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NEW GENERA OF ACROTRETIDS FROM THE CAMBRIAN OF AUSTRALIA AND THE UNITED STATES[1]

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ABSTRACT

Little is known about the paleobiogeography of Cambrian brachiopods. Cooperative studies have shown the presence of three new genera of inarticulate acrotretid brachiopods in Upper Cambrian rocks of both Australia and the United States, but none of their species are common to both regions. *Quadrisonia* (type species *Q. minor*), *Dactylotreta* (type species *D. redunca*), and *Anabolotreta* (type species *A. tegula*) are erected and their type species described from etched material.

INTRODUCTION

Contrary to popular belief, Cambrian brachiopods are abundant, moderately diverse, and morphologically variable. Typically, species of this age are small forms, rarely exceeding 1.5 mm to 2 mm in maximum dimension. Their abundance was not fully realized until Bell (1948) demonstrated that the phosphatic-shelled forms could be recovered from residues of limestones that had been digested in dilute organic acids. In many Middle and Upper Cambrian limestones deposited in open-shelf environments, brachiopods are the most numerous component of the fossil fauna. In terms of biomass, however, trilobites were probably dominant. It is unlikely that representatives of these two phyla interacted to any significant extent. As far as is known, they belonged to two entirely different trophic groups. Some trilobites may have preyed upon, or inadvertently consumed, young brachiopods, but their joint presence in a rock more probably reflects environmental conditions appropriate to both rather than some direct biological linkage between brachiopods and trilobites.

For the past few years, we have been studying Cambrian brachiopods, particularly Upper Cambrian forms. Rowell and his coworkers have been investigating brachiopods of the upper Dresbachian and lower Franconian Pterocephaliid Biomere of the Great Basin of the United States (Rowell & Brady, 1976). More recently, he has initiated a study of the inarticulates of the underlying "*Crepicephalus*" and "*Cedaria*" zones of the lower Dresbachian of that region. Henderson has worked primarily on the inarticulate brachiopods of the Mindyallan and Idamean stages of Queens-

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land, rocks that are of approximately the same age as those investigated by Rowell (Öpik, 1966; Henderson, 1976). Although some information is available on the stratigraphic distribution of brachiopods from the Upper Cambrian of the North American craton (Palmer, 1954; Grant, 1965; Kurtz, 1971; Kurtz et al., 1975), little has been published on the distribution of the much more diverse fauna of the miogeoclinal sequence in the Great Basin (Rowell & Brady, 1976). Essentially nothing is available in the literature on the stratigraphic distribution of Australian Upper Cambrian brachiopods. Furthermore, although the paleobiogeography of Cambrian trilobites has been a subject of concern for over eighty years, almost nothing is known of the past distribution of Cambrian brachiopods. Rowell and Krause (1973) noted that such genera as *Linnarssonia* and *Acrothele* were widespread in Middle Cambrian rocks and seem to be cosmopolitan, but our ignorance of the geographical distribution of most Cambrian brachiopods is virtually complete.

Because we both have systematic manuscripts nearing completion, both lacked information on the degree of endemism of our faunas, and neither had access to the stratigraphic distribution of the taxa recognized by the other, it seemed advantageous that we cooperate. Our immediate objectives were to avoid problems of synonymy and to gain some insight into the geographic distribution of taxa. This contribution bears on the first of these two objectives, making available names for three genera that are common to the Cambrian of both continents.

In the subsequent taxonomic descriptions and discussions, we have employed the morphological terminology used in the *Treatise on Invertebrate Paleontology* (Williams & Rowell, 1965) together with additional terms proposed by Krause and Rowell (1975).

Repositories.—Material described here is held by three institutions: James Cook University (prefixed JCF), the Australian Bureau of Mineral Resources (prefixed CPC) and the Museum of Invertebrate Paleontology, University of Kansas (prefixed UKMIP). Localities are recorded only in terms of reference numbers issued by the institutions to which the individual collections belong. Full descriptions will be published elsewhere.

Acknowledgments.—We are indebted to our colleagues Drs. J. H. Shergold (Bureau of Mineral Resources, Canberra), M. E. Taylor (United States Geological Survey), and A. R. Palmer (State University of New York, Stony Brook) for the loan of material in their charge or collected by them. Henderson's investigations have been supported by the Australian Research Grants Commission. Rowell's studies of North American Cambrian brachiopods have been supported by the National Science Foundation, Earth Sciences Section grants GA-39692 and DES75-21499. The opportunity for Rowell to study Australian Cambrian brachiopods was made possible by a grant from the National Science Foundation International Program (INT76-11757) as a part of the "United States–Australian Cooperative Science Program" administered by the National Science Foundation and the Australian Department of Science. Partial support for this visit was generously provided by the Wallace E. Pratt Fund of the Paleontological Institute, University of Kansas, underwritten by the Exxon U.S.A. Foundation. We share jointly and equally in the authorship of this contribution: the sequence of our names was decided by the toss of a coin.

STRATIGRAPHIC DISTRIBUTION

The stratigraphic distribution of species of the three new acrotretid genera *Quadrisonia*, *Dactylotreta*, and *Anabolotreta* are shown in Figure 1. To avoid the creation of *nomina nuda*, only the type species of each genus is named, the remaining species being left in open nomenclature. These presently undescribed species from Australia are being monographed by Henderson; Rowell and McBride are describing the North American taxa from the Pterocephaliid Biomere (middle Dresbachian *Aphelaspis* Zone to basal Franconian *Elvinia* Zone). Although we are fairly confident of the stratigraphic distribution of the Pterocephialiid Biomere brachiopods, the same claim cannot now be made for lower Dresbachian or higher Franconian and Trempealeauan forms. Lower Upper and upper Upper Cambrian brachiopods of North America are still inadequately known, and recent studies of them have largely been confined to low-diversity cratonic sites (e.g., Palmer, 1954; Bell & Ellinwood, 1962; Grant, 1965; Lochman & Hu, 1960). It is certainly possible that additional work will increase the stratigraphic range of all three of the new genera in North America. Although all three genera are present in both continents, none of the species are known to occur in both Australia and the United States. The closest phenetic similarity is between the late pre-Payntonian *Dactylotreta* sp. 4 and the basal Franconian *Dactylotreta* sp. 6. Even these two taxa may be readily distinguished; and if the suggested chronocorrelation is accurate (Fig. 1), then they are of slightly different ages.

