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DEPARTMENT OF ENERGY, MINES AND RESOURCES

BULLETIN 235

CONTRIBUTIONS TO CANADIAN PALEONTOLOGY

(three papers)

A. J. Boucot, J. G. Johnson, Rolf Ludvigsen
and D. G. Perry

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PREFACE

From time to time it is appropriate to issue several papers on paleontological topics as a single volume under the general title *Contributions to Canadian Paleontology*. This Bulletin contains three papers that present detailed descriptions of Silurian and Devonian brachiopods. Such taxonomic studies provide the basis for precise paleontological determinations that are critical to accurate dating and to stratigraphic and economic analyses of the rocks that form the sedimentary basins of Canada.

D. J. MCLAREN,

Director, Geological Survey of Canada

OTTAWA, April 5, 1974

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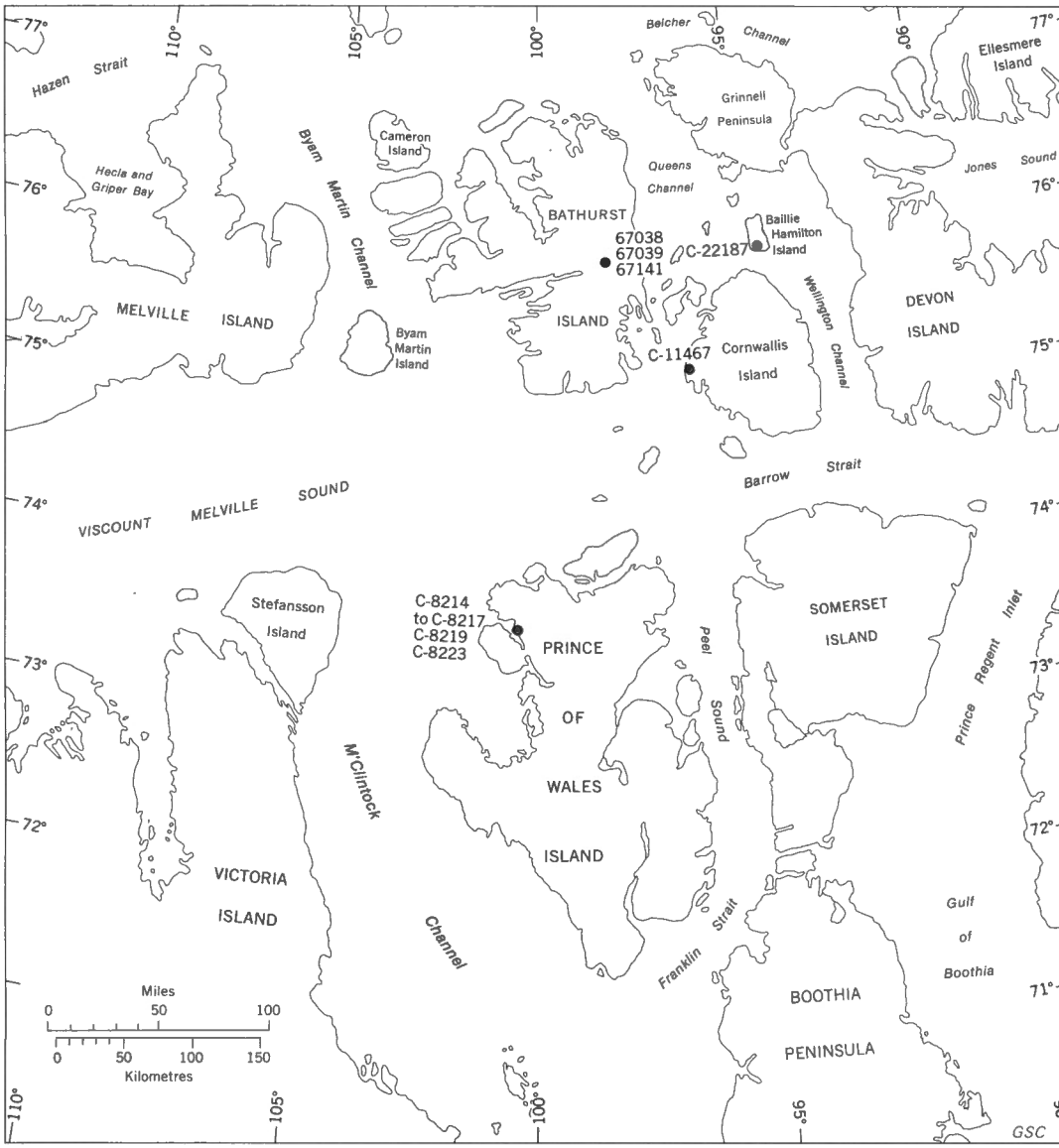

TEXTFIGURE 1. Locality map showing the source of *Quadrithyris* Zone brachiopod collections from the Canadian Arctic Islands (Johnson paper); also showing *Tryblidium* locality (Boucot paper).

TRYBLIDIUM THORSTEINSSONI; FIRST NORTH AMERICAN OCCURRENCE OF THE SILURIAN MONOPLACOPHORAN GENUS

by A. J. Boucot[1]

Abstract

A new species is described, based on a single specimen obtained from etching Wenlockian limestones of the Cape Phillips Formation from Baillie Hamilton Island.

Résumé

L'auteur décrit une nouvelle espèce d'après l'examen d'un échantillon recueilli à l'île Baillie Hamilton et dégagé par décapage des calcaires wenlockiens de la formation de Cape Phillips.

Introduction

The Silurian monoplacophoran genus *Tryblidium* Lindstrom 1880, although well known from Gotland (Lindstrom, 1884), previously has not been reported from North America. In 1971, while attached to a field party headed by R. Thorsteinsson, the author collected a single specimen of *Tryblidium* on the south coast of Baillie Hamilton Island in the Canadian Arctic Archipelago (Textfig. 1, GSC loc. C-22187; UTM Zone 15, 459700 m.E., 8407700 m.N.). The specimen was obtained from a single bed of limestone, replete with silicified brachiopods and lesser amounts of other invertebrates, within the Cape Phillips Formation of dominantly graptolitic shale facies. According to Thorsteinsson (verbal com.), graptolites stratigraphically below and above the bed yielding *Tryblidium* indicate a Wenlockian age.

Acknowledgments

The manuscript benefited from critical reading by R. Thorsteinsson. D. G. Lawrence made the photographs.

Systematic Paleontology

Prefix GSC refers to specimens in the type collections of the Geological Survey of Canada, Ottawa.

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Phylum **MOLLUSCA**

Class ***MONOPLACOPHORA***

Family TRYBLIDIIDA Pilsbry *in* Zittel-Eastman, 1899

Genus ***Tryblidium*** Lindstrom, 1880

Tryblidium thorsteinssoni new species

Plate I, figures 1–5

Diagnosis. Tryblidium thorsteinssoni possesses closely spaced, high, reticulate, thin, frilled lamellae covering the entire shell.

Description. The single specimen (holotype GSC 32601) has an oval, longitudinally elongate outline, slightly less pointed anteriorly than posteriorly. The outer shell surface is covered by an intersecting set of reticulate, frilly, high, thin lamellae. The lamellae originate on either side of the valve, beginning in the umbonal region and then having the point of origin moving forward with increase in shell size. The shell is gently convex both laterally and longitudinally. Since this specimen is relatively small compared to normal specimens of *T. reticulatum*, it is possible, as suggested by Dr. Ellis Yochelson (pers. com.), that many of the features may be associated with an early growth stage. Internally the shell is smooth, there being no evidence for the well-impressed, paired muscle scars or the four concentric zones discussed by Knight and Yochelson (1960) for the genus. The absence both of these four inner concentric zones and of the paired muscle impressions may as well be a function of the small size as of any genetic difference; because of the presence of only a single specimen it would be unwise at this time to attach undue taxonomic significance to absence of internal impressions.

Comparison. Tryblidium thorsteinssoni exhibits reticulate growth lamellae over the entire shell surface whereas *T. reticulatum*, the type species from Gotland, is characterized by such lamellae only in the posterior part of the shell. Additionally, it is clear that the growth lamellae of *T. reticulatum* are far more widely spaced than those of *T. thorsteinssoni*. The lamellae of *T. reticulatum* originate in the umbonal region; those of *T. thorsteinssoni* along the entire lateral margins.

Discussion. One would not normally describe a new species based on a single specimen of a Silurian invertebrate. However, the rarity of early Paleozoic monoplacophorans and the first occurrence of *Tryblidium* in the North American record justify this departure.

Tens of thousands of silicified brachiopods were recovered by etching limestone from the collecting locality, together with a far smaller assortment of other silicified invertebrates. Among these other invertebrates the single specimen of *Tryblidium* was recovered from only one of the five beds containing silicified fossils that were sampled within the zone of *Monograptus riccartonensis*. This extreme rarity in such a large sample of invertebrate material points out the capricious nature of much sampling, particularly for rarer shells, and again calls into question any conclusions based on known distributions of extremely rare taxa.

Bassler (1915) has a number of listings for species of *Tryblidium*. Many of these have been reassigned to other genera, and those which still remain in the genus clearly should be be placed elsewhere. The generic name has been used as a catchall but, outside of the Gotland region, authentic *Tryblidium* is rare both in species and in individuals, though this is not suggested by the literature. Even on Gotland it is not easy to find specimens. During the

summer of 1956 I devoted six weeks to the collection of megafossils on Gotland, but during this work found not a single specimen of *Tryblidium* among many thousands of specimens.

Tryblidium thorsteinssoni is listed here as the "First North American Occurrence" of the genus. Northrop (1939, p. 205) lists the genus from the La Vieille Formation (Wenlockian age) of Gaspé, but gives no illustration of the specimen. His brief description suggests that the specimen is correctly assigned to *Tryblidium.* Through the courtesy of T. E. Bolton, Geological Survey of Canada, Ottawa, the author has borrowed Northrop's original material and finds that it consists of two fragments of shell, probably costate brachiopods, that certainly cannot be shown to be monoplacophorans. The specimens are labelled "*Tryblidium* sp., S.-La Vieille?, just above Island at Ruisseau Creux, Bonaventure River, P. Q., S. A. Northrop Collector, 1928."

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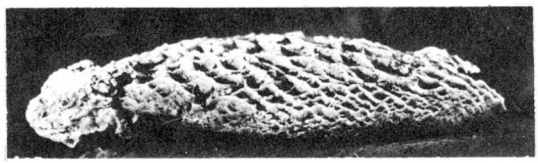
PLATE I



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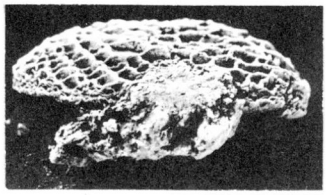

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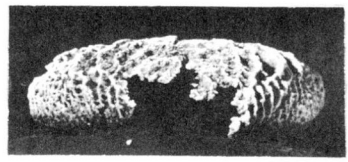

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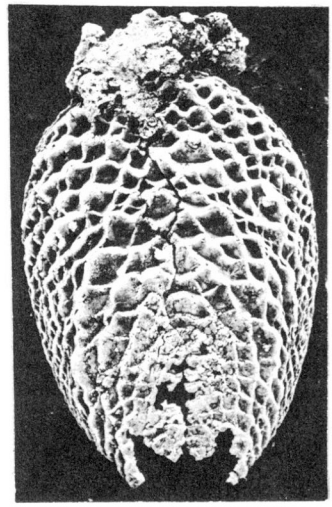

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Tryblidium thorsteinssoni new species

Figures 1–5. Side, anterior, posterior, interior, and exterior views of holotype (GSC 32601); GSC locality C-22187, Cape Phillips Formation, south shore of Baillie Hamilton Island; x3. The umbonal tip is broken (fig. 3); a mass of chert obscures the anterior margin (fig. 4).

DEVONIAN BRACHIOPODS FROM THE *QUADRITHYRIS* ZONE (UPPER LOCHKOVIAN), CANADIAN ARCTIC ARCHIPELAGO

by J. G. Johnson[1]

Abstract

The upper Lochkovian *Quadrithyris* Zone is recognized from Prince of Wales, Bathurst, and Cornwallis Islands, along the western side of the Boothia Uplift. Assemblages from the three islands represent as many faunal communities, each of which is uniquely correlative with the *Quadrithyris* Zone. Species of *Gypidula* and *Carinagypa* appear to be the most useful brachiopods for recognizing *Quadrithyris* Zone assemblages from community to community and for establishing long distance correlations of the zone. Conodonts in *Quadrithyris* Zone collections from Prince of Wales and Cornwallis Islands provide age determinations consistent with those based on brachiopods.

Quadrithyris Zone brachiopod collections from Prince of Wales Island are associated intimately with fossil fish collected and determined by Thorsteinsson and regarded by him as unquestionably older than some part of the upper Gedinnian of northwestern Europe. The *Quadrithyris* Zone and all its correlatives (e.g., upper Lochkovian zone of *Monograptus hercynicus*) must be placed well down in the Gedinnian rather than somewhere in the Rhenish Siegenian Stage.

Twenty-one brachiopod species are described and illustrated. *Carinagypa careopleura, Gypidula thorsteinssoni, Thliborhynchia kerri, Atrypa exquisita,* and *Pinguispirifer carlsi* are described as new species.

Résumé

La zone *Quadrithyris* du Lochkévien supérieur est identifiée à partir de l'île du Prince-de-Galles, de l'île Bathurst de l'île Cornwallis, le long du côté occidental du soulèvement de Boothia. Ces trois îles représentent autant de groupes fauniques et chacun d'eux a pour unique corrélation d'appartenir à la zone *Quadrithyris*. Les espèces de *Gypidula* et de *Carinagypa* s'avèrent les brachiopodes les plus utiles pour identifier les assemblages de la zone *Quadrithyris* d'un groupe et l'autre pour établir les corrélations éloignées de la zone. Les conodontes recueillis dans la zone *Quadrithyris* des îles du Prince-de-Galles et Cornwallis permettent des déterminations d'âge qui correspondent à celles que l'on obtient en se basant sur les brachiopodes.

Les collections de brachiopodes de la zone *Quadrithyris* de l'île du Prince-de-Galles sont intimement associées à un poisson fossile recueilli et identifié par Thorsteinsson et considéré par lui comme indubitablement plus ancien que certaine partie du Gédinnien supérieur du nord-ouest de l'Europe. La zone *Quadrithyris* et toutes

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celles qui lui sont corrélatives (ex. la zone du *Monograptus hercynicus* du Lochkovien supérieur) doivent être placées tout au bas du Gédinnien plutôt que dans l'étage siegenien rhéna.

Vingt et une espèces de brachiopodes sont décrites et illustrées. Les descriptions de nouvelles espèces sont celles des *Carinagypa careopleura*, des *Gypidula thorsteinssoni*, des *Thliborhynchia kerri*, des *Atrypa exquisita* et des *Pinguispirifer carlsi*.

