline as WALCOTT described it, but this is continued posteriorly by a lower, narrower ridge between the *vascula lateralia.* The entire process forms a bulbous, subtriangular projection from the anterior slope of the valve having the same basic shape as that of *Acrothyra urania.* The distribution of muscles in the two species is closely comparable.

Illustrations.—Plate 4, figures *22-31.*——Pl. 4, figs. *22-24.* Int., ext., and post. views of damaged pedicle valve (139494), ×10, ×10, ×15.——Pl. 4, figs. *25-27.* Lat., post., and int. views of damaged brachial valve (139496), all ×15.——Pl. 4, figs. *28-31.* Lat., post., ext., and int. views of damaged pedicle valve (139495), all ×15. [All specimens are topotypes from USNM loc. 54s, early Middle Cambrian, Malade, Idaho.]

Figured Specimens

		USNM
Topotype	fragment of pedicle valve	139494
Topotype	fragment of pedicle valve	139495
Topotype	fragment of brachial valve	139496

All material from USNM loc. 54s (=5b), (*Albertella* zone, early Middle Cambrian—A. R. PALMER, personal communication), "Dark blue-gray Langstan Limestone, just above the Cambrian quartzitic sandstones, north side of Twomile Canyon, near its mouth, 2 miles (3.2 km.) southeast of Malade, Oneida County, Idaho" (WALCOTT, 1912, p. 717).

Superfamily SIPHONOTRETACEA Kutorga, 1848

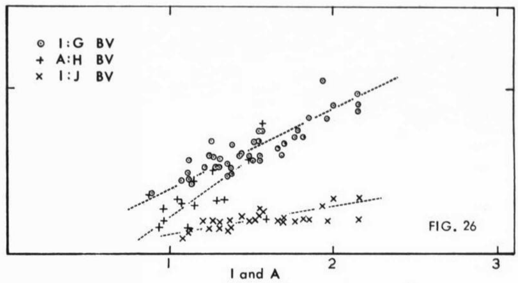
Family SIPHONOTRETIDAE Kutorga, 1848

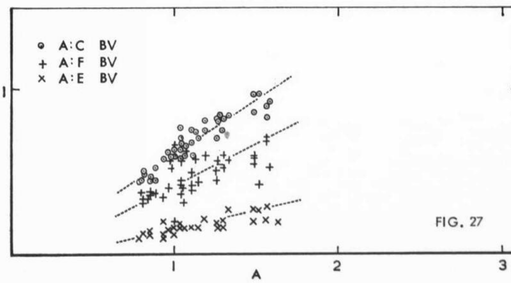
Genus DYSORISTUS Bell, 1944

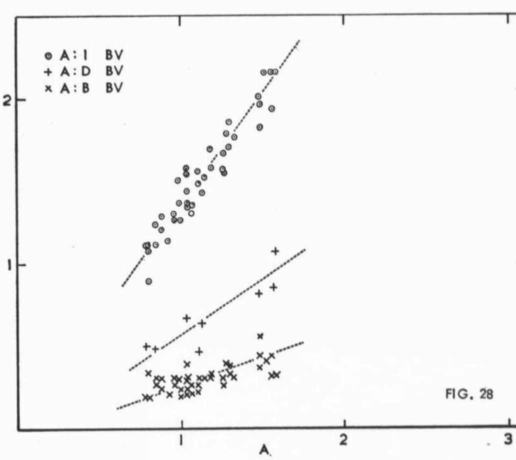
Type species.—*Dysoristus lochmanae* BELL, 1944, by original designation.

Discussion.—The genus was monotypic when erected and included only *Dysoristus lochmanae,* a species then known to be widely distributed in the Upper Cambrian *Cedaria* zone of Montana, Wyoming and Missouri (BELL, 1944, p. 146). The known stratigraphic range of the type species has since been considerably increased, for PALMER (1955, p. 766) has reported it as a rare element of the post-*Aphelaspis* zone faunas of Texas.