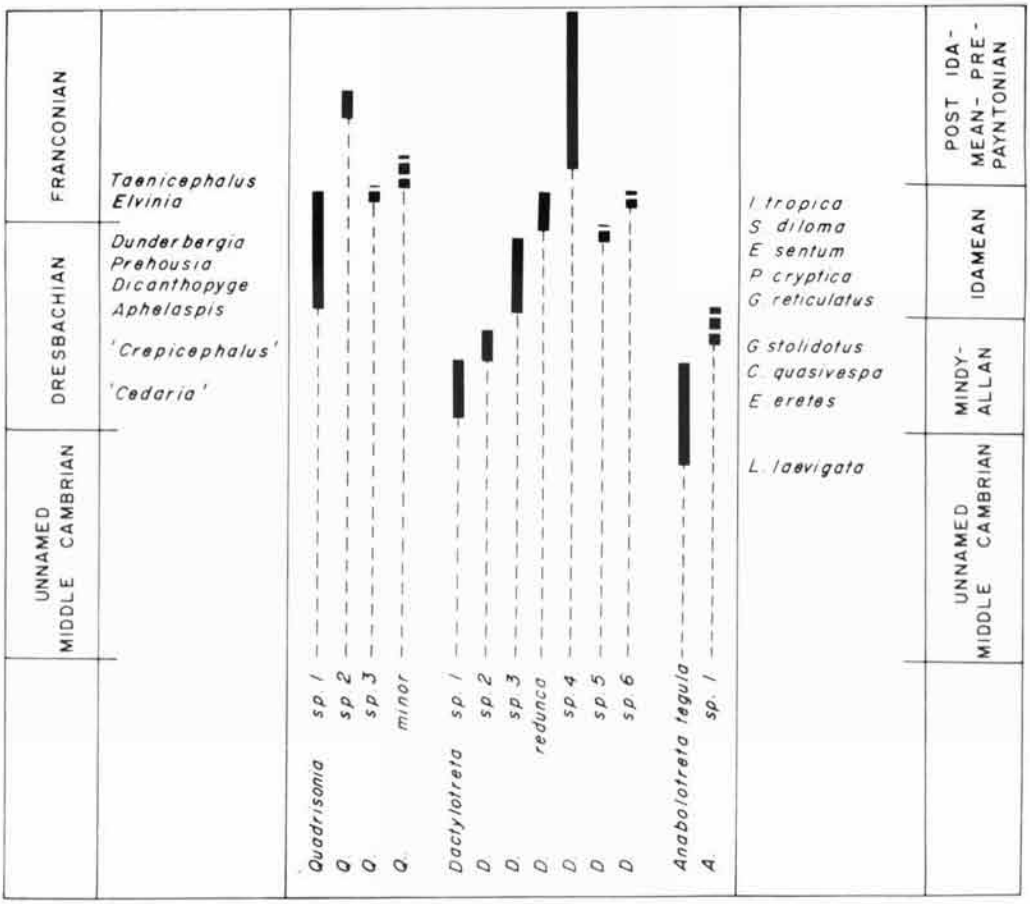

FIG. 1. Stratigraphic ranges of known species of *Quadrisonia, Dactylotreta,* and *Anabolotreta.* Approximate correlation of North American stages and zones (on the left) with those of Australia (on the right) based on Henderson (1976). Australian species ranges in solid black, North American species in heavy broken line.

SYSTEMATICS AND MORPHOLOGY

Order ACROTRETIDA Kuhn, 1949
Superfamily ACROTRETACEA Schuchert, 1893
Family ACROTRETIDAE Schuchert, 1893
Subfamily ACROTRETINAE Schuchert, 1893

Genus DACTYLOTRETA Rowell and Henderson, new

Type species.—*Dactylotreta redunca* ROWELL AND HENDERSON, n. sp.

Diagnosis.—Acutely conical Acrotretinae, ventral valve catacline to slightly procline; unusually large apical process completely occluding apex of valve, flat or slightly ridged medianly, perforated posteriorly by internal pedicle opening. Dorsal pseudointerarea long, relatively large; median plate conspicuous, concave, separating anacline-orthocline propareas, supported by median buttress.

Remarks.—In addition to its type, the genus is represented by six other species, all currently undescribed. In Australia, *Dactylotreta* ranges through most of the Upper Cambrian, but as presently known in North America it occurs in a more restricted stratigraphic interval and has been recorded only from the upper *Dunderbergia* Zone of the Dresbachian Stage and the *Elvinia* Zone of the overlying Franconian Stage (Fig. 1).

All of the species have a relatively high conical ventral valve and tend to be small. They differ from each other in details of profile of the ventral valve and in the degree of development and shape of the dorsal median septum. The latter, a conspicuous feature in some species, is absent in two that are otherwise morphologically very similar to the type species.

The combination of characters found in the genus is not like that in any other acrotretid known to us. A few acrotretids possess high conical ventral valves, particularly from the Ordovician (Cooper, 1956; Biernat, 1973; Krause & Rowell, 1975), but none have such an extensive development of the apical process. In *Dactylotreta,* at least the apical third of the ventral valve, and commonly more, is completely isolated from the body cavity by the dorsal surface of the process.

The functional significance of the relatively large apical process of *Dactylotreta* is not understood, but this is true of the processes of all acrotretids. It is probable that, as in modern pediculate inarticulate brachiopods, muscles were embedded in the wall of the pedicle surrounding an axial lumen, the lumen being an extension of the body cavity. The pedicle muscles may have been attached to the dorso-anterior surface of the process. It is likewise unknown whether the voids between the phosphatic lamellae of the apical process were empty during the life of the animal or whether they were infilled with organic material. Additional work on the ultrastructure of the shell is clearly needed to resolve this point, and such work must be performed on material that has not been processed in formic acid. The composition of the apical process would have had some bearing on the relative buoyancy of the animal which, in turn, would have been an important factor in controlling its mode of life.

DACTYLOTRETA REDUNCA
Rowell and Henderson, new species

Figures 2, 3; Tables 1, 2; Plate 1, figures 1-8.

Holotype.—JCF 10309.

Diagnosis.—*Dactylotreta* with ventral valve of subequal length, height, and width; umbo slightly incurved; posterior and lateral flanks with slight but distinct concavity in profile. Dorsal valve with flattened brim; low, narrow, triangular median septum.