Introduction

The decade of the 1960's was one of remarkable acceleration toward a first realistic understanding of biostratigraphy and correlation of the Late Silurian and of the Early Devonian. It became evident that the graptoloid graptolites continued, with an extensive development, through much of Early Devonian time; and it was the decade in which conodonts first were recognized as important biostratigraphic tools for the Early Devonian. A correlation scheme was developed in which brachiopod, graptolite, and conodont chronologies were interwoven into a zonal scheme of great utility in Europe, North Africa, Asia, western North America, and in Australia.

Because of the long-entrenched nature of the northwest European stage nomenclature of Gedinnian, Siegenian, and Emsian, those names were kept continually in use and loosely applied to the zonal scheme which was based on faunas that could be correlated. In addition, correlations based on very little faunal evidence were drawn between the Rhenish and Bohemian stratigraphic schemes.

We have reached a point in time in which a critical look is necessary at the standards that have lent their names to the stage nomenclature that has been utilized so long. The *Quadrithyris* Zone brachiopod fauna has a well-understood place in the faunal scheme in use today. Consequently, an accurate placement of this fauna in both the Rhenish and Bohemian stage schemes can lead to a significant increase in our understanding of those schemes.

Acknowledgments

J. W. Kerr and R. Thorsteinsson of the Geological Survey of Canada made the collections on which this paper is based. I thank them for the opportunity to study Arctic *Quadrithyris* Zone brachiopods and for stratigraphic information. T. T. Uyeno and Gilbert Klapper identified and dated conodonts from some of the collections and D. C. McGregor the palynomorphs. Peter Carls, Wurzburg, criticized the correlation chart and offered a number of valuable suggestions about European correlations. A. W. Norris and B. S. Norford assisted in the critical reading of the manuscript.

Preparation of internal moulds and serial sections was by Arlene Susan Demaris. Ink drawings were done by Mary Fischer. All photographs of fossils were by Nelson W. Shupe. Work at Corvallis was supported by the Earth Sciences Section, National Science Foundation (U.S.A.), NSF Grant GA-17647.

Correlation of *Quadrithyris* Zone with Rhenish and Bohemian Stages

The *Quadrithyris* Zone was defined at Coal Canyon in central Nevada (Johnson, 1965, p. 370) and subsequently has been identified at a number of localities along a sinuous strip from northeastern Nevada to southeastern California (Johnson, 1970).

The brachiopod fauna of the *Quadrithyris* Zone is principally of Old World type, allowing some conclusions to be drawn about its place in terms of the Old World stage nomenclature. However, its association with a graptolite sequence in the same stratigraphic sections was important. The earliest work of M. A. Murphy in the Coal Canyon section showed that the significant species *Monograptus hercynicus* Perner occurs only a few feet below the main outcropping ledge, which was the source of most *Quadrithyris* Zone brachiopod collections (Berry, 1967; Johnson and Murphy, 1969, fig. 2). Subsequent investigation of the beds with *Quadrithyris* Zone brachiopods at Coal Canyon yielded diagnostic conodonts including *Pedavis pesavis pesavis* (Bischoff and Sannemann) as well as form species *Spathognathodus transitans* Bischoff and Sannemann (Klapper, 1968). As these occurrences were becoming known, similar associations of brachiopods, monograptids, and conodonts were being reported from Yukon Territory (Lenz, 1968a; Klapper, 1969; Lenz and Jackson, 1971), where Lenz's *Spirigerina* Unit is another name for the *Quadrithyris* Zone.

Both in Nevada and in the Yukon, beds that yield *Pedavis pesavis pesavis* also yield brachiopods of the *Quadrithyris* Zone and these horizons follow closely above beds with *Monograptus hercynicus* (Johnson and Murphy, 1969; Lenz and Jackson, 1971, p. 5). The close stratigraphic association between the *Quadrithyris* Zone and *Monograptus hercynicus* is sufficient to accurately place the *Quadrithyris* Zone near the top of the Lochkovian of the Bohemian stage nomenclature. This is a useful correlation whose accuracy has never been debated.

The age assignment of the *Quadrithyris* Zone of Nevada in terms of the Rhenish stage nomenclature, utilizing brachiopods that have some value for correlation, is a different matter. Johnson (1965) suggested a correlation either with the upper Gedinnian or with the lower Siegenian of northwestern Europe. Later (Johnson, 1970, p. 43-48), the evidence was reviewed and a correlation of the *Quadrithyris* Zone with the lower Siegenian was suggested because *Quadrithyris* Zone brachiopods represent an evolutionary advancement over the brachiopod fauna of the Grès de Gdoumont of Belgium, once considered to be a marine equivalent of the upper Gedinnian (*see* the chart of Jaeger, 1965). Although the conclusion was reasonable, some guesswork was involved; the decision that the *Quadrithyris* Zone approximately represents the early Siegenian is now in serious doubt.

Evidence from two widely separated regions leads to a reappraisal of the *Quadrithyris* Zone correlations. In Spain, Carls and Gandl (1968, 1969) and Carls (1969) described sections with interbeds containing brachiopods, conodonts, and trilobites, and Carls (1969, p. 315 and Fig. 2) pointed out the occurrence of *Pedavis pesavis* within a few metres of the last occurrence of the early Gedinnian trilobite *Acastella tiro* (R. and E. Richter). This suggested a much earlier age than early Siegenian for the *Quadrithyris* Zone and a correlation well down in the Gedinnian. Later Carls (1971, p. 210), in a brief note discussing the age of the Grès de Gdoumont, pointed out that the fauna of that unit, as described by Boucot (1960), appears in Spanish sections in a position essentially pre-lower Gedinnian. A surprising consequence of this piece of information is the realization that, once the old acceptance of this fauna as being well up in the Gedinnian is dropped, it is easy to understand that the brachiopods of that formation could be latest Silurian, i.e., of Pridolian age. No *Cyrtina* has been reported from the Gdoumont fauna and the *Shaleria*, *Quadrifarius*, *Protochonetes*, and *Dolerorthis* are not found in the Devonian of Bohemia, Podolia, or Nova Scotia. *Quadrifarius* elsewhere is in beds well identified as of Pridolian age (e.g., Nova Scotia, Berdan *et al.*, 1969, p. 2167; and Podolia, Kozlowski, 1929, Pl. 10, figs. of *Delthyris magnus*). The terebratulid brachiopods of the Gdoumont fauna (Boucot, 1960) pose a final question. Do they occur stratigraphically higher than *Quadrifarius* and other brachiopods of Silurian aspect within the Grès de Gdoumont or with them? No Silurian terebratulid has yet been authenticated.

Irrespective of the solution to these questions, the *Quadrithyris* Zone brachiopods, judged younger than the fauna of the Grès de Gdoumont, need only be younger than basal Gedinnian so that Carls' evidence consistently points to an older age than early Siegenian, in terms of the Rhenish stage nomenclature.

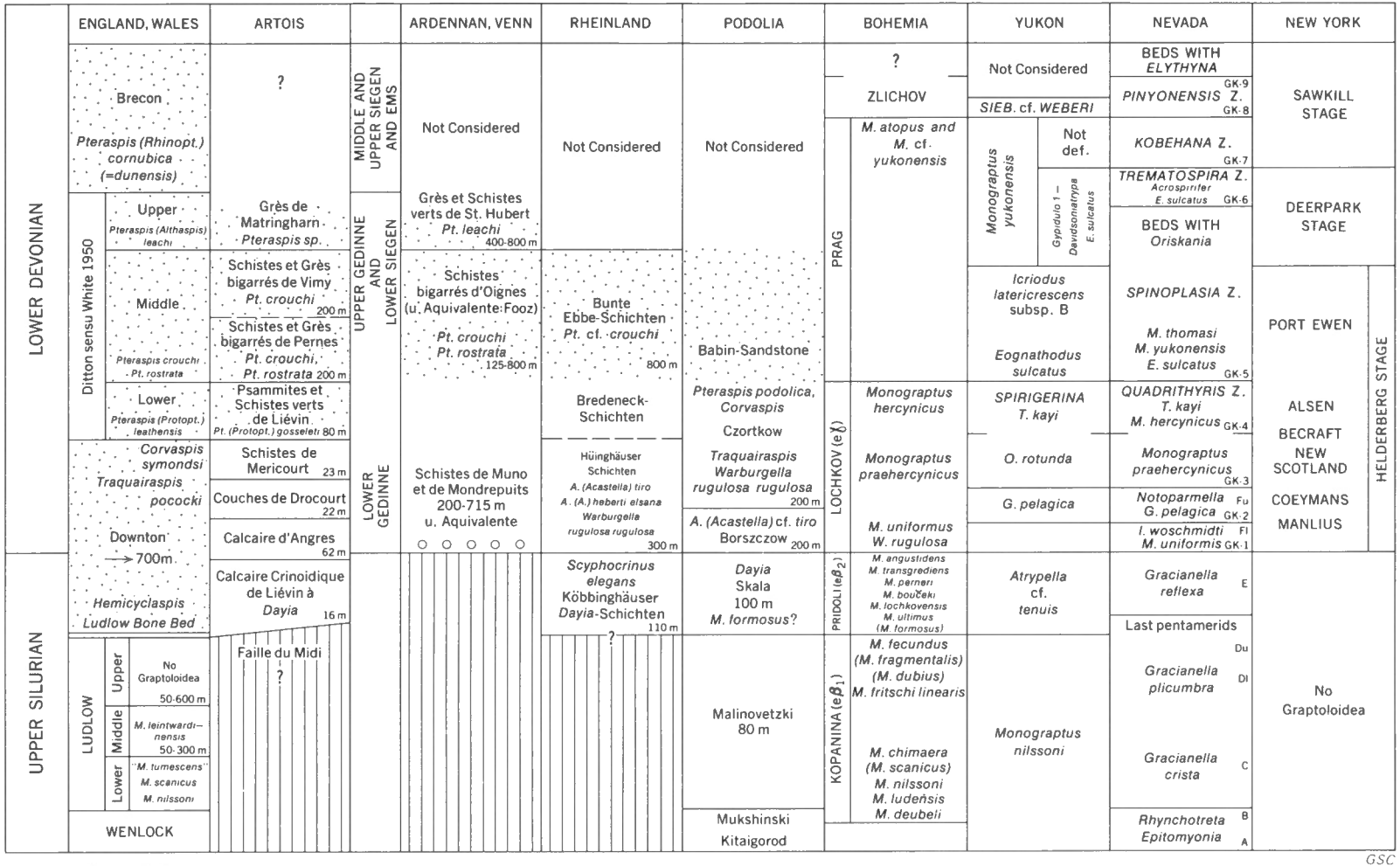
A second and very different line of evidence is provided by fish faunas being studied by R. Thorsteinsson and which were collected by him from strata interbedded with the *Quadrithyris* Zone faunas from western Prince of Wales Island. The fish obtained by Thorsteinsson, associated with the series of collections C-8214, C-8215, C-8216, C-8217, C-8219, and especially the nearby collection C-8223, are distinctly more primitive than the upper Gedinnian forms *Pteraspis crouchi* Lankester and *Pteraspis rostrata* (Asselberghs). Thorsteinsson (oral com., 1971) reported a form very similar to *Protopteraspis primaeva* (Kiaer) from Spitzbergen and *Protopteraspis gosseleti* Leriche from the Psammites de Liévin. The horizon with fish of the *Protopteraspis gosseleti* type (from northern France) and of the *Protopteraspis leathensis* White type (from the lower Dittonian of the Welsh Borderland) usually is correlated with the upper part of the lower Gedinnian (e.g., White, 1956, p. 5; Schmidt, 1960, Table 1, p. 140). Thus, the correlation for the Arctic *Quadrithyris* Zone brachiopods, suggested by the fish, is virtually the same as that suggested by completely different criteria developed by Carls—that the *Quadrithyris* Zone finds its position high in the lower Gedinnian, or possibly, low in the upper Gedinnian. This means that the Lochkovian of the Bohemian nomenclature is largely, if not wholly, lower Gedinnian. It seems likely, therefore, that part of the overlying Pragian is as old as the upper Gedinnian. This makes a consistent picture because, in Nevada, the *Howellella–Acrospirifer* transition (discussed below) occurs about at the *Spinoplasia* Zone-*Trematospira* Zone boundary—far above beds with *Monograptus hercynicus*. These correlations are expressed in Textfigure 2.

The brachiopod evidence of Solle (1963) was an important factor in correlating the upper Lochkovian zone of *Monograptus hercynicus* to the upper middle or upper Siegenian. Solle's conclusions were not widely accepted until Bouček (1966) demonstrated that monograptid graptolites occur in the upper Pragian of Bohemia; thereafter those conclusions were perhaps accepted uncritically. One can suggest, in agreement with Carls (1969, p. 323), that the poorly preserved specimen which was so fundamental to the conclusions of Solle (1963, Pl. 8, figs. 14a, 14b) is not so distinct that it can be assigned confidently to the post-Gedinnian.

Revisions of Brachiopod Ranges

Recognition that the *Quadrithyris* Zone of late Lochkovian age correlates to a level near the middle of the type Gedinnian requires revision of the ranges of a number of brachiopod genera which were at one time determined on the assumption that the *Quadrithyris* Zone was of Siegenian age. A number of Appalachian Province brachiopod genera fall in this category and include those listed in figure 6 of Boucot, Johnson, and Talent (1969).

Correlation of *Quadrithyris* Zone and upper Lochkovian to a position about at the middle of the Gedinnian also is significant to an understanding of the *Howellella–Acrospirifer* lineage. *Howellella* occurs in the Belgian Gedinnian and *Acrospirifer* has its oldest occurrence in the Rhenish Siegenian Stage. Johnson's (1970) assignment of the *Quadrithyris* Zone of central Nevada to the lower Siegenian ignored the fact that the *Howellella–Acrospirifer* transition occurs much higher in Nevada, near the top of the *Spinoplasia* Zone. It now appears that the best estimate for the top of the Gedinnian in the Nevada sequence should be approximately at the top of the *Spinoplasia* Zone. This is not based on direct correlation of fossils, but follows from a partitioning off of the Nevada zones between horizons that can be assigned ages on the basis of correlation. If the *Spinoplasia* Zone does indeed represent the



TEXTFIGURE 2 Correlation chart of lower Lower Devonian beds, zones, and significant fossil species of selected regions. The format of the left columns of the chart is from Jaeger (1965) with modifications. The principal departure from the correlations suggested by Jaeger is a considerable lowering, all across the right part of the chart in the marine sequence, of the *Quadrithyris* Zone, the upper Lochkov, and the *Monograptus hercynicus* Zone.

upper part of the Gedinnian, then it appears that the *Howellella–Acrospirifer* transition actually occurs very close to the Gedinnian–Siegenian stage boundary. The stratigraphic level of the *Howellella–Acrospirifer* transition thus may be very significant for intercontinental correlation.

Is Gedinnian a Viable Stage?