Initially, the relationships of the genus were considered to be obscure; all of the material that formed the basis of the first description was mechanically prepared and every pedicle valve was broken posteriorly (BELL, 1944). Subsequent preparations of material with acetic acid enabled BELL to recover specimens of the type species that were much better preserved. These specimens were described and figured by ROWELL (1962, p. 148) and afforded a ready explanation of the initial failure to obtain undamaged pedicle valves. The pedicle foramen is a relatively large, subcircular to tear-shaped hole cutting through the valve immediately in front of the beak, the shell posterolateral of it being very delicate. When the specimens were prepared mechanically, the plug of matrix through the foramen invariably caused the shell to fracture on both sides of it, and the beak region to be retained in the rock. Even with etched specimens, it is still uncertain whether the pedicle foramen of *D. lochmanae* actually breaches the posterior margin of the value, or whether it is constrained dorsally by a narrow, entire pseudointerarea. In all of the specimens of this species that have been seen, the foramen intersects the margin of the valve and the pseudointerarea is divided into two triangular parts (ROWELL, 1962, pl. 30, figs. 19-20). It is quite possible however, that this condition is an artifact caused by damage either before or during preparation of the material. The plausibility of this suggestion is supported by examination of large collections of etched specimens of *Dysoristus transversus* (WALCOTT), a species that is certainly closely related to *D. lochmanae.* The majority of the pedicle valves of *D. transversus* are either broken posteriorly or have a pedicle foramen comparable to that described for the type species of the genus, intersecting the margin of the valve. Fortunately, a few specimens are found in a collection from Lincoln Canyon, Nevada, that are seemingly better preserved and show more detail of the extreme posterior margin of the pedicle valve. In these fossils, the margin of the valve is entire, the pseudointerarea forming an undivided, triangular plate dorsal of the foramen; moreover, the foramen, which has clearly grown anteriorly by resorption, is restricted posteriorly by an externally convex, triangular plate (Pl. 3, fig. *13, 14*). These features of the pedicle valve, together with what is known of the musculature, mantle canals, and gross morphology of the opposing brachial valve, suggest that *Dysoristus* is an early representative of the Siphonotretidae (ROWELL, 1962), differing conspicuously from later genera in being nonspinose.







FIGS. 26-28. *Dysoristus transversus* (WALCOTT). Biometric diagrams (see text for descriptions).

DYSORISTUS TRANSVERSUS (Walcott), 1908

Linnarssonella transversa WALCOTT, 1908, p. 92, pl. 9, fig. 6; WALCOTT, 1912, p. 670, pl. 78, figs. 6, 6a-6c.

Thin-shelled, ventribiconvex, rounded transversely subtriangular in outline; beak of pedicle valve marginal, perforated by relatively large tear-shaped pedicle track, typically extending forward about 0.25 of valve length from beak, closed posteriorly by externally convex, triangular plate, depressed slightly below level of adjacent shell and forming posterior margin of subcircular foramen; in lateral profile gently convex, slightly more strongly rounded posteriorly, maximum height of valve about 0.3 of length occurring near mid-length; in outline length about 0.7 of width, posterolateral margins of valve slightly convex to straight, strongly rounded anterolaterally, gently rounded anteriorly; valve ornamented by fine concentric growth lines. Brachial valve with slightly incurved marginal beak, umbonal region inflated somewhat above adjacent lateral flanks, convex in lateral profile, more strongly rounded posteriorly, maximum height of valve about 0.25 of length, occurring slightly behind mid-length of valve, outline comparable to that of pedicle valve,

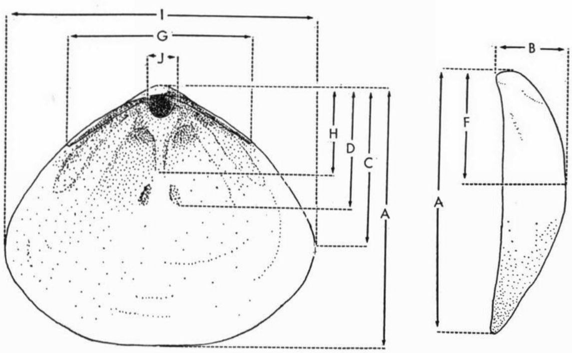
TABLE 7

DYSORISTUS TRANSVERSUS

Statistics of sample of topotype specimens

Bivariate statistics for allometric growth given only when α differs significantly from 1 (P = 0.05)