Description.—Shells of moderate size, conical, height usually less than 1.5 mm. Protegula with pitted ornament, post-protegular growth stages with fine, closely spaced growth lines.

Ventral valve with height and width subequal, both slightly exceeding length. Early growth procline, becoming catacline. Typically, posterior slope gently concave and anterior slope distinctly convex in lateral profile, rare individuals with one or both of these slopes straight. Lateral slopes with faint but distinctive concavity in early ontogeny becoming straight in posterior profile with later growth; posterior apical angle about 55°. Apex bluntly rounded; small subcircular external foramen, opening posteriorly or posteroventrally, on end of short, delicate pedicle sheath in well-preserved specimens. Pseudointerarea poorly defined, crossed by narrow, shallow intertrough, growth lines continuous across intertrough, deflected dorsally. Internally, apical process plugging apical half of valve; process consisting of successive laminae forming complete partitions between valve walls and separated by pillars. Surface of apical process with median ridge bounded laterally by bacculate *vasula lateralia.* Internal pedicle tube embedded in apical process, adjacent to, but not on, posterior sector of valve, terminating in small, subcircular pedicle opening.

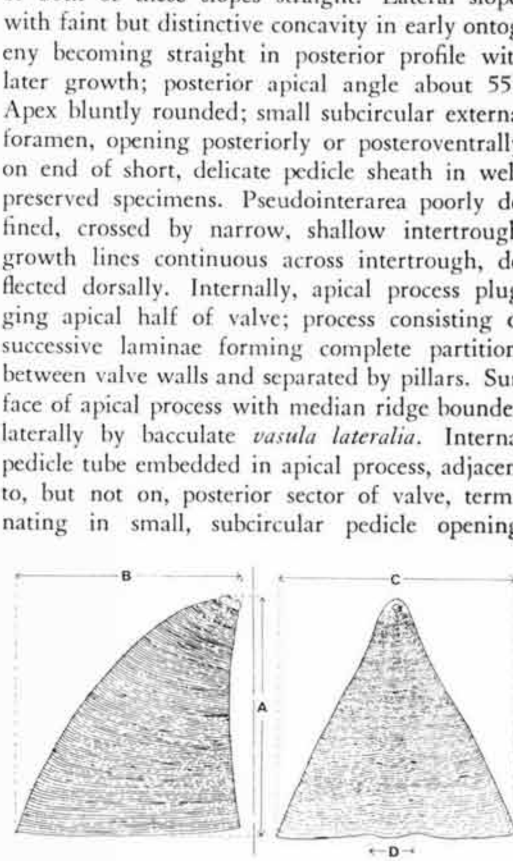

FIG. 2. Diagrammatic representation of the location of measurements on the ventral valve of *Dactylotreta redunca.*

TABLE 1. *Basic Statistics of* Dactylotreta redunca *Ventral Valve. (Measurements in mm as in Fig. 2.)*

	A	B	C	D
Vector of Means				
	0.80	0.79	0.87	0.20
Variance–Covariance Matrix				
A	0.0196			
B	0.0164	0.0159		
C	0.0194	0.0181	0.0218	
D	0.0024	0.0022	0.0025	0.0006
	A	B	C	D

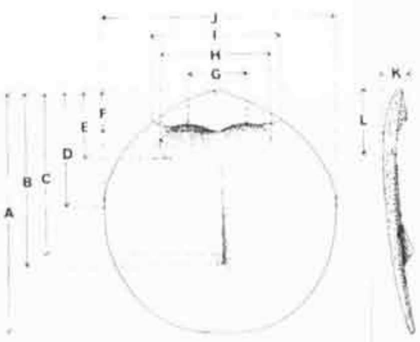

FIG. 3. Diagrammatic representation of the location of measurements on the dorsal valve of *Dactylotreta redunca*.

Apical process commonly broken immediately anterior of pedicle opening. Apical pits well defined, immediately dorsal of pedicle opening, close together on posterior sector of valve; cardinal muscle scars posterolaterally located.

Dorsal valve typically slightly longer than wide. In commissural view posterolateral margins nearly straight, subtending angle of about 120° at pointed apex. Protegulum with pair of nodes. Valve very gently convex, commonly almost flat, with shallow median sulcus arising short distance in front of apex and extending to valve margin. Pseudointerarea elongate with broad, weakly concave median plate separated by faint ridges from small, anacline propareas. Posterolateral and lateral margins of valve flattened to form brim. Cardinal muscle scars narrowly set, bounded laterally by brim and medially by cardinal buttress, anterior margin of scars poorly defined. Median septum low, narrow, triangular in profile, extending forward about two-thirds valve length, maximum height immediately behind anterior limit.

Material and stratigraphic horizon.—The species is presently known from approximately 100 valves. It occurs sporadically in the upper part of the *Stigmatoa diloma* Zone and in the overlying *Irvingella tropica* Zone of the Idamean Stage in the Georgina basin of Queensland.

TABLE 2. *Basic Statistics of* Dactylotreta redunca *Dorsal Valve. (Measurements in mm as in Fig. 3.)*

	A	B	C	D	E	F	G	H	I	J	K	L
Vector of Means												
	0.92	0.70	0.69	0.55	0.32	0.18	0.30	0.49	0.54	0.95	0.10	0.16
Variance–Covariance Matrix												
A	0.0219											
B	0.0144	0.0156										
C	0.0049	0.0090	0.0084									
D	0.0127	0.0081	0.0031	0.0071								
E	0.0060	0.0060	0.0027	0.0035	0.0032							
F	0.0034	0.0035	0.0017	0.0020	0.0018	0.0011						
G	0.0053	0.0049	0.0023	0.0030	0.0023	0.0014	0.0023					
H	0.0091	0.0096	0.0049	0.0052	0.0046	0.0028	0.0038	0.0089				
I	0.0104	0.0092	0.0035	0.0060	0.0044	0.0027	0.0039	0.0078	0.0092			
J	0.0214	0.0161	0.0098	0.0126	0.0083	0.0045	0.0073	0.0133	0.0133	0.0292		
K	0.0022	0.0023	0.0015	0.0011	0.0009	0.0005	0.0007	0.0014	0.0013	0.0031	0.0006	
L	0.0019	0.0000	0.0022	0.0011	0.0000	0.0000	0.0001	0.0000	0.0000	0.0014	0.0004	0.0046
	A	B	C	D	E	F	G	H	I	J	K	L

Genus QUADRISONIA
Rowell and Henderson, new

Type species.—*Quadrisonia minor* ROWELL AND HENDERSON, n. sp.