The term Gedinnian has had labelling value because it seemed to connote a single, simple biostratigraphic entity lacking a multiplicity of faunas between boundaries. Now, when the Gedinnian interval is seen to include a succession of distinguishable faunas in Nevada (Johnson, 1973b), its significance seems to have waned. It covers so long a time period that to say "the Gedinnian fauna" or "the Gedinnian Stage" is to be needlessly vague, and it is too poorly known faunally to have summary value.

Perhaps we should dare to ask if we would accept the Belgian Gedinnian as a standard if we could choose today. The fossil groups that have proven biostratigraphic value in this part of the column (graptolites and conodonts and, to a lesser extent, brachiopods, corals, and ostracodes) are absent or rare. There is no known succession of faunas through the stage in the type area. It is not in a single rock facies so that evolution of even a single faunal group can be studied. Faunally defined boundaries are virtually unknown or are unknowable in any detailed sense of which some use could be made today. The answer must be that, if we were searching today for stage stratotypes, the Belgian Gedinnian would not be considered.

If we are not to employ "Gedinnian" as a stage name, what are we to use? A new name? A new area? Pragmatism makes such sanguine notions unrealistic. Possibly a compromise solution will better suit immediate needs: i.e., use of the Bohemian stage names Lochkovian, Pragian, Zlichovian (Svoboda, 1960, p. 510, 511). These also have their deficiencies, but Lochkovian at least has the advantage of proceeding upward from the youngest Silurian stage, the Pridolian. The Lochkovian is graptolite-defined in simple, exposed fossiliferous sections (Horný, 1962; Chlupác, 1972). It can be correlated with many sections around the world. The Bohemian stage names exist now in Devonian stratigraphic nomenclature and can be used meaningfully as an expedient. Whether their use will be sanctioned by stratigraphic commissions that apply official stamp to a consensus of world specialists is a question still to be answered. For the present, realism in Lower Devonian correlation and age assignment can be served best by utilization of the Bohemian nomenclature.

Correlation of Arctic Brachiopod Assemblages

The assemblages of brachiopods in the several collections from Prince of Wales Island, Bathurst Island, and Cornwallis Island (Textfig. 2) are different for each island and have their own characteristics. They do not represent a single fauna, but they do represent a single brachiopod assemblage zone. Each group of collections is recognizable as of *Quadrithyris* Zone age (Johnson, 1970) on the basis of contained brachiopods, and a comparison of the faunal content of the three assemblages helps to delineate which fossils occur consistently as usable guides to the zone. With the aid of Table 1, these can be discussed individually.

Dolerorthis sp. occurs in only one collection. It is not significant because the genus occurs in younger beds in Yukon Territory (Lenz, 1968a) and in New South Wales, Australia (A. J. Wright, oral com.). *Schizophoria* sp. and *Protocortezorthis* cf. *P. fornicatimcurvata* have no value for detailed correlation and are not abundant in any collection. The presence of *Cortezorthis* cf. *C. windmillensis* indicates an age no older than *Quadrithyris* Zone because *C. windmillensis* is the initial species of the *Cortezorthis* lineage and the specimens from

TABLE 1 Distribution of species and number of individuals in *Quadrithyris* Zone collections from the Arctic Islands.

Species \ G.S.C. localities (see figure 1)	C-8214	C-8215	C-8216	C-8217	C-8219	C-8223	67038	67039	67141	C-11467
**Dolerorthis* sp.										3
Schizophoria sp.		2			1			1		7
**Protocortezorthis* cf. *fornicatimcurvata* (Fuchs)	1(?)									2
**Cortezorthis* cf. *windmillensis* (Johnson)										9
Leptaena sp. A Johnson					1(?)	1				2
Iridistrophia? sp.	2	2								3
**"Brachyprion" mirabilis* Johnson		1(?)			5		3	1	83	6(?)
"Chonetes" sp.									1	1
Anastrophia sp.									1	
**"Camerella"*? sp.							3			
**Gypidula thorsteinssoni* n. sp.	20		24	7	9	3	2		23	
**Carinagypa careopleura* n. sp.						1			28	6
**Gypidula* cf. *kayseri (*(Peetz)										25
**Procerulina*? sp.									2	
**Machaeraria* sp.	2	1			1			2	3	
**Thliborhynchia kerri* n. sp.							4			9
**Ancillotoechia* sp. A						2				
**Ancillotoechia* sp. B									2	6
**Katunia* sp.									2	
aff. *"Plethorhyncha" diana* (Barrande)									1	
indet. rhynchonellid				1		2	5		3	
**Atrypa exquisita* n. sp.									46	
**Atrypa* sp.	14	21	3	2	9	4	9	1		31
Spinatrypa sp.									1	
**Spirigerina supramarginalis* (Khalfin)							33	32		
**Dubaria* cf. *thetis* (Barrande)			1					5		
Toquimaella kayi Johnson									11	1
**Ogilviella* cf. *rotunda* Lenz							39	10		
Nucleospira sp.					2					
**Pinguispirifer carlsi* n. sp.									20	
**Undispirifer*? sp.			2	1	2	6				12
Cyrtina sp.							1			

*Species illustrated in this paper

GSC

Cornwallis Island have a slightly better developed median septum than do the Nevada specimens, suggesting at least a slight advance in development of the *Cortezorthis* morphology. *Leptaena* sp. A and *"Brachyprion" mirabilis* suggest the *Quadrithyris* Zone correlation, but the total range of these species is poorly known. *Iridistrophia?* sp., *"Chonetes"* sp., *Anastrophia* sp., and *"Camerella"?* sp. are all poorly represented in numbers and of little value for correlation.

Gypidulids offer the best means of correlation within the Arctic Islands. *Gypidula thorsteinssoni* n. sp. appears in all but one of the Prince of Wales Island collections and is the most abundant species in the Prince of Wales assemblage, but it is present also in two of the collections from Bathurst Island and is abundant in one of them. *Carinagypa careopleura* n. sp. also provides a tie between assemblages. It occurs as a single specimen in one collection from Prince of Wales Island, but is abundant with *G. thorsteinssoni* in the largest collection

from Bathurst Island (GSC 67141) and it occurs also in the lone collection from Cornwallis Island. *Gypidula* cf. *G. kayseri* occurs only in the Cornwallis Island collection (GSC C-11467), but it is abundant there, occurring with a lesser number of specimens of *Carinagypa careopleura*. Possibly, *C. careopleura* is a geographic variant of the smooth gypidulid that occurs in the *Quadrithyris* Zone of Nevada under the name *Gypidula* cf. *G. pseudogaleata* (Hall) (Johnson, 1970, Pl. 15). *Gypidula* cf. *G. kayseri* is a probable geographic variant of the Nevada *Quadrithyris* Zone fossil illustrated as *Sieberella* cf. *S. problematica* (Barrande) (Johnson, 1970, Pl. 13). The brachial plate structure of the latter two forms is different and this difference in morphology requires separate generic assignments, but I have seen variation of this kind in other Early Devonian gypidulids, suggesting that it occurs in response to something other than genetic factors. So, the distributions of *C. careopleura* and *Gypidula* cf. *G. kayseri* both provide evidence for the *Quadrithyris* Zone assignment of the Arctic collections containing them. *Gypidula kayseri* is a Siberian species which has been used as a guide to a mid-Lower Devonian zone of *Quadrithyris* Zone position by Rzhonsnitskaya (1968), suggesting that it has very wide utility as a stratigraphic guide.

Procerulina? is an unusual gypidulid brachiopod of uncertain correlative value. *Machaeraria* is a genus that appears to have some value as a marker in the *Quadrithyris* Zone in the Arctic Islands. It has not yet been seen there out of the zone and in Nevada has its only occurrence within the *Quadrithyris* Zone. Exceptions have been reported in Yukon Territory (Lenz, 1968a, p. 593). A related form, *Thliborhynchia kerri* n. sp., is a most unusual species of a distinctive rhynchonellid genus whose type species is a coarser ribbed form which occurs in post-*Quadrithyris* Zone beds (Lenz, 1967). *Thliborhynchia kerri* occurs in collections from Bathurst and Cornwallis Islands and provides a tie, but it is not known outside the Arctic Islands. The two species of *Ancillotoechia* have no obvious value for correlation. The genus *Katunia*, present in one collection, was defined from the Solovian Limestone of the Altai Mountains of the U.S.S.R. (Kulkov, 1963). That formation includes a fauna of the *Gypidula kayseri* Zone of Rzhonsnitskaya, suggesting distant correlation at the *Quadrithyris* Zone level. The same can be said for the atrypid *Spirigerina supramarginalis* which occurs typically in the Solovian Limestone and also occurs in the *Quadrithyris* Zone of Nevada and its Yukon Territory analog, the *Spirigerina* Unit of Lenz (1968a). The indeterminate species of rhynchonellids, including the "*Plethorhyncha*", atrypids of the *reticularis* type, and *Spinatrypa*, are of no value for correlation at present. *Dubaria* cf. *D. thetis* also is too poorly known in its occurrences to be of value for detailed correlation. *Toquimaella kayi* is a constituent of the *Quadrithyris* Zone of Nevada and also occurs in Yukon Territory (Johnson, 1970, p. 160). *Ogilviella* cf. *O. rotunda* suggests a correlation with the *Spirigerina* Unit of Lenz (1968a).

The final four forms in Table 1, *Nucleospira* sp., *Pinguispirifer carlsi* n. sp., *Undispirifer?* sp., and *Cyrtina* sp., have no detailed value for correlation at present, but *Pinguispirifer carlsi* has potential significance. The type species of *Pinguispirifer* is younger, a constituent of the Pragian Stage of Bohemia and, because of the unique morphology of the genus, it may prove to be biostratigraphically useful.

Several brachiopods have been mentioned that suggest a correlation with the *Gypidula kayseri* Zone of Rzhonsnitskaya (1968). That zone generally falls within the "Gedinnian" as has been used by various Russian authors over the years. Two brachiopods in the Arctic *Quadrithyris* Zone fauna suggest a possible correlation above the *G. kayseri* Zone within the Lower Devonian. The first is the species reported by Khodalevich (1951, Pl. 15) from the Soviet Union as *Atrypa vijaica* Khodalevich. It appears likely to be a *Toquimaella* and is very close morphologically to *Toquimaella kayi*. The second is a form reported from the Soviet Unit by Alekseeva *et al.* (1970, Pl. 3, fig. 13) as *Gypidula problematica*, which bears a remarkable resemblance to *Gypidula thorsteinssoni* n. sp. The Russian occurrence from the Salair

Range on the margin of the Kuznetzk Basin is from the Malobatsch Beds, approximately the same age as the so-called "Koblenzian" occurrence of *Atrypa vijaica* of the Ural Mountains, and slightly younger than *Quadrithyris* Zone correlatives. These Russian occurrences may represent range extensions of forms that are *Quadrithyris* Zone guides in western and Arctic North America, but they also suggest that completely reliable correlations with the Russian stratigraphic scheme are still to be formulated.

Associated Fossils

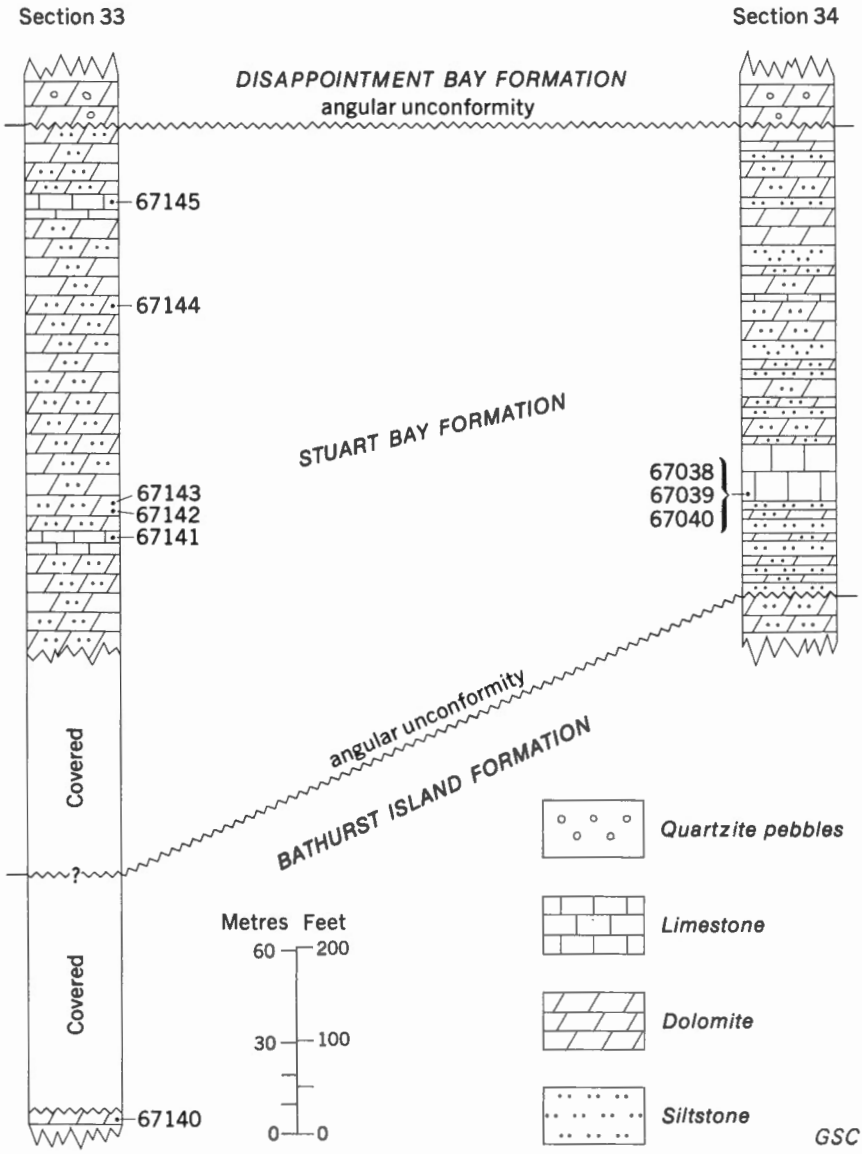
Conodonts obtained from the collection from GSC locality C-8223, Prince of Wales Island, and identified by T. T. Uyeno (written report, June 13, 1972) include *Pedavis pesavis* cf. *P. pesavis pesavis* (Bischoff and Sannemann), *Ozarkodina remscheidensis* (Ziegler) and indeterminate elements of *Ozarkodina* sp. The same collection yielded microfossils identified by D. C. McGregor in a report dated September 10, 1971:

> Spores, chitinozoans and scolecodonts are present in this sample. The spores consist of rather simple forms, the most abundant of which are *?Stenozonotriletes irregularis* Schultz and small, obligate, tetrahedral tetrads. They suggest an Early Devonian age, probably not younger than early Emsian, but their stratigraphic ranges are not well known.
>
> In the Arctic islands, the most closely comparable assemblage I have seen is in the lower fifteen hundred feet of the Bathurst Island Formation east of Young Inlet, on northern Bathurst Island. The similarity between the two assemblages suggests some degree of correlation in age and biofacies, but it should not be construed as proving synchroneity.