Variable x	Variable y	$\overline{x}$	var(x)	$\overline{y}$	var(y)	r'	a	var(a)	$\overline{\log(x)}$	var(log x)	$\overline{\log(y)}$	var(log y)	r	α	var(α)	n	valve
A	C	1.13	0.053	0.68	0.023	0.935	0.6610	0.00134	0.100	0.0403	-0.407	0.0522	0.940	1.1377	0.00367	43	brachial
A	E	1.14	0.058	0.17	0.003	0.841	0.2160	0.00045	0.107	0.0448	-1.840	0.0924	0.845	1.4362	0.01962	32	brachial
A	B	1.13	0.053	0.30	0.006	0.737	0.3474	0.00134	0.100	0.0403	-1.247	0.0671	0.718	1.2902	0.01970	43	brachial
A	F	1.13	0.053	0.47	0.014	0.634	0.5145	0.00386	0.100	0.0403	-0.797	0.0748	0.622	1.3624	0.02779	43	brachial
A	H	1.19	0.050	0.35	0.025	0.549	0.7036	0.02472	0.157	0.0345	-1.152	0.2154	0.500	2.5000	0.33498	16	brachial
A	D	1.19	0.100	0.69	0.046	0.891	0.6817	0.01591	......	......	......	......	......	......	......	8	brachial
I	G	1.51	0.099	0.63	0.023	0.886	0.4815	0.00125	......	......	......	......	......	......	......	42	brachial
I	J	1.54	0.098	0.20	0.003	0.716	0.1757	0.00054	0.410	0.0409	-1.658	0.0762	0.741	1.3653	0.03005	30	brachial
A	I	1.13	0.053	1.51	0.096	0.955	1.3538	0.00397	......	......	......	......	......	......	......	43	brachial



Diagrammatic representation of measurements

A = maximum length of valve B = maximum height of valve C = length of valve to line of maximum width of valve D = length of valve to front of the anterior muscle scars E = inclined length of median plate F = length of valve to point of maximum height of valve G = maximum width of pseudo - interarea H = length of valve to front of ridge I = maximum width of valve J = maximum width of median plate

maximum width developed at about 0.6 of valve length; large specimens with poorly defined weak median sulcus; ornament as pedicle valve.

Pedicle valve interior with triangular pseudointerarea, slightly depressed ventral of commissure plane, dorsally concave but essentially orthocline, interior feebly marked by fine radiating striae, muscle scars not identified.

Pseudointerarea of brachial valve anacline, closely adnate to inner surface of valve, width about 0.4 that of valve, propareas narrowly triangular, separated by diamond-shaped median plate, curvature of plate slightly less than that of inner surface of valve, its anterior margin elevated gently above valve floor, may be supported medianly by very low median ridge, ridge typically extending forward to about 0.3 of valve length, dichotomizing before termination; muscle scars poorly impressed, 2 small elliptical scars close together near center of valve, 2nd pair of long scars, probably muscular in origin, posterolaterally located, separated by pair of anterolaterally diverging bacculate *vascula lateralia*.

Illustrations.—Figures 26-28; Plate 3, figures *1-14;* Table 7.—Figs. 26-28. Scatter diagrams and reduced major axis growth lines for topotype specimens of *Dysoristus transversus*. [Symbols for variables as in Table 7. Variable plotted along abscissa cited first in pair. BV=brachial valve. All dimensions in millimeters.]——Pl. 3, figs. *1-3*. Ext., int., and lat. views of pedicle valve, extreme posterodorsal part of valve damaged (139524), all ×20.——Pl. 3, figs. *4-6*. Int., oblique int. and ext. views of brachial valve (specimen rotated in fig. *5* to show shape of median plate) (139522), all ×12.5.——Pl. 3, figs. *7-8*. Ext. and int. views of pedicle valve, extreme posterodorsal part of valve damaged (139523), both ×15.——Pl. 3, figs. *9-11*. Post., int. and ext. views of brachial valve (139521), all ×15.——Pl. 3, figs. *12-14*. Int., post., and ext. views of complete pedicle valve showing pseudointerarea dorsal of pedicle foramen (139471), all ×15. [Specimens 139521-139524 inclusive are topotypes from USNM loc. 30j, early Late Cambrian, House Range, Utah: specimen 139471 from the top of the Lincoln Canyon Formation, early Late Cambrian, south side of Lincoln Canyon, Snake Range, Nevada.]