Diagnosis.—Ventribiconvex Acrotretinae; ventral valve procline to catacline; ventral pseudointerarea narrow, externally concave or planar, undivided or with a very shallow intertrough. Apical process bridging posterior and anterior internal surfaces, extending forward along the latter, variable in outline, commonly subrectangular to anteriorly expanding when adult, perforated posteriorly by internal pedicle tube, maximum height of process immediately in front of pedicle opening, anteriorly descending gently to valve floor. Dorsal valve with narrow, typically orthocline propareas; median septum low to absent, never reaching level of commissure plane, commonly a rounded ridge.

Remarks.—The genus is presently represented by four species. In Australia it ranges through most of the Idamean and occurs in association with pre-Payntonian A assemblages. Within North America it is currently known only from the Franconian *Elvinia* and *Taenicephalus* zones, where it is locally abundant.

In its gross morphology, the ventral valve is externally similar to that of many of the Linnarssoniinae, particularly *Linnarssonia* Walcott and *Pegmatreta* Bell. The presence of a deeply incised intertrough in species of the latter two genera allows them to be readily distinguished from *Quadrisonia*. There are further differences. The cardinal muscle scars of *Linnarssonia* are typically set on raised bases. Moreover, the dorsal valve of *Quadrisonia* has well-defined propareas, even in juvenile specimens. The dorsal propareas of the Linnarssoniinae are vestigal in young forms and are inconspicuous even in larger specimens.

Considerable variation exists in the form of the apical process, even between individuals of one species obtained from the same sample. The variation is, in part, a function of the age of the individual and is controlled largely by the degree of development of medial trunks of the *vascula lateralia*. This variation is discussed in more detail for the type species, *Q. minor*.

The dorsal valve of all four species shows less variation. The posterior margin is typical of the Acrotretinae: a conspicuous concave median plate divides the pseudointerarea into two narrow, typically orthocline propareas; the median plate is supported by a modestly developed median buttress. The median septum shows more interspecific variation. Commonly it is a broad, rounded ridge, but may form a low blade or, at the other extreme, be absent. It commonly arises at or slightly in front of the median buttress and extends forward half to three-quarters of the valve length.

QUADRISONIA MINOR
Rowell and Henderson, new species

Figures 4-6; Tables 3, 4; Plate 1, figure 9; Plate 2, figures 1-6

Holotype.—UKMIP 115501.

Diagnosis.—*Quadrisonia* with dorsal valve not thickened posteriorly, median septum a low ridge, beak of ventral valve in posterior quarter of valve length.

Description.—Shell ventribiconvex, valves typically thin and translucent when wet. Protegulum with fine pitted ornament, post-protegular ornament of delicate, closely spaced, concentric growth lines.

Ventral valve typically 10 to 20 percent wider than long, maximum height about 35 to 40 percent of valve length, occurring at the beak. Commissural outline with straight posterior margin, strongly rounded lateral margins, and more gently curved anterior margin. Valve procline, beak typically situated 5 to 10 percent of valve length in front of posterior margin. In lateral profile, posterior slope straight, becoming concave apically, concavity formed by apex overhanging ventral pseudointerarea; anterior slope straight, or slightly concave immediately in front of beak, becoming externally convex near front of valve. Lateral slopes straight to gently convex in posterior profile. Pseudointerarea essentially flat, apical angle approximately 80°, lateral margins with flanks of valve not clearly demarcated. Free margin of pseudointerarea deflected dorsally to produce medial projection; growth lines continuous across pseudointerarea with slight medial bow, forming trace of projection, sometimes bearing exceedingly shallow intertrough. External pedicle opening circular, posteriorly directed, borne on short pedicle sheath in well-preserved specimens. Internally, apical process anteriorly expanding, lying mostly on anterior slope of valve, typically extending to 30 to 40 percent of valve length. Process pierced posteriorly by internal pedicle opening, whose anterior surface grooves process. Major trunks of *vascula lateralia* diverging anterolaterally from apex, each trunk with medially directed branch arising short distance in front of valve apex. Apical pits on lateral slopes of apical process, immediately lateral of internal pedicle opening. Cardinal muscle scars on posterolateral flanks of valve.

Dorsal valve typically 10 to 20 percent wider than long. In commissural outline posterolateral margins of valve subtending angle of 140 to 160° at obtusely pointed apex. Valve gently and rather evenly convex, maximum height typically 15 to 20 percent of valve length attained between a third and half valve length in front of beak. Pseudointerarea well developed, broad concave median plate separating orthocline to slightly anacline triangular propareas. Central part of median plate supported by median buttress; lateral sectors of plate and median part of propareas projecting as narrow shelf into valve, overhanging posterior region of cardinal muscle scars. Cardinal muscle scars closely set on posterior part of valve immediately in front of pseudointerarea, laterally bounding the median buttress. Low median ridge arising in front of buttress and extending forward to center of valve, more rarely terminating about two-thirds of valve length in front of beak. Pair of small central scars lateral to median ridge about 40 percent of valve length in front of beak, sometimes forming low radial muscle tracks.

Remarks.—The species shows considerable variation in the form of the apical process, particularly its outline. This variation is closely related

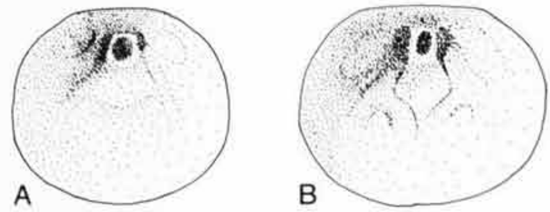

FIG. 4. Variation in form of apical process of *Quadrisonia minor*.

to the depth of insertion and degree of development of the mantle canal pattern, which, in turn, is related to the size of the shell. In young individuals (Fig. 4A), the lateral boundaries of the process are bordered by the major trunks of the diverging *vascula lateralia*. Maximum height of the process occurs immediately in front of the internal pedicle opening, and the surface of the process descends to merge with the valve floor. In older specimens (Fig. 4B) medially directed branches from the main trunks of the mantle canals may cut across and into the front of the