Conodonts also were identified from GSC locality C-11467, Cornwallis Island, by T. T. Uyeno (written report dated June 13, 1972) and include the following: *Pedavis pesavis* (Bischoff and Sannemann), *Ozarkodina optimus* (Moskalenko), *Ozarkodina excavatus* (Branson and Mehl). According to Uyeno,

> The single I element in *Pedavis pesavis* is fragmentary making its definite specific assignment difficult. Its gross morphology appears to be that of the nominate subspecies. *Ozarkodina optimus* occurs in the same bed with *Monograptus hercynicus* Perner in the Zeravshan Range, Central Asia (Moskalenko, 1966). At Royal Creek, Yukon Territory, the P element of *Ozarkodina optimus* occurs in the intervals between 342 feet to 750 feet (at section R.C. 1) and 624 feet to 638 feet (at section R.C. 2) above the base (Klapper, 1969).
>
> The association of *P. pesavis* and *O. optimus* suggests correlation with the interval between 342 feet and 354 feet, at section R.C. 1. This interval falls within the *Spirigerina* Unit of Lenz and the *Quadrithyris* Zone of Johnson (Klapper, 1969).

In addition to collections of *Quadrithyris* Zone age, plotted on columnar sections 33 and 34, Bathurst Island (Textfig. 3), a collection of silicified megafossils was examined from a higher level. The collection, from GSC locality 67145 (section 33), includes the following (with number of individuals): *Skenidioides* sp. 5, *Isorthis* cf. *canalicula* (Schnur) 20, *Cortezorthis* spp. 28, *Schizophoria?* sp. 3, *Muriferella* sp. 3, *Dalejina* sp. 37, *Gypidula* sp. 8, *Leptaena* sp. 5, "*Schuchertella*" sp. 1, *Strophonella* sp. 1, *Stropheodonta* sp. (very fine ribbed) 2, *Phragmostrophia* sp. 150, *Chonetes* sp. 5, indet. rhynchonellids 2 spp. 13, *Werneckeella* sp. 1, *Atrypa "reticularis"* 9, *Spinatrypa* sp. 3, *Anatrypa?* sp. 3, *Nucleospira* sp. 9, *Howellella?* sp. 5, *Quadrithyris?* sp. 1, indet. reticulariid (aseptate) 6, and *Cyrtina* sp. 8. The age of this collection is probably Pragian, based on the presence of *Werneckeella*, large specimens of *Cortezorthis*, and the presence of *Muriferella* and *Phragmostrophia*. Eighty-five feet higher in the section, the Stuart Bay Formation is overlain unconformably by the Disappointment Bay Formation which has yielded faunas at several localities, both on Bathurst and Cornwallis Islands, of Zlichovian or probable late Emsian age (Johnson *in* Berdan *et al.*, 1969, p. 2171; Johnson, 1973a).



TEXTFIGURE 3. Columnar sections of Stuart Bay Formation yielding brachiopod collections of *Quadrithyris* Zone age, east-central Bathurst Island (see Textfig. 1). The collections assigned to the *Quadrithyris* Zone include GSC locs. 67038, 67039, and 67141.

Subdivision of *Quadrithyris* Zone

The *Spirigerina* Unit of Royal Creek, Yukon Territory (Lenz, 1968a) and the *Quadrithyris* Zone are similar in their brachiopod assemblages and can be regarded reasonably as a single assemblage zone, i.e., the *Quadrithyris* Zone. But it should be noted that Lenz (1968a, p. 592) found the diagnostic brachiopods *Ogilviella rotunda* and *Toquimaella kayi* at lower and higher horizons, respectively, within his R.C. 2 *Spirigerina* Unit. The same relative occurrence is demonstrated by new collections from R.C. 1 (Lenz and Pedder, 1972, p. 15), where *O. rotunda* occurs at 284 to 293, 322 to 324, and 346 to 357 feet, but does not occur with *T. kayi* at 375 to 395 feet, or higher in the section. These two species also occur in different collections from Bathurst Island (Table 1).

According to Klapper (oral com., Feb. 7, 1973) conodont collections from the newly collected R.C. 1 section indicate that the lower beds, with *O. rotunda*, correlate to Klapper's fauna 3 and that the higher beds, with *T. kayi*, correlate to Klapper's fauna 4, both of central Nevada (Klapper *et al.*, 1971, Fig. 1). At Royal Creek both faunas have been regarded as part of the *Spirigerina* Unit. In Nevada, conodont fauna 3 occurs with non-diagnostic brachiopods below the ledge with the type fauna of the *Quadrithyris* Zone (Textfig. 2). Evidence from Canadian localities suggests that the *Quadrithyris* Zone can be divided into lower and upper subzones that contain conodont faunas 3 and 4.

Brachiopod Communities

The brachiopod collections from the three principal collection areas, Prince of Wales, Bathurst, and Cornwallis Islands, have their own characteristics, which suggest that they represent different brachiopod biofacies of *Quadrithyris* Zone age. Yet all apparently characterize a more broadly defined community, the *Gypidula–Atrypa–Schizophoria* biofacies first noted by Johnson and Dasch (1972). That biofacies includes the major outer, or relatively deeper, brachiopod communities in a two-way breakdown. Very little is known about the shallower and presumably near-shore communities of *Quadrithyris* Zone age which should include coarse-ribbed spiriferids and terebratulids, and this may explain the fact that no terebratulid has yet been found in strata of Lochkovian age in western or Arctic North America. In Nevada, several brachiopod zones compose the Lochkovian (the F fauna of Johnson *et al.*, 1968, the *Notoparmella* fauna of Johnson, 1973b, and the fauna of the *Quadrithyris* Zone, Johnson, 1970). Throughout the interval of these several zones in western North America, correlation on a zonal basis can be made with considerable ease along the whole distance of the continental margin, from Baillie Hamilton Island, north of Cornwallis Island, to central Nevada and southeastern California. However, above the level of the *Quadrithyris* Zone, the similarity of faunas between Nevada and northwestern Canada disappears, evidently because the fossiliferous Nevada localities experienced a faunal shift that brought in shallower water fossils (e.g., the coarse-ribbed *Howellella–Leptocoelia* community) as noted by Johnson and Dasch (1972).

The single collection from the west side of Cornwallis Island (C-11467) more closely resembles the fauna from the type *Quadrithyris* Zone (of central Nevada) than does any of the other collections from the Arctic Islands. The diversity of the assemblage from C-11467 is high and includes a good representation of orthid and dalmanellid brachiopods, almost all preserved as disarticulated shells in dark limestone. This assemblage undoubtedly has

undergone some small amount of postmortem transportation, perhaps downslope from an original close association with a biostromal development, as appears to be the situation at Coal Canyon in central Nevada.

The collections from Bathurst Island differ somewhat in content as well as in preservation, including as they do some shells that are exquisitely preserved as articulated specimens. The collection from GSC locality 67141 is a rich one, derived from a greenish tan limestone. By contrast with the Cornwallis Island locality, the collection from GSC locality 67141 is notable because of the absence of dalmanellids and orthids. The collection may well represent a faunule that existed in a sheltered area associated with a biostrome or small reef. Two additional collections from Bathurst Island (GSC locs. 67038, 67039) are from a cream-coloured, coarsely crystalline limestone, a kind of rock strongly reminiscent of the Koněprusy Limestone of the Pragian Stage of Bohemia and which is supposed to represent a reefal lithology. The brachiopods from GSC localities 67038 and 67039, like those from locality 67141, are mostly well-preserved, articulated specimens. The two former collections contain an abundance of *Spirigerina* and *Ogilviella*, atrypid genera which do not occur in any of the other collections, and the diversity of these collections is surprisingly small.

The collections from Prince of Wales Island were taken from a slightly argillaceous grey limestone and are relatively sparse in the diversity of brachiopods represented. These collections commonly are characterized by an abundance of gypidulids and atrypids about which little can be said except that the association of these two forms is not uncommon. Both genera occur in the Prince of Wales Island collections as well-preserved articulated specimens, suggesting that they have been moved little, if any, from their habitat while living.

Systematic Paleontology

Prefix GSC refers to specimens in the type collections of the Geological Survey of Canada, Ottawa.

Phylum **BRACHIOPODA**

Superfamily ORTHACEA Woodward, 1852

Family HESPERORTHIDAE Schuchert and Cooper, 1931

Subfamily DOLERORTHINAE Öpik, 1934

Genus ***Dolerorthis*** Schuchert and Cooper, 1931

Dolerorthis sp.

Plate II, figures 1–4

Material. Hypotypes (GSC 31792, 31793) GSC loc. C-11467, Cornwallis Island.

Discussion. The available material is sparse, serving mainly to document the occurrence of the genus in the Devonian fauna of Cornwallis Island. The brachial valve is convex with a median sulcus, the latter being a possible point of distinction from more typical species of *Dolerorthis*. It is not possible to say if the species at hand is the same as the one from the Nevada *Quadrithyris* Zone (Johnson, 1970, Pl. 1). The specimens from Cornwallis Island are possibly more strongly sulcate.

Superfamily DALMANELLACEA Schuchert, 1931

Family DALMANELLIDAE Schuchert, 1931

Subfamily CORTEZORTHINAE Johnson and Talent, 1967

Genus *Cortezorthis* Johnson and Talent, 1967

Cortezorthis aff. *C. windmillensis* (Johnson and Talent, 1967)

Plate II, figures 5–11, 16, 17

Protocortezorthis windmillensis Johnson and Talent, 1967, p. 158, Pl. 21, figs. 1–13.
Protocortezorthis windmillensis Johnson, 1970, p. 78, Pl. 4, figs. 3–19.

Material. Hypotypes (GSC 31794, 31795, 31796, 31797, 31798) GSC loc. C-11467, Cornwallis Island.

Discussion. The Cornwallis Island specimens must be assigned to *Cortezorthis* and they are similar to the species *C. windmillensis*, which originally was assigned to the genus *Protocortezorthis*. When the initial work was done on the *Cortezorthis* lineage and its origin in *Protocortezorthis* was determined, it was thought that the species *windmillensis* was the end member of the *Protocortezorthis* lineage, the last species without a fully developed dorsal median septum. Subsequently, and particularly through the work of A. C. Lenz, it was made clear that *Protocortezorthis*, of a type closely allied to the type species *P. fornicatimcurvata*, continues into younger beds. Earlier, the problem was even more difficult because of the transitional nature of morphology of some of the available specimens of *C. windmillensis*. That species is typified by an incipient dorsal median septum and peripheral radial septa, developed only anteriorly (Johnson, 1970, Pl. 4, fig. 13), but it also has a variable development of the dorsal adductor muscle scar and its bounding ridges. For example, the specimens in figures 4 and 14 of Johnson's (1970) Plate 4 conform to a simple, elongate outline of a type typical of *Protocortezorthis*. Other specimens, particularly exemplified by figure 15 of Johnson's (1970) Plate 4, have a broader, or rhomboidal, dorsal adductor muscle field with an outline similar to what is typically developed on *Cortezorthis*. My present feeling is to retain the generic name *Protocortezorthis* only for the taxon with essentially stable morphology, i.e., species resembling *P. fornicatimcurvata* (Fuchs). The species *C. windmillensis* has divergent characters of a type that herald the morphology of typical *Cortezorthis* clearly developed in the form of the incipient dorsal median septum and in the variable development of the dorsal adductor muscle field of *Cortezorthis* type.

The specimens from Cornwallis Island differ from *Cortezorthis windmillensis* from Nevada only in having the dorsal septum moderately well developed. The specimens from Cornwallis Island have a low septum that is continuous from the myophragm which divides the dorsal adductor field, anteriorly to the commissure. Specimens of *Cortezorthis windmillensis* from Nevada commonly have a relatively flat area between the anterior end of the adductor field and the peripheral medial development of the incipient septum.

The few pedicle valves available (Pl. II, figs. 5, 8) assigned to *Cortezorthis* aff. *windmillensis* can be distinguished from *Protocortezorthis* because of the presence of prominent peripheral crenulations of the valve margins and because, as is so noticeable on the specimen in Plate II, figure 8, there is a narrow, prominent median carina which is typical of *Cortezorthis* and which results from accommodation of the dorsal median septum.

Genus ***Protocortezorthis*** Johnson and Talent, 1967

Protocortezorthis aff. *P. fornicatimcurvata* (Fuchs, 1919)

Plate II, figures 12–15

Synonymy. See Johnson and Talent, 1967, p. 157.

Material. Hypotypes (GSC 31799, 31800) GSC loc. C-11467, Cornwallis Island.

Discussion. Only a few specimens are available and none is a pedicle valve. In addition, there is a possibility of specimens of *P.* aff. *P. fornicatimcurvata* being confused with those of *Cortezorthis* aff. *C. windmillensis*. They can be distinguished on the following characters: most species of *Protocortezorthis*, including *P. fornicatimcurvata* (Johnson and Talent, 1967, Pl. 21, figs. 14–22, and *see* especially fig. 15), have radial and subradial striations, reflecting the costae, on internal moulds (*see also* Walmsley, 1965, Pl. 63, figs. 5, 6 for illustrations of this morphological character). The specimens illustrated here, from Cornwallis Island, display this to some extent and contrast with specimens of *Cortezorthis* aff. *C. windmillensis* which have very strong peripheral crenulations, but which lack striae over the whole interior. In addition, brachial valves of *P.* aff. *P. fornicatimcurvata* lack a dorsal median septum and have a trim, elongate development of dorsal adductor muscle scars, unlike the more rhomboidal outline that is characteristic of *Cortezorthis*.

A. C. Lenz first brought to the author's attention the presence of *Protocortezorthis* of the *fornicatimcurvata* type in beds younger than the *Quadrithyris* Zone, making it clear that *Protocortezorthis* did not give rise orthogenetically to *Cortezorthis*. Rather, *Cortezorthis* must be regarded as a branch from the continuing *Protocortezorthis* lineage so that they co-existed for a time during the Early Devonian. No *Protocortezorthis* is known in beds as young as Middle Devonian and none of the known species of *Cortezorthis* is as young as Middle Devonian even though this was once suggested (Johnson and Talent, 1967, p. 153, 154).