Figured Specimens

		USNM	Length (mm.)
Topotype	brachial valve	139521	1.35
Topotype	brachial valve	139522	1.60
Topotype	pedicle valve damaged posteriorly	139523	......
Topotype	pedicle valve damaged slightly posteriorly	139524	0.95
	pedicle valve	139471	......

Specimens 139521-139524 from USNM loc. 30j, (*Dicanthopyge* Zone, early Late Cambrian—A. R. PALMER, personal communication) "near the base of the arenaceous shales and limestones forming 1e of the Orr Formation, on Orr Ridge, about 5 miles (8 km.) south of Marjum Pass, House Range, Millard County, Utah" (WALCOTT, 1912, p. 670).

Specimen 139471 from top of Lincoln Canyon Formation, early Late Cambrian, south side of Lincoln Canyon, Snake Range, Nevada.

Discussion.—The species was initially assigned to *Linnarssonella* (WALCOTT, 1908), but BELL (1944, p. 147) suggested that it might be congeneric with *Dysoristus lochmanae,* although at that time *D. transversus* was only known from partly exfoliated brachial valves. Subsequently, etched material made available by Dr. A. R. PALMER from the Lincoln Canyon Formation of Lincoln Canyon, Nevada, seemingly substantiated BELL's opinion (ROWELL, 1962, p. 149) and his views are confirmed by the present study of etched topotype specimens of *"Linnarssonella" transversa.*

Unfortunately, all topotype pedicle valves are damaged posteriorly to a greater or lesser extent, and in the above description details of the ventral pseudointerarea and plate closing the pedicle track posteriorly are based on the Lincoln Canyon specimens. The damage to the pedicle valves precludes citing statistics involving the length of this valve and Table 7 is concerned only with the brachial valve.

Order LINGULIDA Waagen, 1885

Superfamily LINGULACEA Menke, 1828

Family OBOLIDAE King, 1846

Subfamily LINGULELLINAE Schuchert, 1893

Genus TROPIDOGLOSSA Rowell, n. gen.

Etymology.—Greek, *tropis,* keel, and Greek, *glossa,* tongue.

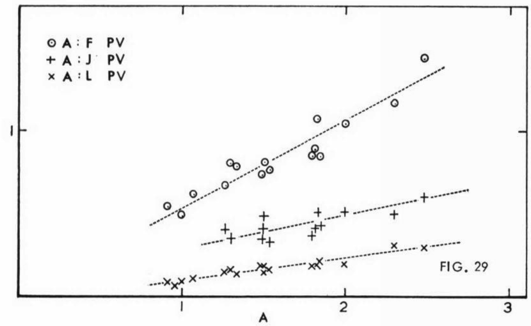
Type species.—*Linnarssonella modesta* WALCOTT, 1908.

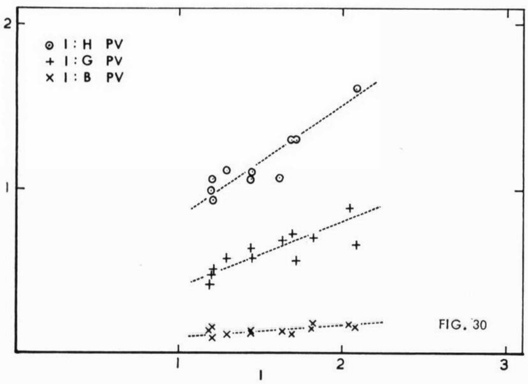
Diagnosis.—Small for family, thin-shelled, ornament of fine growth lines; dorsibiconvex, elongate oval in outline; pedicle valve exterior characterized by short, conspicuous keel extending anteriorly from beak, umbonal region of brachial valve externally bearing two ridges diverging slightly from beak, separated by pronounced groove. Pedicle valve with orthocline pseudointerarea divided into propareas by pedicle groove, flexure lines prominent. Pseudointerarea of brachial valve narrow, medianly depressed.