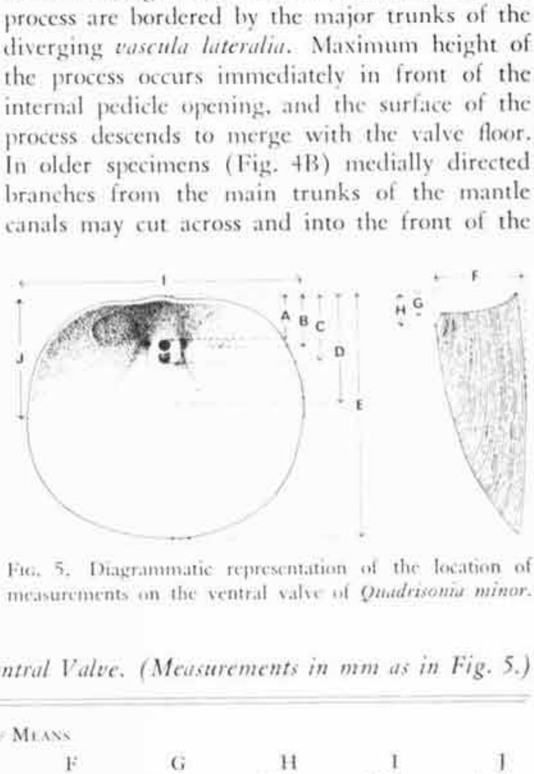

FIG. 5. Diagrammatic representation of the location of measurements on the ventral valve of *Quadrisonia minor*.

TABLE 3. *Basic Statistics of* Quadrisonia minor *Ventral Valve. (Measurements in mm as in Fig. 5.)*

VECTOR OF MEANS

A	B	C	D	E	F	G	H	I	J
0.22	0.34	0.36	0.55	1.41	0.53	0.13	0.13	1.62	0.69

VARIANCE–COVARIANCE MATRIX

A	0.0026									
B	0.0000	0.0050								
C	0.0029	0.0028	0.0065							
D	0.0050	0.0018	0.0116	0.0209						
E	0.0044	0.0053	0.0141	0.0251	0.0591					
F	0.0018	0.0023	0.0057	0.0119	0.0219	0.0122				
G	0.0005	0.0005	0.0016	0.0018	0.0015	0.0019	0.0020			
H	0.0005	0.0005	0.0016	0.0018	0.0015	0.0019	0.0020	0.0020		
I	0.0046	0.0080	0.0211	0.0347	0.0745	0.0296	0.0036	0.0036	0.1072	
J	0.0026	0.0038	0.0089	0.0154	0.0254	0.0097	0.0010	0.0010	0.0377	0.0176
	A	B	C	D	E	F	G	H	I	J

TABLE 4. *Basic Statistics of* Quadrisonia minor *Dorsal Valve. (Measurements in mm as in Fig. 6.)*

	VECTOR OF MEANS												
	A	B	C	D	E	F	G	H	I	J	K	L	M
	1.40	0.82	0.72	0.35	0.15	0.71	0.38	0.73	0.69	0.46	1.59	0.20	0.53
	VARIANCE–COVARIANCE MATRIX												
A	0.1034												
B	0.0757	0.0632											
C	0.0410	0.0291	0.0212										
D	0.0244	0.0219	0.0106	0.0144									
E	0.0123	0.0100	0.0058	0.0039	0.0022								
F	0.0522	0.0383	0.0199	0.0117	0.0059	0.0270							
G	0.0260	0.0209	0.0118	0.0102	0.0042	0.0122	0.0131						
H	0.0443	0.0292	0.0142	0.0152	0.0063	0.0204	0.0206	0.0298					
I	0.0532	0.0403	0.0231	0.0128	0.0075	0.0263	0.0153	0.0229	0.0318				
J	0.0311	0.0197	0.0133	0.0044	0.0035	0.0153	0.0085	0.0114	0.0169	0.0159			
K	0.1211	0.0892	0.0526	0.0281	0.0144	0.0615	0.0291	0.0545	0.0630	0.0390	0.1494		
L	0.0069	0.0033	0.0062	0.0007	0.0007	0.0034	0.0016	0.0057	0.0033	0.0030	0.0081	0.0026	
M	0.0486	0.0398	0.0233	0.0142	0.0053	0.0260	0.0133	0.0206	0.0237	0.0133	0.0603	0.0038	0.0334
	A	B	C	D	E	F	G	H	I	J	K	L	M

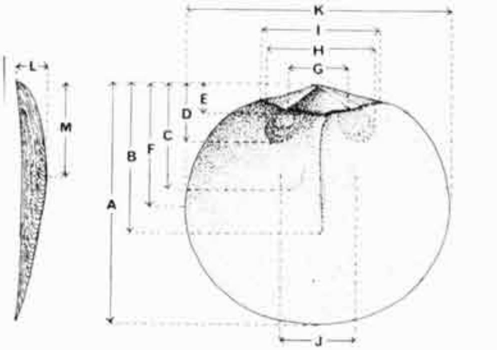

FIG. 6. Diagrammatic representation of the location of measurements on the dorsal valve of *Quadrisonia minor.*

apical process, giving it a pointed, almost diamond-shaped outline.

Material and stratigraphic horizon.—The species is known from approximately 200 valves. It is common in the uppermost beds of the *Elvinia* Zone of western Utah and occurs more rarely at this stratigraphic level in eastern and central Nevada. The species is also locally abundant in the basal 5 cm of the overlying *Taenicephalus* Zone in Utah.

Subfamily LINNARSSONIINAE Rowell, 1965

Genus ANABOLOTRETA Rowell and Henderson, new

Type species.—*Anabolotreta tegula* ROWELL AND HENDERSON, n. sp.

Diagnosis.—Biconvex, procline Linnarssoniinae, ventral pseudointerarea weakly concave externally or flat, intertrough weakly developed to absent; apical process low, elongate, subtriangular, grooved from crest to internal pedicle foramen. Dorsal valve lacking median buttress, with or without low median ridge.

Remarks.—The genus is presently known from two species. The type species, an Australian form, occurs in the uppermost Middle Cambrian and the lower part of the Mindyallan. The second species occurs in slightly younger strata of the "*Crepicephalus*" and lower *Aphelaspis* zones of the Great Basin of the United States. The two species may be readily distinguished from each other in that the Australian taxon has a well-developed lamellose ornament and, characteristically, is substantially smaller than the American species.