Superfamily PENTAMERACEA M'Coy, 1844

Family GYPIDULIDAE Schuchert and LeVene, 1929

Subfamily GYPIDULINAE Schuchert and LeVene, 1929

Genus ***Carinagypa*** Johnson and Ludvigsen, 1972

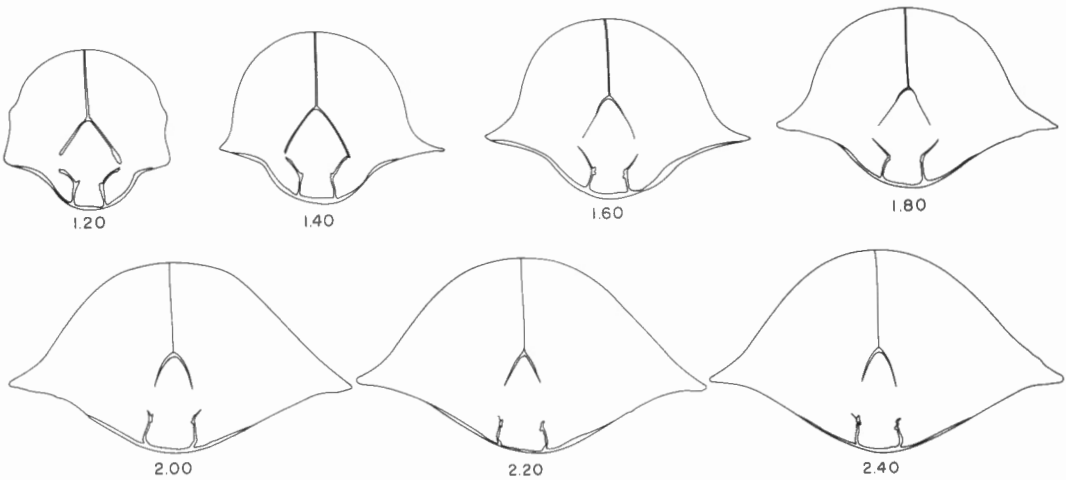
Carinagypa careopleura new species

Plate V, figures 1–9; Textfigure 4

Material. Holotype (GSC 31821) and paratypes (GSC 31822, 31823, 31875) GSC loc. 67141, Bathurst Island. Hypotype (GSC 31824) GSC loc. C-11467, Cornwallis Island.

Discussion. As the name implies, the species is devoid of any kind of plication, but more important the diagnostic feature of the species is the virtual absence of a ventral fold. This is best detected and understood with the aid of a well-preserved anterior commissure (Pl. V, figs. 5, 9). The external morphology and stratigraphic position suggest that this species is ancestral to *Carinagypa loweryi* (Merriam).

Description. Large, ventri-biconvex, pedicle valve three to four times as deep as brachial valve. Outline subcircular to angularly equidimensional with very broad, strongly curved



TEXTFIGURE 4. Serial sections of *Carinagypa careopleura* n. sp.; x4; GSC 31875, GSC loc. 67141, Bathurst Island. Distances are in mm.

ventral umbo. Exterior smooth except for faintest anterior deflection of medial part of commissure, shown by poorly developed concentric growth lines.

Pedicle valve with spondylium and short ventral septum. Brachial valve (as seen with three prepared internal moulds) with well-defined, discrete outer plates diverging laterally and extending slightly past one-third valve length (similar on moulds to those of *Gypidula thorsteinssoni*, Pl. IV, fig. 6). Tiny, inward projecting double carinae faintly developed. All structures of both valves constructed of thin plates of lamellar calcite.

Comparison. Carinagypa careopleura n. sp. differs from *C. loweryi* (Merriam) in completely lacking anterior plications and in having a less well developed ventral fold. Before sectioning, the author regarded *careopleura* as a geographic variant of *Gypidula pseudogaleata* (Hall) and its Nevada counterpart *G.* cf. *pseudogaleata* (Johnson, 1970, Pl. 15, figs. 9–11). Both of the latter are narrow and more elongate than *C. careopleura*, but the geographically intermediate specimens from Nevada are morphologically intermediate in shape. Both are yet to be studied internally with the aid of serial sections, but this kind of investigation is now indicated.

Genus ***Gypidula*** Hall, 1867

Gypidula thorsteinssoni new species

Plate III, figures 6–25; Plate IV, figures 1–25; Textfigure 5

(?) *Gypidula problematica* Alekseeva *et al.*, 1970, Pl. 3, fig. 13; not Barrande.

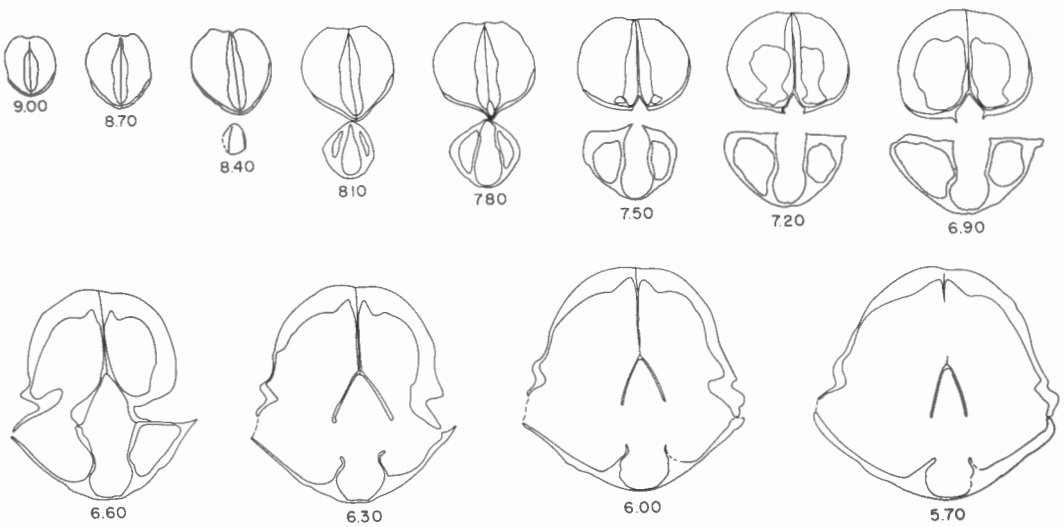
Material. Holotype (GSC 31805) and paratypes (GSC 31807, 31808, 31809, 31876) GSC loc. C-8216, Prince of Wales Island. Hypotypes (GSC 31806, 31819) GSC loc. C-8217, Prince of Wales Island; (GSC 31820) GSC loc. C-8219, Prince of Wales Island; (GSC 31810, 31811) GSC loc. C-8223, Prince of Wales Island; (GSC 31817, 31818) GSC loc. 67038, Bathurst Island; (GSC 31812, 31813, 31814, 31815, 31816) GSC loc. 67141, Bathurst Island.

Discussion. This species is characterized by smooth flanks and by an anterior development of a biplicate ventral fold.

Description. Small specimens transverse-oval, lenticular ventri-biconvex, and smooth with only a trace of fold and sulcus; flexure of anterior commissure toward pedicle valve developed even at early growth stage (Pl. IV, fig. 16). Considerable size attained without greatly altering transverse-oval outline; some specimens slightly elongate (e.g., Pl. III, fig. 13). Flanks smooth. Ventral fold progressively more elevated anteriorly, splitting to form biplicate fold of variable strength, extending from about one-third valve length, on larger specimens, to anterior commissure. Brachial valves have broad, slightly flaring sulcus with a median plication.

Spondylium and short supporting septum of pedicle valve and gypidulid-style brachial plates all composed of lamellar calcite. Pedicle valve with thick inner prismatic layer. Traces of outer plates intersect exterior at high angles, well defined and divergent, reaching a third to almost half length of valves (Pl. IV, figs. 5, 6). Brachial plates lie within and on slopes of dorsal sulcus.

Comparison. Gypidula thorsteinssoni n. sp. probably is closest to *Gypidula* (or *Sieberella*) *problematica* (Barrande). Barrande's (1879, Pl. 26, figs. 3–5) illustrations show a small, slightly transverse biconvex species with a pair of low, subangular plications forming the ventral fold and with these adjoined by one or two low plications on each flank. The specimens from Prince of Wales Island and from Bathurst Island are similar to *G.? problematica* but appear to have relatively more strongly convex pedicle valves and tend to be more elongate (possibly because they are larger). The major point of distinction is that *G. thorsteinssoni* lacks the lateral plications that are characteristic of *G.? problematica;* this is a consistent feature. It appears also that *G.? problematica* has stronger plications, considering the size of the specimens illustrated. Plications barely can be discerned on some of the Prince of Wales Island specimens that are similar in size to the Bohemian specimens.



TEXTFIGURE 5. Serial sections of *Gypidula thorsteinssoni* n. sp.; x3; GSC 31876, GSC loc. C-8216, Prince of Wales Island. Distances are in mm.

Gypidula cf. *G. kayseri* (Von Peetz, 1901)

Plate III, figures 1–5

Pentamerus kayseri Von Peetz, 1901, p. 377, Pl. 3, figs. 8A–C.
Gypidula kayseri Alekseeva *et al.*, 1970, Pl. 3, fig. 14.

Material. Hypotypes (GSC 31803, 31804) GSC loc. C-11467, Cornwallis Island.

Discussion. Von Peetz' (1901) original illustrations show an elongate, plicate specimen from ventral, dorsal, and side views. It is a relatively strongly biconvex gypidulid with a few strong plications. Particularly, the ventral fold is modified by a strong V-shaped median furrow extending all the way from the umbo so that the fold consists essentially of a pair of strong, angular plications. In addition, there is a single well-developed pair of plications on the flanks, joining the furrows that bound the ventral fold. This condition is duplicated closely in the few specimens available from Cornwallis Island (GSC loc. C-11467). Von Peetz' work did not determine the nature of the brachial plates but, in recent years, Rzhonsnitskaya (1968) has listed *Gypidula kayseri* as a diagnostic element of one of the Early Devonian faunas of the U.S.S.R. The material from Cornwallis Island has divergent, discrete outer plates and thus conforms to the internal structure of *Gypidula* (Belanski, 1928, p. 7, Fig. 2). Only the fact of few and poorly preserved specimens occurring in the Cornwallis Island collection and the lack of comparative material from the U.S.S.R. deter a confident assignment. There are no points of contradictory morphology of any consequence that can be recognized at this time.

Genus ***Procerulina*** Andronov, 1961

Procerulina? sp.

Plate II, figures 18–21

Material. Hypotypes (GSC 31801, 31802) GSC loc. 67141, Bathurst Island.

Discussion. Two pedicle valves of an unusual gypidulinid brachiopod have been recovered from GSC locality 67141 on Bathurst Island and the identification as a gypidulid seems to be firmly grounded on the presence of a spondylium (Pl. II, fig. 20). The striking feature of this form is its unusually high angular ventral fold which splits anteriorly. This is a basic feature of the external morphology of the type species of *Procerulina*, but the available specimens are not close to any described form.

Superfamily UNCERTAIN

"*Camerella*"*?* sp.

Plate XI, figures 10–15

Material. Hypotype (GSC 31874) GSC loc. 67038, Bathurst Island.

Discussion. Of the three specimens in the collections, one shows the camerellid form, but generic assignment and even assignment to superfamily is uncertain because available specimens are inadequate for study of internal structures. It is possible that the Arctic specimens are congeneric with "*Camerella*" sp. of Nevada (Johnson, 1970, Pl. II, figs. 9–18). The

latter are rare in the *Spinoplasia* Zone and very rare in the *Quadrithyris* Zone. They also occur in the Pillar Bluff Limestone which has a *Quadrithyris* Zone conodont fauna (Boucot and Johnson, 1967, p. 60).

A second possibility is that the Arctic specimens are related to forms like the so-called *Clorinda parva* which Kulkov (1963, Pl. 1, fig. 5) illustrated from the Solovian Limestone. True *Clorinda* Barrande (Johnson and Ludvigsen, 1972) is greatly different from the Nevada and Texas "*Camerella*". A solution to the questions raised awaits more adequate collections.

Superfamily STROPHEODONTACEA Caster, 1939

Family STROPHEODONTIDAE Caster, 1939

Subfamily STROPHEODONTINAE Caster, 1939

Genus ***Brachyprion*** Shaler, 1865

"*Brachyprion*" *mirabilis* Johnson, 1970

Plate V, figures 10–17

cf. *Shaleria* sp. Boucot, *in* Boucot *et al.*, 1960, p. 12, Pl. 2, figs. 23–26, Pl. 3, figs. 1–8.
"*Brachyprion*" *mirabilis* Johnson, 1970, p. 115, Pl. 22, figs. 1–12.

Material. Hypotypes (GSC 31825, 31827, 31828) GSC loc. 67141, Bathurst Island; (GSC 31826) GSC loc. 67038, Bathurst Island; (GSC 31829, 31830) GSC loc. C-8219, Prince of Wales Island.

Discussion. There are a number of specimens, especially in the collections from Bathurst Island, that have well-preserved shell material, but they break away from the matrix with difficulty. In addition, there is so little space between conjoined valves that internal moulds are difficult to prepare. Two internal moulds of pedicle valves are illustrated (Pl. V, figs. 14, 15) revealing the simple, poorly impressed, broad diductor muscle field without the well-differentiated muscle bounding ridges that characterize the group of *Douvillina* and *Mesodouvillina*. No brachial valve interior has yet been seen.

Superfamily RHYNCHOTREMATACEA Schuchert, 1913

Family RHYNCHOTREMATIDAE Schuchert, 1913

Subfamily ORTHORHYNCHULINAE Cooper, 1956

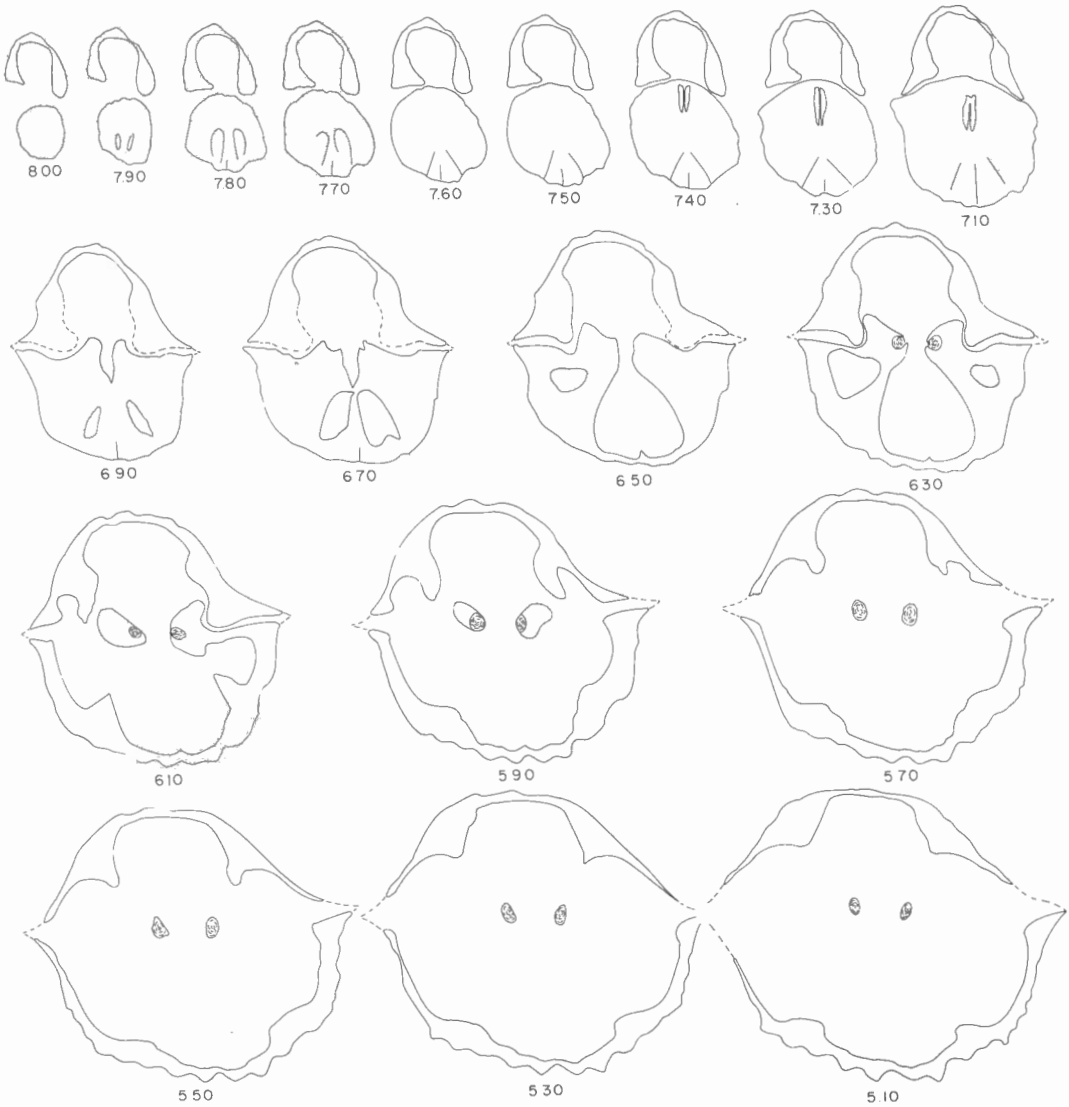
Genus ***Machaeraria*** Cooper, 1955

Machaeraria sp.