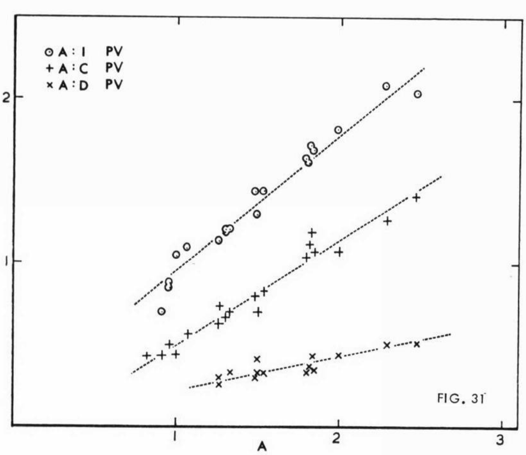
Age.—Late Cambrian.

Discussion.—Were it not for the fact that the collection recovered from etching contains a number of complete shells, with both valves in apposition to each other, one might feel some lack of confidence in asserting that the two valves belonged to one species. The external form of the brachial valve, with its rounded outline and paired protuberances, recalls that of many acrotretaceans (e.g. *Linnarssonella, Apsotreta*) and it is not surprising that WALCOTT, dealing only with mechanically prepared specimens, considered the species an acrotretid. The resemblance is rather superficial, however, for the protuberances of *Tropidoglossa* are distinct ridges rather than short nodes as in the acrotretids and the form of the dorsal pseudointerarea is more like that of a lingulacean than an acrotretacean. The morphology of the interior of the pedicle valve leaves little doubt of the suprageneric affinities of the species. The complex of characters associated with the ventral pseudointerarea is virtually identical with that of *Lingulella* and the elongate outline and low convexity of the pedicle valve are typical features of many of the Lingulellinae.

The genus may be distinguished readily on external features from all other members of the subfamily by the short ventral keel and paired







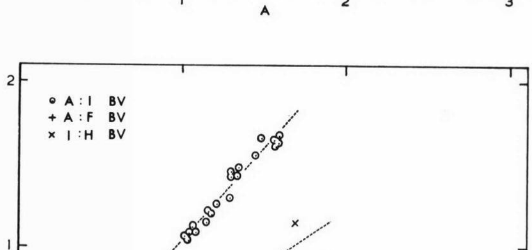
FIGS. 29-31. *Tropidoglossa modesta* (WALCOTT). Biometric diagrams (see text for descriptions).

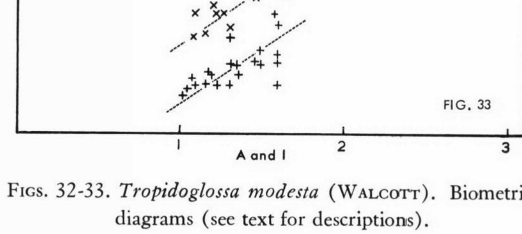
ridges diverging from the dorsal beak. The function of these structures is problematic; possibly both were directly associated with the pedicle. The ventral keel, at least at its posterior end, is a fold in the shell and its inner surface forms part of the pedicle groove. The groove separating the two ridges on the dorsal beak lies against the anterior end of the pedicle groove of the opposite valve; in modern lingulids the pedicle expands greatly in diameter immediately behind the pedicle opening with the beaks of both valves virtually buried in it and it is conceivable that a comparable expansion occurred in *Tropidoglossa,* the pedicle resting in the groove on the external surface of the brachial valve.

TROPIDOGLOSSA MODESTA (Walcott), 1908

Linnarssonella modesta WALCOTT, 1908, p. 90, pl. 9, figs. 8, 8a; WALCOTT, 1912, p. 668, pl. 78, figs. 8, 8a-8f.

Dorsibiconvex, inequivalved, ornament of fine growth lines more conspicuous anteriorly; pedicle valve elongate in outline, about 0.1 longer than wide, maximum width occurring near mid-length of valve; posterolateral margins nearly straight, typically subtending angle of about 100 degrees at beak, anterolateral and anteror margins more strongly and uniformly rounded; in lateral profile gently convex, convexity interrupted only by keel, valve about 10 times as long as high, maximum height occurring near mid-length of valve; narrow, low, short keel arising as ventrally directed deflection from beak extending forward about 0.25 mm.; brachial valve about 0.1 shorter





FIGS. 32-33. *Tropidoglossa modesta* (WALCOTT). Biometric diagrams (see text for descriptions).