The genus, along with *Opisthotreta* Palmer, is one of the youngest of the Linnarssoniinae, a group that is numerically more abundant in Middle Cambrian rocks. *Opisthotreta* differs from *Anabolotreta* in having an apsacline ventral pseudointerarea, which is strongly demarcated from the lateral flanks of the valve, and in possessing only a minute apical process. *Linnarssonia* Walcott and *Pegmatreta* Bell show the greatest resemblance to the new genus. Rowell (1965, 1966) regarded *Pegmatreta* as a junior synonym of *Linnarssonia;* the two taxa are undoubtedly very similar, but this action may have been premature. The type species of neither genus is known from etched material and consequently some of the details of valve morphology are inadequately understood. However, the morphological differences between the two type species, *Linnarssonia transversa* (Hyatt) and *Pegmatreta perplexa* Bell, seem to be characteristic of two groups of species. The two groups differ primarily in the form of the apical process and, to a lesser extent, in the development of muscle bases. At least until these Middle Cambrian taxa are adequately monographed, there would seem to be advantages in recognizing these two groups of species as genera. The name *Linnarssonia* would then be restricted to those species with a high, pillarlike apical process and thickened, slightly elevated cardinal muscle scar bases. *Pegmatreta* would be used for species that are externally similar but have a relatively low, almost hemispherical apical process and lack pronounced thickening of muscle scar bases. With this suggested usage, *Anabolotreta* is morphologically most similar to *Pegmatreta*, and the two are probably cladistically related. The new genus, however, may be distinguished from *Pegmatreta* by its lack of a well-defined, relatively deep intertrough and by details of the form of the apical process.

Neotreta Sobolev, an Upper Cambrian genus from the Khabarovsk region of the eastern Soviet Union, has tentatively been referred to the Linnarssoniinae (Sobolev, 1976). The genus differs from *Anabolotreta*, and indeed any other described acrotretid, in its subequal biconvex form and exceedingly low catacline ventral pseudointerarea.

ANABOLOTRETA TEGULA
Rowell and Henderson, new species

Figures 7, 8; Tables 5, 6; Plate 2, figures 7-14

Holotype.—JCF 10311.

Diagnosis.—*Anabolotreta* with well-developed lamellose ornament on both valves.

Description.—Shell small, wider than long, maximum width occurring slightly in front of midlength of valve. Ventral valve low, subconical, procline, slightly higher than dorsal valve,

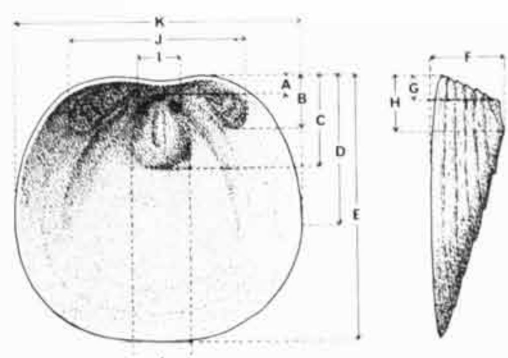

FIG. 7. Diagrammatic representation of the location of measurements on the ventral valve of *Anabolotreta tegula*.

TABLE 5. *Basic Statistics of* Anabolotreta tegula *Ventral Valve. (Measurements in mm as in Fig. 7.)*

	A	B	C	D	E	F	G	H	I	J	K	L
VECTOR OF MEANS	0.07	0.18	0.26	0.36	0.68	0.20	0.04	0.15	0.19	0.36	0.77	0.18
VARIANCE–COVARIANCE MATRIX												
A	0.0085											
B	0.0003	0.0011										
C	0.0004	0.0012	0.0035									
D	0.0004	0.0015	0.0030	0.0054								
E	0.0008	0.0027	0.0051	0.0093	0.0163							
F	0.0002	0.0008	0.0014	0.0023	0.0039	0.0013						
G	0.0000	0.0004	0.0007	0.0010	0.0020	0.0004	0.0005					
H	0.0000	0.0006	0.0005	0.0009	0.0020	0.0003	0.0006	0.0015				
I	0.0000	0.0008	0.0005	0.0009	0.0018	0.0005	0.0004	0.0006	0.0009			
J	0.0005	0.0011	0.0021	0.0037	0.0067	0.0017	0.0008	0.0009	0.0008	0.0031		
K	0.0011	0.0030	0.0060	0.0104	0.0182	0.0044	0.0021	0.0020	0.0021	0.0074	0.0206	
L	0.0000	0.0002	0.0007	0.0012	0.0022	0.0004	0.0002	0.0002	0.0001	0.0010	0.0024	0.0008
	A	B	C	D	E	F	G	H	I	J	K	L

ornament of later growth stages of both valves of fine, irregular, anastomosing growth lines together with conspicuous growth lamellae, frequency of lamellae variable.

Ventral valve with broad, externally concave pseudointerarea, typically with poorly developed intertrough; commissural margin of pseudointerarea bowed dorsally. Valve outline in commissural plane with anterior and lateral margins broadly rounded, posterior margin concave, reflecting pseudointerarea. Posterior and anterior slopes nearly straight in lateral profile, lateral flanks gently convex to nearly straight in posterior profile, profiles invariably interrupted by steplike growth lamellae. Pedicle foramen small, subcircular, apical. Internally, apical process low, broad, typically subtriangular, anterior margin broadly rounded, rising smoothly to poorly defined apex near its anterior margin, posterior slope grooved, groove reaching to internal foramen. Apical pits weakly indented, adjacent to apical process, immediately anterior of internal foramen. Cardinal scars lobate, weakly impressed, posterolaterally located, separated by broad *vascula lateralia* from apical process.

Dorsal valve gently convex in lateral and anterior profile, maximum height half of valve length, occurring in front of midlength of valve. Pseudointerarea not strongly developed, orthocline, with concave, triangular median plate bordered by minute propareas.

Remarks.—The species shows considerable variation in the development of growth lamellae (compare Pl. 2, fig. 10a,11b), and in extreme variants they are entirely lacking. Variation occurs both within and between samples but shows no stratigraphically significant pattern. It may be environmentally rather than genetically induced.

Material and stratigraphic horizon.—The species is known from approximately 250 valves. It is represented by sparse specimens from the *Lejopyge laevigata* Zone of the Middle Cambrian and is abundant in the lower part of the Mindyallan Stage of the Georgina basin of Australia.