Plate VIII, figures 1–12; Textfigure 6

Material. Hypotypes (GSC 31845, 31846) GSC loc. C-8214, Prince of Wales Island; (GSC 31847) GSC loc. 67039, Bathurst Island; (GSC 31877) GSC loc. 67141, Bathurst Island.

Discussion. Species of *Machaeraria* occur throughout the Lower Devonian of the world, and within several provinces, with a total range from Late Silurian to early Middle Devonian. It appears that these various species encompass a small range of variation from place to place



TEXTFIGURE 6. Serial sections of *Machaeraria* sp.; x4; GSC 31877, GSC loc. 67141, Bathurst Island. Distances are in mm.

and at different stratigraphic levels. The relatively stable morphology combines with a small number of available specimens of the species that are known and with essentially inadequate illustrations so that little is to be gained in attempting to compare and contrast the few available specimens from the Arctic Islands with those described previously.

Machaeraria does not seem to be a marker for the *Quadrithyris* Zone in the Arctic, as it is in Nevada. To date, the author has not seen the genus outside of the *Quadrithyris* Zone in the Arctic Islands, but it has been reported at several levels within the Lower Devonian at Royal Creek in the Yukon by Lenz (1968a, p. 593). *Machaeraria* also occurs in a fauna

described (Kulkov, 1963, Pl. 3) from the Solovian Limestone, a fauna that the author believes to be correlative with the *Quadrithyris* Zone.

The specimens at hand are small and have numerous subangular costae that uncommonly split on fold or sulcus (e.g., Pl. VIII, figs. 6, 7). Internally, there are short dental lamellae present on small specimens, but these become obsolescent by infilling of secondary shell material on larger specimens, this shell material building up to outline an impressed diductor muscle field. The brachial valve lacks any trace of a median septum although a myophragm may be developed. The plate-like cardinal process has been distinguished both by internal moulds and in serial sections. Crural plates are absent or are extremely short, but they have been detected (Textfig. 6, sections 6.50 and 6.30).

Genus ***Thliborhynchia*** Lenz, 1967

Thliborhynchia kerri new species

Plate VI, figures 1–23; Plate VII, figures 1–3; Textfigure 7

Material. Holotype (GSC 31831), paratypes (GSC 31832, 31833, 31834) GSC loc. 67038, Bathurst Island; paratypes (GSC 31835, 31836, 31837, 31838, 31839) GSC loc. C-11467, Cornwallis Island.

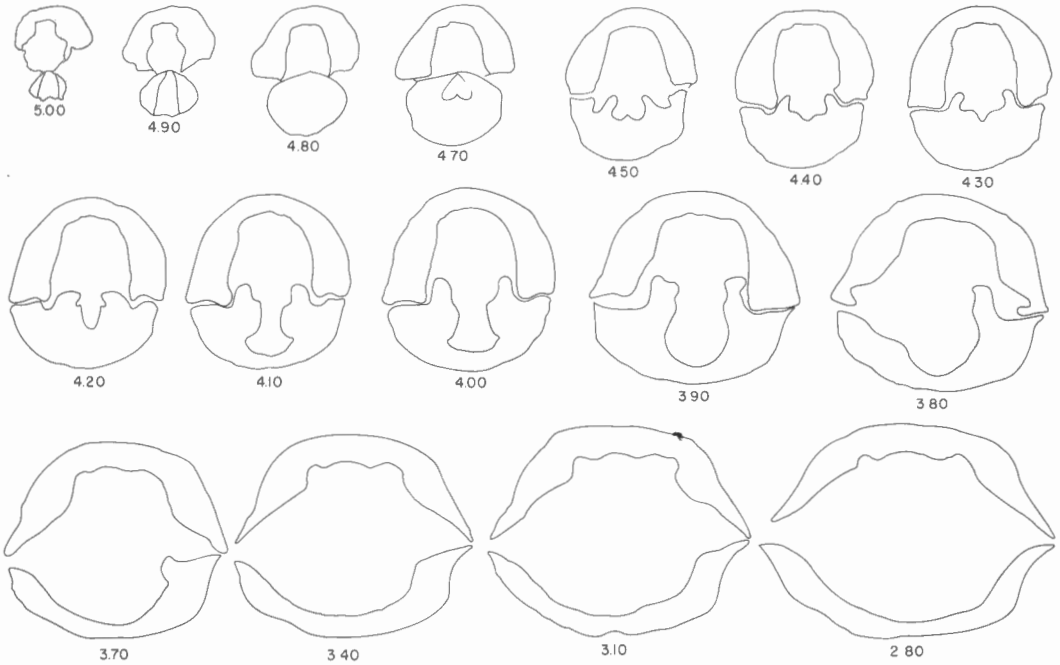
Discussion. This remarkable brachiopod is a fine-ribbed analog of the type species *T. julli* Lenz.

Description. Outline subtriangular to almost rhomboidal, lateral profile lenticular, subequally biconvex. Available specimens poorly preserved in beak region, hindering accurate description. Principal development of posterior of both valves involves long straight, or even concave, posterolateral margins, developed along angulated slopes to an extreme point so that maximum width develops anterior to midlength. Anterior commissure may be arcuate or gently lobed medially, depending on strength of development of flat ventral sulcus and strongly elevated, broad dorsal fold. Anterior parts of ventral flanks flat, reflexed in some specimens so that anterolateral extremities twist ventrally. Corresponding development of anterior flanks of brachial valve develops pair of concave or trough-like surfaces adjacent to dorsal fold. Costae fine and rounded, almost wire-like, increasing in number anteriorly by bifurcation and by implantation.

Dental lamellae short and widely spaced. Diductor muscle field not well developed on prepared specimens. Dorsal interior characterized by small, divergent socket plates and by discrete hinge plates, defining an elongate, trough-like notothyrial cavity unsupported by median septum and cleft at its apex by very small, blade-like cardinal process. Dorsal adductor scars elongate-oval, divided by low myophragm and situated in posterior one-third of valve by impression, without muscle bounding ridges. Interiors of both valves crenulated anteriorly by impress of costae.

Comparison. The new species is much more finely costate than the type species *T. julli*. No other named species is available for comparison.

Havlíček (1961) proposed a genus *Sicorhyncha* with which *Thliborhynchia kerri* is undoubtedly related. *Sicorhyncha* is a much less lenticular genus, lacking the degree of angulation and extreme cuneate outline of *Thliborhynchia*. The type species of *Sicorhyncha* also differs in having parietal slopes of the fold and sulcus so well differentiated that median plications are added laterally within the ventral sulcus rather than being radial as they are in *T. kerri*.



TEXTFIGURE 7. Serial sections of *Thliborhynchia kerri* n. sp.; x4.5; GSC 31834, GSC loc. 67038, Bathurst Island Distances are in mm.

Family UNCERTAIN

Genus ***Katunia*** Kulkov, 1963

Discussion. Kulkov's genus *Katunia*, based on specimens from the Lower Devonian Solovian Limestone of the Gorni Altai, is a small, pauciplicate rhynchonellid with obsolescent dental lamellae and lacking a dorsal median septum. It is an external homeomorph of the septate genus *Werneckeella* Lenz (1971). Especially, this is true of the species that Kulkov (1963, Pl. 4, figs. 2–4) illustrated under the name *Katunia*(?) *postmodica* (Scupin). Another external homeomorph is the species *Isopoma alecto* (Barrande). This species was illustrated by Havlíček (1961, p. 40, Pl. 6), but it differs from *Katunia* in having thin rather than ponderous hinge plates and in the presence of free-hanging crural bases. Lenz (1971) pointed out the similarity of another Bohemian Lower Devonian species, "*Linguopugnoides*" *praecox* (Barrande), from the Vinařice Limestone. Unfortunately, that species is unknown internally.

Katunia sp.

Plate VII, figures 9–18

Material. Hypotypes (GSC 31841, 31842) GSC loc. 67141, Bathurst Island.

Discussion. This species resembles the so-called *Katunia? postmodica* illustrated by Kulkov (1963, Pl. 4), but in my opinion that form is not sufficiently close to Scupin's (1906, Pl. 13) own illustrations of *postmodica* to warrant retention of the name either for the Altai or for the

Canadian specimens. Consequently, the form is listed here as *Katunia* sp. The species *postmodica*, if it is indeed a *Katunia*, is more rounded, narrower at midlength and in the anterior half, and contains slightly fewer costae than the specimens from the Canadian Arctic.

The identification here is based on the external form and on a prepared internal mould made from one of the specimens after photography. That specimen reveals tiny, almost completely obsolescent dental lamellae, no median septum, and a well-defined notothyrial cavity blocked off by prominent, thick hinge plates laterally.

Family TRIGONIRHYNCHIIDAE Schmidt, 1965

Genus ***Ancillotoechia*** Havlíček, 1959

Ancillotoechia sp. A

Plate VII, figures 4–8

Material. Hypotype (GSC 31840) GSC loc. C-8223, Prince of Wales Island.

Discussion. This is a narrowly triangular, coarsely costate species of moderate size. Of the two available specimens, one was photographed unprepared, while the second was prepared as an internal mould, revealing short, widely spaced, thin dental lamellae. In the brachial valve there is a thin, blade-like median septum, reaching about two-fifths of the total length of the valve, supporting a V-shaped septalium which is partly, or possibly wholly, covered by inner hinge plates. The outer hinge plates are flat and triangular.

Ancillotoechia sp. B

Plate VII, figures 19–28

Material. Hypotypes (GSC 31843, 31844) GSC loc. 67141, Bathurst Island.

Discussion. This is a moderately large, strongly costate species of rhynchonellid in which the two available specimens show variation from two to three costae in the ventral sulcus and from three to four costae on the dorsal fold. After photography, one of the specimens (Pl. VII, figs. 19–23) was prepared as an internal mould, revealing short, thin, plate-like, dental lamellae. In the brachial valve there is a thin, blade-like median septum supporting a V-shaped septalium. Very faint, splaying ridges originate at about one-fifth valve length and surround what apparently were the adductor impressions. The septum extends about to midlength or slightly beyond it.

Superfamily ATRYPACEA Gill, 1871

Family ATRYPIDAE Gill, 1871

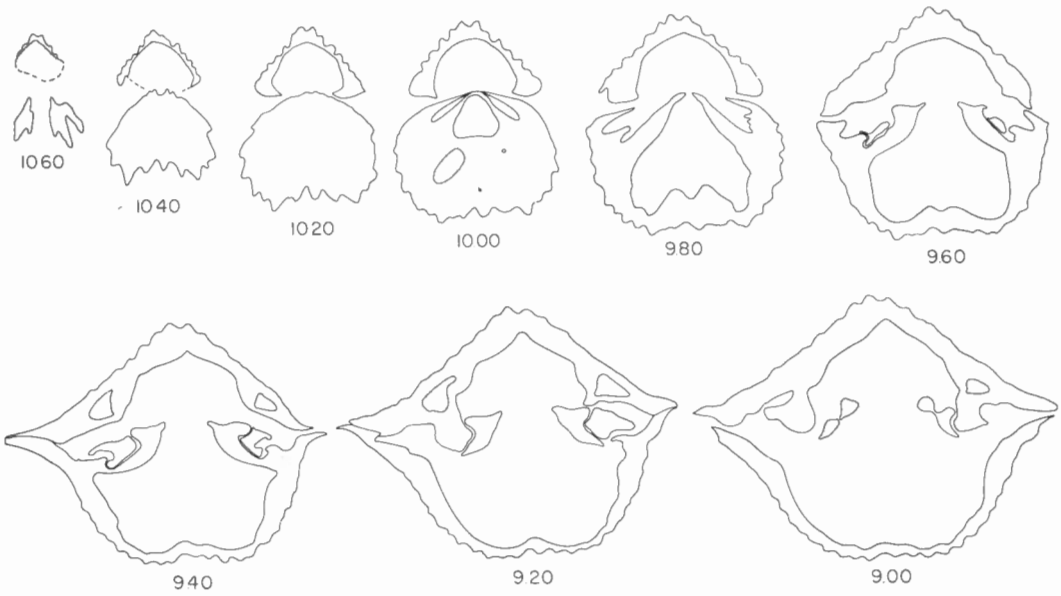
Subfamily ATRYPINAE Gill, 1871

Genus ***Atrypa*** Dalman

Atrypa exquisita new species

Plate VIII, figures 19–28; Textfigure 8

Material. Holotype (GSC 31850), paratypes (GSC 31851, 31852, 31853, 31854, 31878), GSC loc. 67141, Bathurst Island.



TEXTFIGURE 8. Serial sections of *Atrypa exquisita* n. sp.; x4; GSC 31878, GSC loc. 67141, Bathurst Island. Distances are in mm.

Discussion. Paleontologic methods have not yet reached a point where they can prove satisfactory means by which to realistically distinguish the numerous forms, variants, and species of the genus *Atrypa*. The Arctic species, here named *Atrypa exquisita*, cannot be compared or contrasted with named species with any sense of reality and is a form that ordinarily appears on faunal lists as *Atrypa "reticularis"*. By some rules this would be reason not to distinguish it as a new species, but it is hypocritical to invoke such rules at the paleontologist's whim. Better is the practice of always avoiding impractical rules. *Atrypa exquisita* n. sp. does have morphologic features that can be used to characterize it within the Arctic Early Devonian. *Atrypa* sp. of Plate VIII, figures 13–18, from Prince of Wales Island, is distinctly dorsi-biconvex compared to the subequally biconvex *A. exquisita*.