TABLE 8

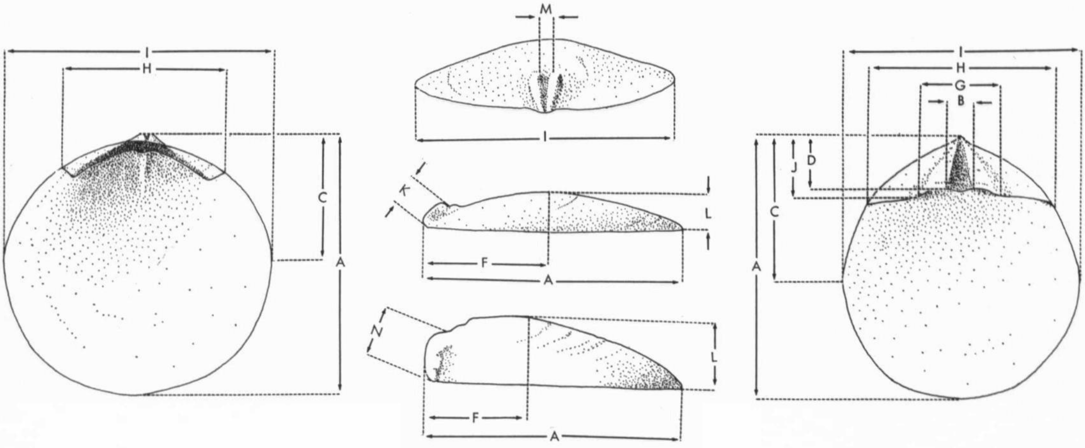
TROPIDOGLOSSA MODESTA

Statistics for sample of topotype specimens

Bivariate statistics for allometric growth given only when α differs significantly from 1 (P = 0.05)

Variable x	Variable y	$\bar{x}$	var(x)	$\bar{y}$	var(y)	r'	a	var(a)	$\overline{\log(x)}$	var(log x)	$\overline{\log(y)}$	var(log y)	r	α	var(α)	n	valve
A	I	1.50	0.223	1.37	0.155	0.987	0.8340	0.00109	....							19	pedicle
A	C	1.50	0.223	0.82	0.090	0.979	0.6370	0.00100	0.359	0.1016	-0.262	0.1417	0.981	1.1811	0.00315	19	pedicle
A	L	1.55	0.202	0.17	0.004	0.944	0.1423	0.00014	0.400	0.0862	-1.840	0.1458	0.951	1.3002	0.01012	18	pedicle
A	F	1.59	0.191	0.84	0.054	0.946	0.5332	0.00200	....							17	pedicle
A	D	1.71	0.138	0.37	0.006	0.884	0.2110	0.00081	....							14	pedicle
I	G	1.56	0.099	0.63	0.015	0.813	0.3913	0.00519	....							12	pedicle
A	J	1.74	0.134	0.44	0.006	0.772	0.2151	0.00170	....							13	pedicle
I	B	1.56	0.099	0.15	0.001	0.623	0.0746	0.00034	....							12	pedicle
I	H	1.48	0.082	1.16	0.039	0.914	0.6900	0.00978	....							10	pedicle
A	I	1.30	0.040	1.37	0.051	0.972	1.1257	0.00365	....							21	brachial
A	C	1.30	0.038	0.59	0.008	0.762	0.4622	0.00472	....							21	brachial
A	E	1.33	0.034	0.14	0.001	0.580	0.1731	0.00142	....							16	brachial
A	L	1.31	0.040	0.30	0.003	0.446	0.2637	0.00279	....							22	brachial
A	F	1.31	0.040	0.41	0.017	0.682	0.6591	0.01162	0.259	0.0238	-0.948	0.0916	0.716	1.9634	0.09392	22	brachial
I	H	1.38	0.042	0.81	0.020	0.812	0.6887	0.01244	....							15	brachial