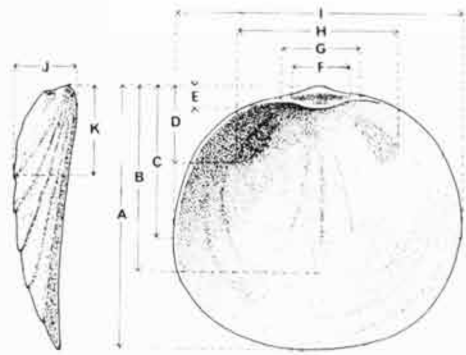

FIG. 8. Diagrammatic representation of the location of measurements on the dorsal valve of *Anabolotreta tegula*.

TABLE 6. *Basic Statistics of* Anabolotreta tegula *Dorsal Valve. (Measurements in mm as in Fig. 8.)*

VECTOR OF MEANS

A	B	C	D	E	F	G	H	I	J	K
0.72	0.51	0.37	0.23	0.06	0.12	0.19	0.38	0.80	0.17	0.21

VARIANCE–COVARIANCE MATRIX

	A	B	C	D	E	F	G	H	I	J	K
A	0.0157										
B	0.0102	0.0133									
C	0.0084	0.0060	0.0051								
D	0.0041	0.0042	0.0020	0.0024							
E	0.0011	0.0004	0.0005	0.0004	0.0001						
F	0.0018	0.0014	0.0009	0.0007	0.0001	0.0006					
G	0.0023	0.0018	0.0012	0.0006	0.0001	0.0003	0.0004				
H	0.0060	0.0059	0.0028	0.0027	0.0005	0.0008	0.0010	0.0052			
I	0.0162	0.0109	0.0086	0.0047	0.0013	0.0017	0.0024	0.0068	0.0176		
J	0.0030	0.0021	0.0015	0.0009	0.0002	0.0004	0.0005	0.0013	0.0031	0.0009	
K	0.0047	0.0026	0.0024	0.0010	0.0003	0.0006	0.0007	0.0016	0.0046	0.0009	0.0019
	A	B	C	D	E	F	G	H	I	J	K

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EXPLANATION OF PLATES

PLATE 1

FIGURE

1-8. *Dactylotreta redunca* Rowell & Henderson, n. gen. and sp., Georgina Limestone, Glenormiston district, western Queensland. ——1a,b. Internal and external views of ventral valve, JCF 10304, Locality L423, ×40. ——2. Internal view of ventral valve, JCF 10305, Locality L423, ×40. ——3a,b. External and internal views of ventral valve, JCF 10306, Locality L423, ×50. ——4a,b. Anterior and lateral views of ventral valve, JCF 10307, Locality L423, ×30. ——5a,b. Posterior and lateral views of ventral valve, JCF 10308, Locality L423, ×30. ——6a,b. External and internal of dorsal valve, holotype JCF 10309, Locality L138, ×40. ——7a,b. Ventral valve broken longitudinally to show construction of apical process, Locality L423 (specimen discarded), ×35 and enlargement ×600. ——8a,b. Internal and posterior views of dorsal valve, JCF 10310, Locality L423, ×40.

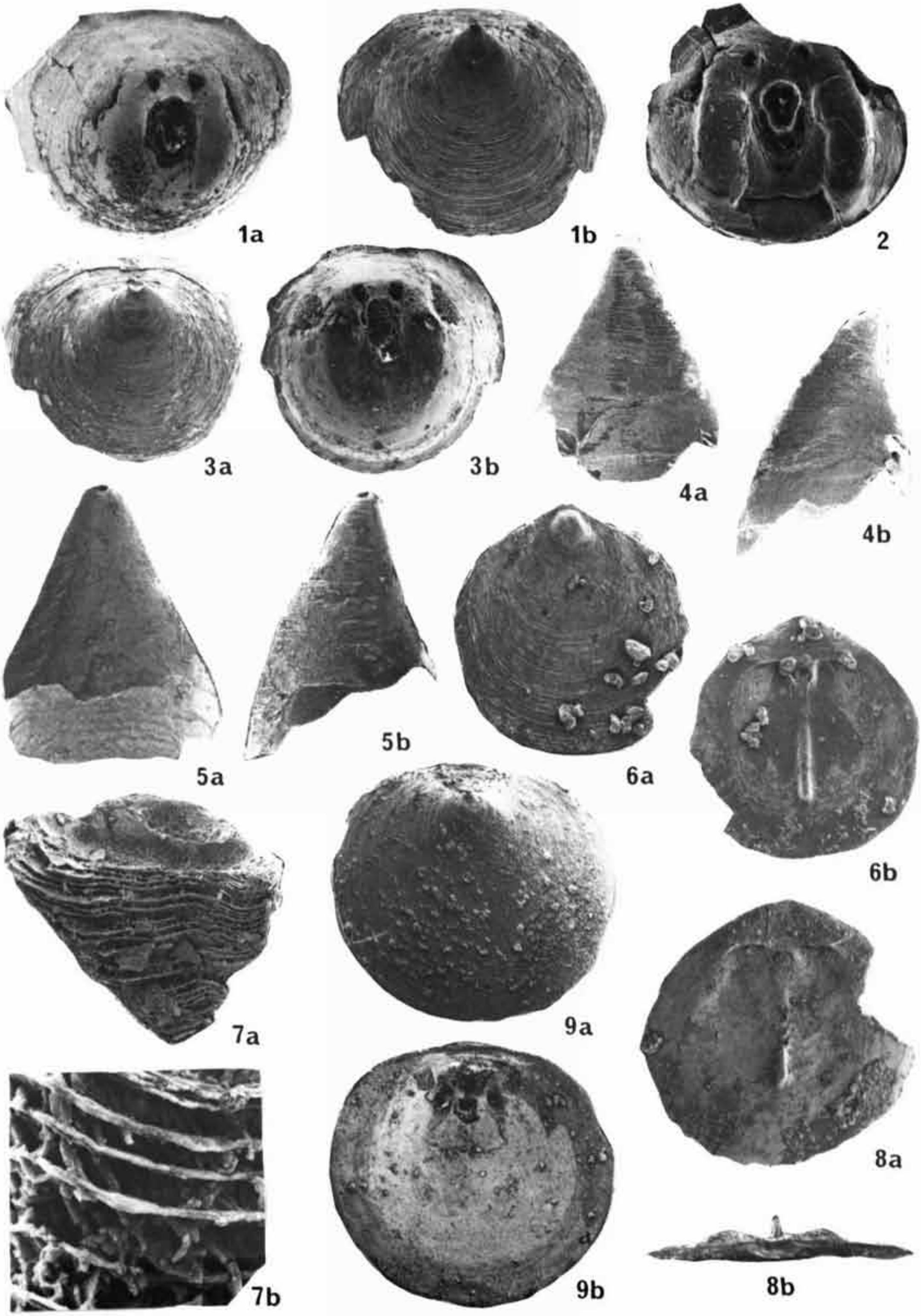
9a,b. *Quadrisonia minor* Rowell & Henderson, n. gen. and sp., *Taenicephalus* Zone, Orr Formation, Steamboat Pass, Utah. External and internal views of ventral valve, UKMIP 115502, Locality 75/20, ×25.