Description. Valves oval in outline, varying from elongate to transverse, with maximum width commonly near midlength. Lateral profile subequally biconvex. Ventral beak small and incurved. Cardinal angles broadly rounded and obtuse. Fold and sulcus lacking; anterior commissure rectimarginate or gently arched toward brachial valve.

External ornament consists of rounded costae approaching tubular type; these swell and attenuate at intersections with concentric growth lines where prominent frills were attached.

Atrypa reticularis Linnaeus, studied by Harper (1969), has strong growth lines which, upon removal of the frill, leave growth line imbrications and discontinuity of the costae across these. *Atrypa exquisita* n. sp. has, by contrast, semicontinuous radial costae that terminate, on the best-preserved specimens, in a large marginal frill in which costae of normal size over the body of the shell split into numerous, very fine, wire-like costellae (Pl. VIII, figs. 26–28). Costae of *Atrypa exquisita* n. sp. are of medium size, spreading on the pedicle valve from a posterior median ridge into two pairs of radially disposed median costae. The brachial valve has a complementary development of costae.

Dental lamellae present but small. Ventral muscle scars faintly impressed. Cardinalia include typical development of discrete inner socket ridges bisected longitudinally by denticular ridge.

Subfamily ZYGOSPIRINAE Waagen, 1883

Discussion. Amsden's (*in press*) recent work demonstrates that *Plectatrypa* and *Spirigerina* are primitive zygospirid stocks. Only *Spirigerina* persists into the Lower Devonian. The onetime supposition that *Spirigerina* should be classified with the carinatinids is known now to be untenable (Johnson and Boucot, 1972).

Genus *Spirigerina* d'Orbigny, 1849

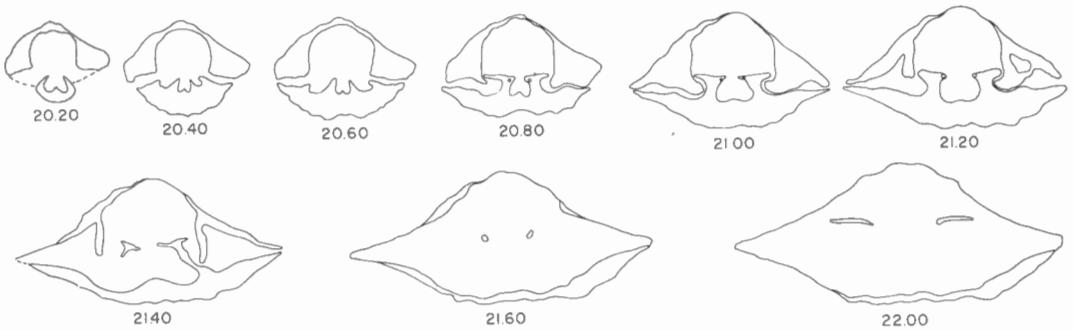
Spirigerina supramarginalis (Khalfin, 1948)

Plate IX, figures 1–26; Textfigure 9

Atrypa supramarginalis Khalfin, 1948, p. 159, Pl. 2, fig. 10; p. 176, Pl. 4, figs. 4–7.
Spirigerina supramarginalis Kulkov, 1963, p. 70, Pl. 5, figs. 11–13.
Spirigerina supramarginalis Johnson, 1970, p. 157, Pl. 42, figs. 1–10.

Material. Hypotypes (GSC 31855, 31856, 31857, 31858) GSC loc. 67038, Bathurst Island; (GSC 31859, 31860, 31861, 31879) GSC loc. 67039, Bathurst Island.

Discussion. Spirigerina is an atrypid of immense variability. For this reason it is difficult to characterize with a few words the variations of any one species. *Spirigerina supramarginalis* is no exception and, while no attempt is made here to redescribe it, the illustrations demonstrate some of the variations that the species displays. The particular characteristic of this species that helps set it apart from other Early Devonian species is the relatively small number of costae developed. Specimens from Bathurst Island are comparable to specimens illustrated by Khalfin (1948) and by Kulkov (1963) from the Altai Mountains. By contrast, those illustrated from Nevada (Johnson, 1970, Pl. 42) more commonly fall in the group with more numerous plications such as the specimen illustrating the end of that range of variation on Plate IX, figures 22–26. Savage (1970, Pl. 102) described and illustrated some specimens of *Spirigerina* from beds of probable early *Quadrithyris* Zone age from New South Wales. These also fall in the range of variation of specimens with more numerous costae than is usual. The assignment may be correct, but no judgment is made here.



TEXTFIGURE 9. Serial sections of *Spirigerina supramarginalis* (Khalfin); x3.5; GSC 31879, GSC loc. 67039, Bathurst Island. Distances are in mm.

Subfamily SEPTATRYPINAE Kozlowski, 1929

Genus *Dubaria* Termier, 1936

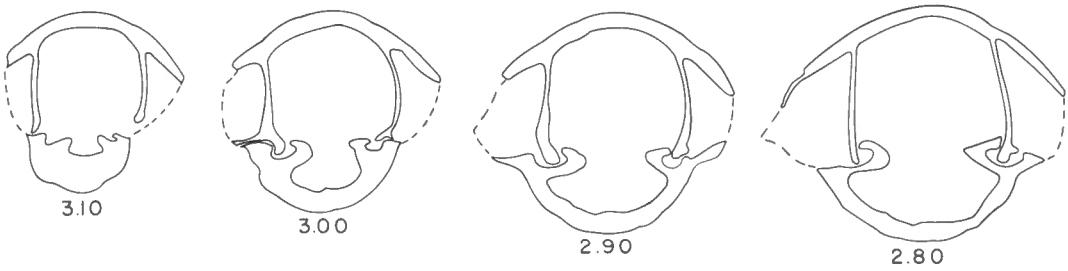
Dubaria cf. *D. thetis* (Barrande, 1847)

Plate X, figures 1–10; Textfigure 10

Terebratula thetis Barrande, 1847, p. 349. Pl. 14, fig. 5.
Atrypa thetis Barrande, 1879, p. 54, Pl. 86, case IV; ?Pl. 133, case I.
Septatrypa thetis Khodalevich, 1951, p. 84, Pl. 21, figs. 4–6.
Rhynchatrypa thetis Siehl, 1962, p. 200, Pl. 28, figs. 1, 2; Pl. 37, fig. 11; Pl. 38, figs. 1, 2.
Atrypopsis thetis Kulkov, 1963, p. 67, Pl. 5, figs. 3–10.

Material. Hypotypes (GSC 31862) GSC loc. C-8216, Prince of Wales Island; (GSC 31863, 31880) GSC loc. 67039, Bathurst Island.

Discussion. The form of the few available specimens of this small smooth brachiopod are suggestive of *Dubaria thetis*, a lenticular Early Devonian species. The serial sections available from a single specimen show that widely spaced and well-developed dental lamellae are present along with discrete inner socket ridges, but that outer hinge plates which lie along a horizontal line in serial sections (Siehl, 1962, Pl. 28) are not evident. The significance of this morphologic feature is greatly in need of study.



TEXTFIGURE 10. Serial sections of *Dubaria* cf. *D. thetis* (Barrande); x8; GSC 31880, GSC loc. 67039, Bathurst Island. Distances are in mm.

Superfamily CARINATINACEA Rzhonsnitskaya, *nom. transl.* herein

Family CARINATINIDAE Rzhonsnitskaya, 1960

Subfamily CARINATININAE Rzhonsnitskaya, 1960

Discussion. Since the revision of the carinatinids (Johnson and Boucot, 1972), done for the first time on a phylogenetic basis, it has become clear that carinatinids, together with the related notanopliids, constitute an atrypid superfamily which is distinct from Atrypacea by the ubiquitous presence of a ventral median costa and a unique mode of flank costae insertion, contrasting with the ventral median costal pair and radial flank costae typical of Atrypacea (Johnson, 1973b).

Genus *Ogilviella* Lenz, 1968

Ogilviella cf. *O. rotunda* Lenz, 1968

Plate X, figures 11–24

Ogilviella rotunda Lenz, 1968b, p. 181, Pl. 31, figs. 1–35.

Material. Hypotypes (GSC 31864, 31865, 31866, 31867) GSC loc. 67038, Bathurst Island.

Discussion. The available specimens are small and badly exfoliated; moreover, the interiors are crystalline, making worthwhile serial sections difficult to obtain. The material from Bathurst Island differs slightly from the type material illustrated by Lenz (1968b, Pl. 31), principally in having a less well developed bifurcation of the median ventral plication, although this is developed on one small specimen illustrated in figures 23 and 24 of Plate X.

There is an Australian species of this genus, *Ogilviella prolifica* Savage, 1970. There is little to differentiate between these species except perhaps that the type species *O. rotunda* Lenz appears more circular because of its less prominent ventral beak and it appears to have its median ventral carina slightly better differentiated from the flanks than that same structure on *Ogilviella prolifica* Savage.

Superfamily CYRTIACEA Frederiks, 1924

Family CYRTIIDAE Frederiks, 1924

Subfamily PINGUISPIRIFERINAE Havlíček, 1971

Genus *Pinguispirifer* Havlíček, 1957

Discussion. In his comprehensive monograph on the Bohemian Silurian and Devonian spiriferids, Havlíček (1959) provided serial sections of the type species of *Pinguispirifer* which did not show crural plates to be present. He did show, in those sections, that the pedicle valve is characterized by closely spaced, nearly obsolescent dental lamellae. That second observation on morphology was emphasized by the internal mould provided by Boucot (1962, Textfig. 1). However, Boucot (1962, Textfig. 2) also illustrated an internal mould of the brachial valve, showing that short crural plates are present. The external features that characterize *Pinguispirifer* are an ordinary development of ventral sulcus and dorsal fold and very low, indistinct rounded plications on the flanks, and with the external surface having a radial sculpture crossed by concentric growth lines. This feature of external ornament led Havlíček (1959) to include *Pinguispirifer* within the eospiriferids. Boucot (1962, p. 420) rejected the eospiriferid assignment, but did not make an alternative suggestion. More recently, Havlíček (1971, Pl. 5) has provided an excellent new illustration of the fine external ornament of *Pinguispirifer infirmus* (Barrande) and has proposed a subfamily Pinguispiriferinae of the family Cyrtiidae. Havlíček made this family assignment provisionally, on the basis of the presence of the radial pattern of fine ornament, but he noted, following Boucot (1962), that the presence of a striated site of dorsal diductor attachment is a non-eospiriferid feature. Although this is true, the comparison is based largely on Silurian eospiriferids and takes no account of the probability that *Pinguispirifer* was derived from these same Silurian eospiriferids.

The high, short, and closely spaced dental lamellae that characterize *Pinguispirifer* do not detract from the suggested eospiriferid origin. *Cyrtia* has a somewhat similar arrangement of dental plates. Additionally, it is clear that striation of the dorsal diductor site is very minor in *P. carlsi* n. sp. Thus, it provides a temporal and morphologic intermediate between Silurian *Eospirifer* and the Pragian type species of *Pinguispirifer*.

Pinguispirifer carlsi new species

Plates X, figures 30–34; Plate XI, figures 1–7; Textfigure 11

Material. Holotype (GSC 31870), paratypes (GSC 31871, 31872, 31873, 31881) GSC loc. 67141, Bathurst Island.

Discussion. Pinguispirifer carlsi n. sp. is a relatively lenticular species with a narrow, U-shaped ventral sulcus and a low, narrow dorsal fold.

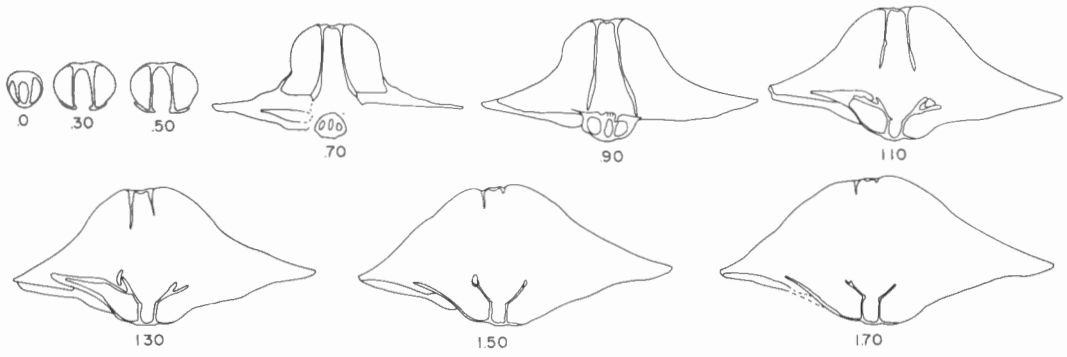
Description. Valves transversely oval in outline and ventri-biconvex in lateral profile, with pedicle valve about twice as deep as brachial valve. Ventral beak short, incurved, and only slightly overhanging a low, triangular, apsacline interarea with width equal to about two-thirds maximum width of valves. Cardinal angles strongly rounded; maximum width in posterior half. Ventral sulcus relatively narrow and U-shaped, equal in width to about two of adjacent plications. Dorsal fold very low, rising only slightly above curvature of valve. Flanks of both valves commonly with four distinct, low rounded plications, separated by very shallow, U-shaped interspaces. Exterior covered by regularly spaced, fine concentric growth lines and indistinct radial striae.

Dental lamellae thin, closely spaced, lying entirely within narrow umbonal extension of ventral sulcus (Pl. XI, fig. 3), projecting only about one-sixth maximum length of valves. Very narrow area between dental lamellae may be divided by thin myophragm.

It is difficult to make the distinction, in the figures, between a myophragm and a blade-like septum, but the thin median groove in the external mould (Pl. XI, figs. 3–5) is no more than a low ridge. There is no obvious delineation of a ventral muscle field and the interior is smooth except for faint radial corrugations, reflecting the plication of the shell and its radial striae (Pl. XI, fig. 5).

Crural plates thin, of subparallel cross-section, diverging slightly along base of valve, supporting thin, inclined, inner hinge plates. Crura originate from juncture of these plate pairs. Crural plates delineate posterior margins of slightly impressed, elongate, triangular adductor muscle field. Interior smooth, except for faint radial corrugations, reflecting plication of valves.

Comparison. Pinguispirifer carlsi n. sp. is more evenly oval than *P. infirmus* from the Pragian of Bohemia (Havlíček, 1959, Pl. 17) which has a somewhat rounded quadrate outline. *Pingui-*



TEXTFIGURE 11. Serial sections of *Pinguispirifer carlsi* n. sp.; x3; GSC 31881, GSC loc. 67141, Bathurst Island. Distances are in mm.

spirifer carlsi is more lenticular than *P. infirmus* and has a much narrower ventral sulcus and dorsal fold. The relatively broad fold and sulcus of *Pinguispirifer infirmus* are characteristic.