Variable	K	N	M
Mean	0.23	0.12	0.11
Var.	0.001	0.001	0.000
Valve	pedicle	brachial	brachial
n	21	21	21



Diagrammatic representation of measurements

A = maximum length of valve B = maximum width of pedicle groove C = length of valve to line of maximum width of valve D = length of pedicle groove E = inclined length of median plate F = length of valve to point of maximum height G = maximum width between flexure lines H = maximum width of pseudointerarea I = maximum width of valve J = length of pseudointerarea to front of flexure lines K = length of keel L = maximum height of valve M = maximum width of internodal groove N = inclined length of internodal groove

than pedicle, subrounded outline, maximum width typically about equal to length occurring near mid-length of valve, posterolateral margins less strongly rounded than anterior or anterolateral, subtending very obtuse angle at beak; beak slightly incurved, umbonal region inflated above lateral flanks; in lateral profile gently convex anteriorly, more strongly rounded posteriorly, profile interrupted by ridges near beak, maximum height of valve about 0.25 of length, occurring about 0.3 of valve length in front of beak; umbonal region with 2 short ridges, about 0.1 mm. in length diverging slightly from beak separated by groove of comparable width.

Pedicle valve with strong orthocline pseudointerarea, broadly triangular, width about 0.8 maximum width of valve, divided by narrowly triangular pedicle groove, pedicle groove extending forward about 0.2 length of valve, maximum width of groove typically about 0.1 width of valve; propareas either side of groove divided by flexure lines diverging from beak, parts of propareas median of flexure lines elevated relative to those lateral to them; floor of valve immediately anterior of pseudointerarea slightly thickened; muscle scars and mantle canals not clearly impressed.

Pseudointerarea of brachial valve relatively inconspicuous, commonly closely adpressed to inner surface of valve, median segment depressed dorsally relative to remainder of pseudointerarea, margins of depressed plate not sharply defined, width of pseudointerarea about 0.6 maximum width of valve; muscle scars and mantle canal markings not clearly impressed.

Illustrations.—Figures 29-33; Plate 2, figures *1-7;* Plate 4, figures *33-36;* Table 8.——Figs. 29-33. Scatter diagrams and reduced major axis growth lines for topotype specimens of *Tropidoglossa modesta.* [Symbols for variables as in Table 8. Variable plotted along abscissa cited first in pair. BV =brachial valve. PV=pedicle valve. All dimensions in millimeters.]——Pl. 2, figs. *1-4.* Int., ext., post., and lat. views of brachial valve (139519), all ×15.——Pl. 2, figs. *5-7.* Ext., post., and lat. views of pedicle valve (139516), all ×10. [All specimens are topotypes from USNM loc. 30k, early Late Cambrian, House Range, Utah.]——Pl. 4, figs. *33-34.* Int. and ext. views of brachial valve (139520), both ×15.——Pl. 4, fig. *35.* Ext. view of pedicle valve (139518), ×15.——Pl. 4, fig. *36.* Int. view of pedicle valve (139517), ×12.5. [All specimens are topotypes from USNM loc. 30k, early Late Cambrian, House Range, Utah.]

Figured Specimens

		USNM	Length (mm.)
Topotype	pedicle valve	139516	2.35
Topotype	pedicle valve	139517	1.80
Topotype	pedicle valve	139518	1.55
Topotype	brachial valve	139519	1.35
Topotype	brachial valve	139520	1.60

All specimens from USNM loc. 30k (lower *Dunderbergia* Zone, early Late Cambrian—A. R. Palmer, personal communication), ". . . at the top of the arenaceous shales and limestones forming 1e of the Orr Formation," "on Orr Ridge, about 5 miles (8 km.) south of Marjum Pass, House Range, Millard County, Utah" (Walcott, 1912, p. 669).

Discussion.—When considering the outside of the valves, Walcott (1908, 1912) seemingly misidentified them, confusing brachial with pedicle. He described a pair of ridges on each side of the ventral beak, these ridges now considered to be features of the brachial valve.

No other species are known with which close comparison may be made. Although similar to many of the Lingulellinae, it differs from them in possession of the ventral keel and paired ridges on the beak of the brachial valve.

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[Rejected names enclosed within square brackets]