PLATE 2

FIGURE

1-6. *Quadrisonia minor* Rowell & Henderson, n. gen. and sp., Locality 75/20—*Taenicephalus* Zone, Orr Formation, Steamboat Pass, Utah. Locality 74/139—***Elvinia*** Zone, Windfall Formation, Cherry Creek, Nevada. ——1a-c. Internal, external and lateral views of ventral valve, UKMIP 115503, Locality 75/20, ×25. ——2a,b. Internal and lateral views of ventral valve, holotype UKMIP 11501, Locality 75/20, ×25. ——3. Internal of ventral valve, UKMIP 115504, Locality 74/139, ×20. ——4. Internal of ventral valve, UKMIP 115505, Locality 75/20, ×25. ——5a-c. External, lateral, internal views of dorsal valve, UKMIP 115506, Locality 75/20, ×25. ——6. Internal view of dorsal valve, UKMIP 115507, Locality 75/20, ×25.

7-14. *Anabolotreta tegula* Rowell & Henderson, n. gen. and sp., Mungerebar Limestone, Dajarra district, western Queensland. ——7a,b. Lateral and posterior views of whole specimen, CPC 17933, Locality G8, ×40. ——8. Internal view of ventral valve, holotype JCF 10311, Locality L192, ×40. ——9. Exterior view of ventral valve, CPC 17934, Locality G8, ×40. ——10a,b. External and internal views of dorsal valve, CPC 17935, Locality G8, ×40.——11a,b. Internal and external views of dorsal valve, JCF 10312, Locality L212, ×30. ——12. Internal view of ventral valve, CPC 17936, Locality G8, ×40. ——13. Internal view of ventral valve, JCF 10313, Locality L191, ×40. ——14a,b. Lateral and posterior views of whole specimen, CPC 17937, Locality G412, ×60.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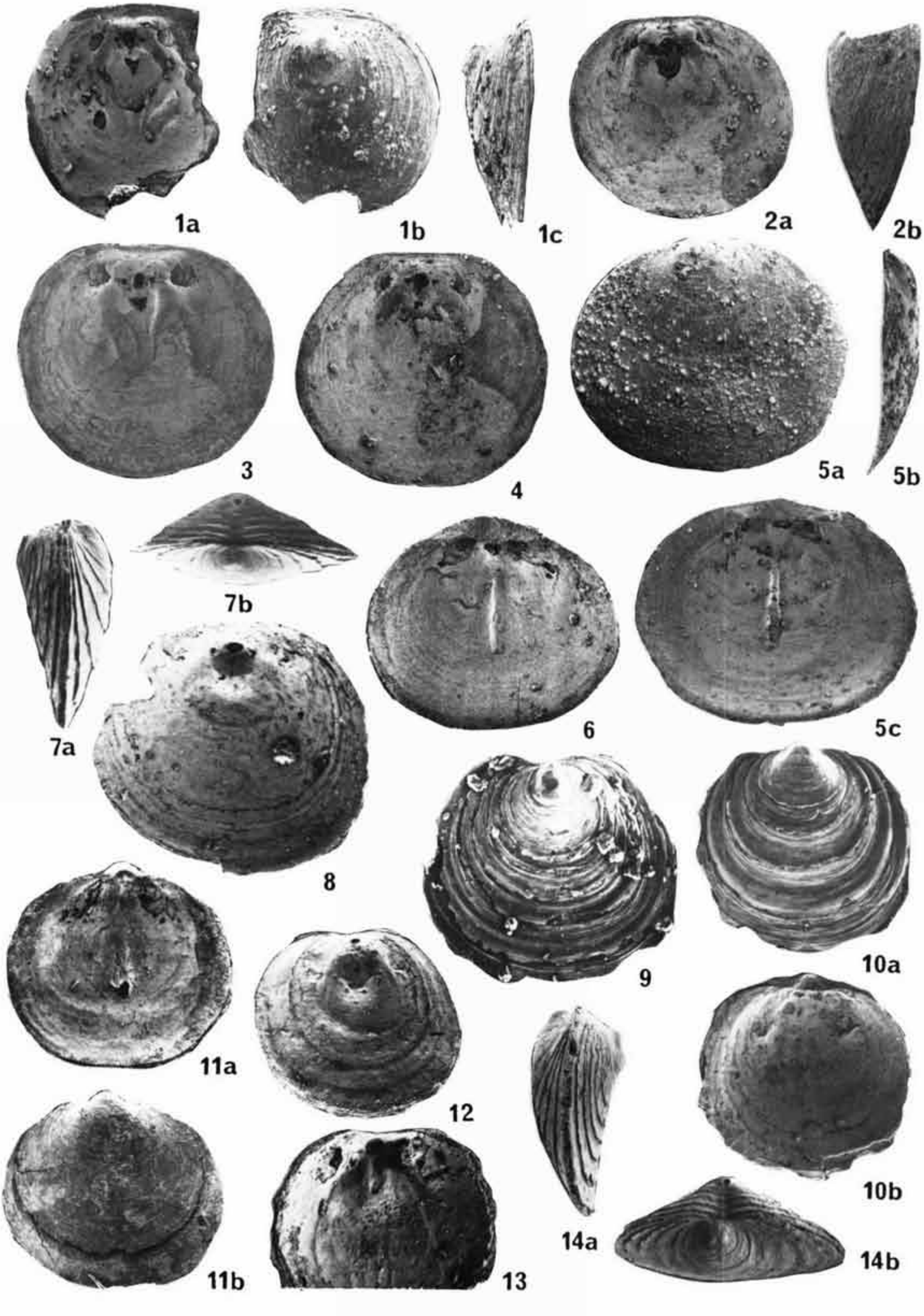
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