Superfamily RETICULARIACEA Waagen, 1883

Family RETICULARIIDAE Waagen, 1883

Genus ***Undispirifer*** Havlíček, 1957

Undispirifer? sp.

Plate X, figures 25–29; Plate XI, figures 8, 9

Material. Hypotypes (GSC 31868) GSC loc. C-8219, Prince of Wales Island; (GSC 31869) GSC loc. C-8216, Prince of Wales Island.

Discussion. The author has examined hypotype specimens of *Undispirifer undiferus* (Roemer) from the German Middle Devonian. *Undispirifer* is a plicate reticulariid genus with prominent dorsal fold and a U-shaped ventral sulcus. The ornament is of well-developed concentric growth lines and short spine-bases, not forming ridges across the whole width of each growth lamella. Internally, *Undispirifer* has plate-like dental lamellae that are relatively wide-spaced and of moderate length, not made obsolescent by the presence of secondary shell material. The brachial valve has crural plates and may or may not have a slight elevation of its notothyrial cavity. A number of the collections from the *Quadrithyris* Zone of the Arctic Islands include spirifers of this type, generally distinguished from the type species by even less well developed radial plications and by a very slight impression of the ventral muscle field. The available specimens also have short crural plates and, although the assignment of Early Devonian reticulariid species to *Undispirifer* gives that genus a relatively long range, it is not obvious how the Early Devonian species at hand could be distinguished in any important way from Middle Devonian representatives of *Undispirifer.*

It is worth noting that the appearance of an *Undispirifer* in the *Quadrithyris* Zone beds of the Canadian Arctic is not unexpected. The genus has been reported (Johnson *et al.*, 1968) in beds of early Lochkovian age in the Roberts Mountains of Nevada where they have been assigned provisionally to the Podolian species of similar age, *Undispirifer laeviplicatus* (Kozlowski, 1929, Pl. 10).

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List of Localities

Collections are marked on Figure 5 of GSC Memoir 378 on Bathurst Island (Kerr, J. W., 1974).

67038–67040 75°45′30″N, 98°21′W (517600E; 8408050N; UTM Zone 14), Section 34 of Kerr (1974), about 2 miles north of Polar Bear Pass on eastern Bathurst Island. Stuart Bay Formation, 100–160 ft. above base, from a patch reef, now preserved as a thin pillar. Collection by J. W. Kerr, 1964.

67141 75°44′30″N, 98°25′W. North of central part of Polar Bear Pass, eastern Bathurst Island. Section 33 of Kerr (1974) is on the east side of main stream flowing to Goodsir Inlet, 3 miles north of main right angle bend in that stream. Stuart Bay Formation, 350 ft. above base. Collected by J. W. Kerr, 1964.

67142 Same as above. Stuart Bay Formation, 375 ft. above base. Collected by J. W. Kerr, 1964.

67143 Same as above. Stuart Bay Formation, 385 ft. above base. Collected by J. W. Kerr, 1964.

67144 Same as above. Stuart Bay Formation, 600 ft. above base. Collected by J. W. Kerr, 1964.

67145 Same as above. Stuart Bay Formation, 705 ft. from base. Collected by J. W. Kerr, 1964.

C-8214 449700E; 8156750N. UTM Zone 14, Prince of Wales Island. Unnamed formation (mainly limestone and dolomite) which occurs in western parts of Prince of Wales Island and represents a facies equivalent of the Peel Sound Formation in eastern parts of the island; 2 ft. above base of measured section (640 ft. thick) that is entirely within the formation. Collected by R. Thorsteinsson, 1970.

C-8215 Same as above, 5 ft. above base of same section. Collected by R. Thorsteinsson, 1970.

C-8216 Same as above, 26 ft. above base of same section. Collected by R. Thorsteinsson, 1970.

C-8217 Same as above, 28 ft. above base of same section. Collected by R. Thorsteinsson, 1970.

C-8219 Same as above, 74 ft. above base of same section. Collected by R. Thorsteinsson, 1970.

C-8223 451100E; 8161750N. UTM Zone 14, Prince of Wales Island (northwest). Same unnamed formation as at C-8214, 30 ft. above base of exposures in creek. Collected by R. Thorsteinsson, 1970.

C-11467 570550E; 8337250N. UTM Zone 14, Cornwallis Island (west coast). Probably same unnamed formation as C-8214; isolated exposure. Collected by R. Thorsteinsson, 1971.

Plates II to XI

PLATE II

Dolerorthis sp. (PAGE 16)

Figures 1, 2. Rubber replica of dorsal exterior and dorsal external mould (GSC 31792); GSC locality C-11467, Cornwallis Island; x2.

Figures 3, 4. Rubber replica of dorsal interior and dorsal internal mould (GSC 31793); same locality; x2.

Cortezorthis cf. *C. windmillensis* (Johnson and Talent) (PAGE 17)

Figures 5, 6. Ventral internal mould and rubber impression (GSC 31794); GSC locality C-11467, Cornwallis Island; fig. 5, x3; fig. 6, x2.

Figure 7. Exterior of exfoliated brachial valve (GSC 31795); same locality; x4.

Figures 8, 9. Ventral internal mould and rubber impression (GSC 31796); same locality; fig. 8, x3; fig. 9, x2.

Figures 10, 11. Dorsal internal mould and rubber impression (GSC 31797); same locality; x2.

Figures 16, 17. Dorsal internal mould and rubber impression (GSC 31798); same locality; x2.

Protocortezorthis cf. *P. fornicatimcurvata* (Fuchs) (PAGE 18)

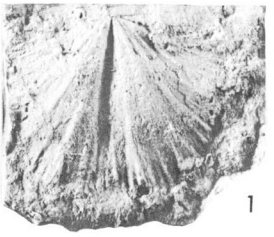
Figures 12, 13. Internal mould of brachial valve and rubber impression (GSC 31799); GSC locality C-11467, Cornwallis Island; x2.

Figures 14, 15. Internal mould of brachial valve and rubber impression (GSC 31800); same locality; x2.

Procerulina? sp. (PAGE 21)

Figures 18, 19. Ventral and posterior views of pedicle valve (GSC 31801); GSC locality 67141, Bathurst Island; x2.

Figures 20, 21. Dorsal and posterior views of pedicle valve (GSC 31802); same locality; x2.



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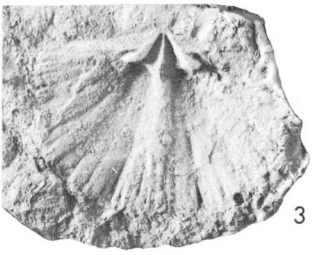

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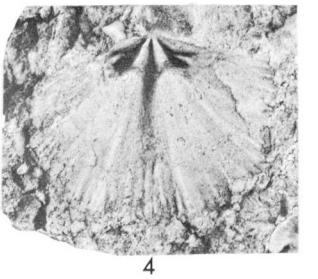

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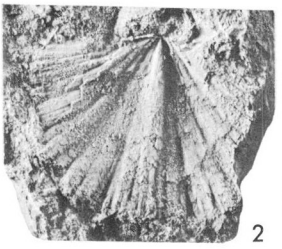

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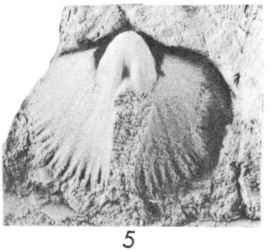

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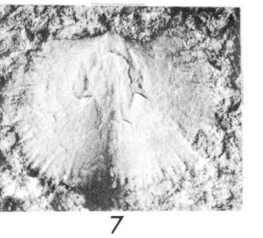

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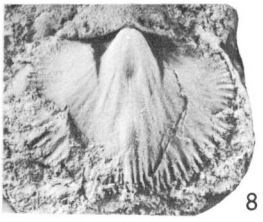

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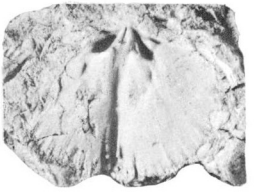

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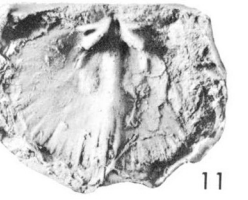

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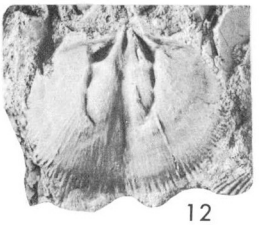

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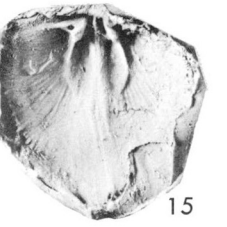

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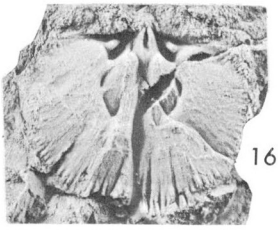

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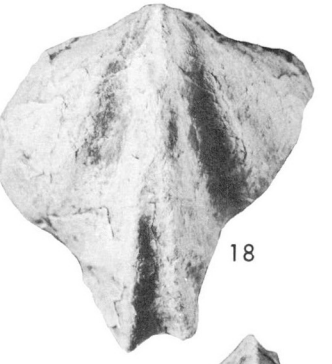

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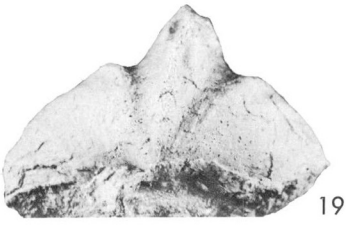

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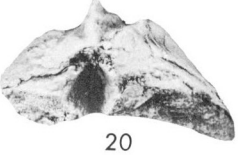

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PLATE III

Gypidula cf. *G. kayseri* (Von Peetz) (PAGE 21)

Figure 1. Exterior of brachial valve (GSC 31803); GSC locality C-11467, Cornwallis Island; x2.

Figures 2–5. Posterior, side, anterior, and ventral views of pedicle valve (GSC 31804); same locality; x2.

Gypidula thorsteinssoni new species (PAGE 19)

Figures 6–10. Ventral, dorsal, side, posterior, and anterior views of internal mould (GSC 31806); GSC locality C-8217, Prince of Wales Island; x2.

Figures 11, 12. Anterior and dorsal views (GSC 31807); GSC locality C-8216, Prince of Wales Island; x2.

Figures 13–15. Ventral, side, and anterior views (GSC 31808); same locality; x2.

Figures 16–20. Anterior, side, dorsal, ventral, and posterior views of holotype (GSC 31805); same locality; x2.

Figures 21–25. Ventral, dorsal, side, anterior, and posterior views (GSC 31809); same locality; x2.

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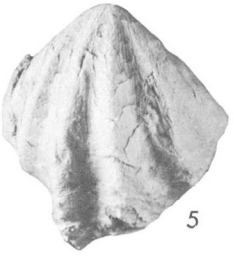
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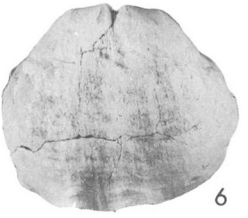
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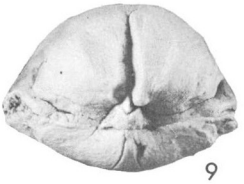
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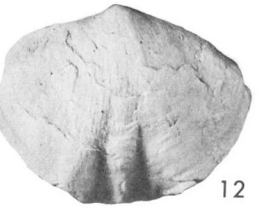
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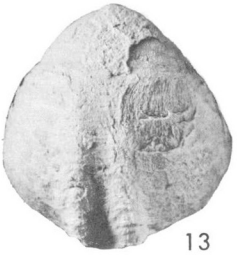
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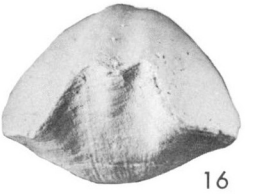
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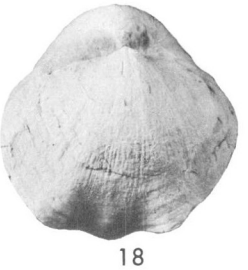
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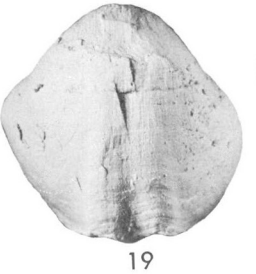
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PLATE IV

Gypidula thorsteinssoni new species (PAGE 19)

Figure 1. Exterior of pedicle valve (GSC 31810); GSC locality C-8223, Prince of Wales Island; x1.5.

Figures 2, 3. Posterior and ventral views of pedicle valve (GSC 31811); same locality; x1.5.

Figure 4. Exterior of pedicle valve (GSC 31812); GSC locality 67141, Bathurst Island; x2.

Figure 5. Internal mould of brachial valve (GSC 31813); same locality; x2.

Figure 6. Internal mould of brachial valve (GSC 31814); same locality; x2.

Figures 7–10. Side, anterior, ventral, and dorsal views (GSC 31815); same locality; x2.

Figure 11. Ventral view of pedicle valve (GSC 31816); same locality; x2.

Figures 12, 13. Anterior and posterior views of pedicle valve (GSC 31817); GSC locality 67038, Bathurst Island; x1.5.

Figures 14–18. Ventral, dorsal, anterior, posterior, and side views (GSC 31818); same locality; x3.

Figures 19–23. Side, anterior, posterior, ventral, and dorsal views (GSC 31819); GSC locality C-8217, Prince of Wales Island; x2.

Figures 24, 25. Anterior and ventral views (GSC 31820); GSC locality C-8219, Prince of Wales Island; x2.

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PLATE V

Carinagypa careopleura new species (PAGE 18)

Figures 1, 2. Ventral and posterior views of pedicle valve (GSC 31822); GSC locality 67141, Bathurst Island; x1.5.

Figures 3, 4. Posterior and ventral views of pedicle valve (GSC 31823); same locality; x1.5.

Figures 5, 6. Anterior and side views of holotype (GSC 31821); same locality; x1.5.

Figures 7–9. Posterior, ventral, and anterior views of pedicle valve (GSC 31824); GSC locality C-11467, Cornwallis Island; x1.5.

"*Brachyprion*" *mirabilis* Johnson (PAGE 22)

Figures 10, 11. Ventral and dorsal views (GSC 31825); GSC locality 67141, Bathurst Island; x2.

Figures 12, 13. Ventral and dorsal views (GSC 31826); GSC locality 67038, Bathurst Island; x3.

Figure 14. Internal mould of pedicle valve (GSC 31827); same locality as figs. 10, 11; x2.

Figure 15. Internal mould of pedicle valve (GSC 31828); same locality as figs. 10, 11; x2.

Figure 16. Ventral view of pedicle valve (GSC 31829); GSC locality C-8219, Prince of Wales Island; x1.25.

Figure 17. External mould of brachial valve (GSC 31830); same locality; x1.25.

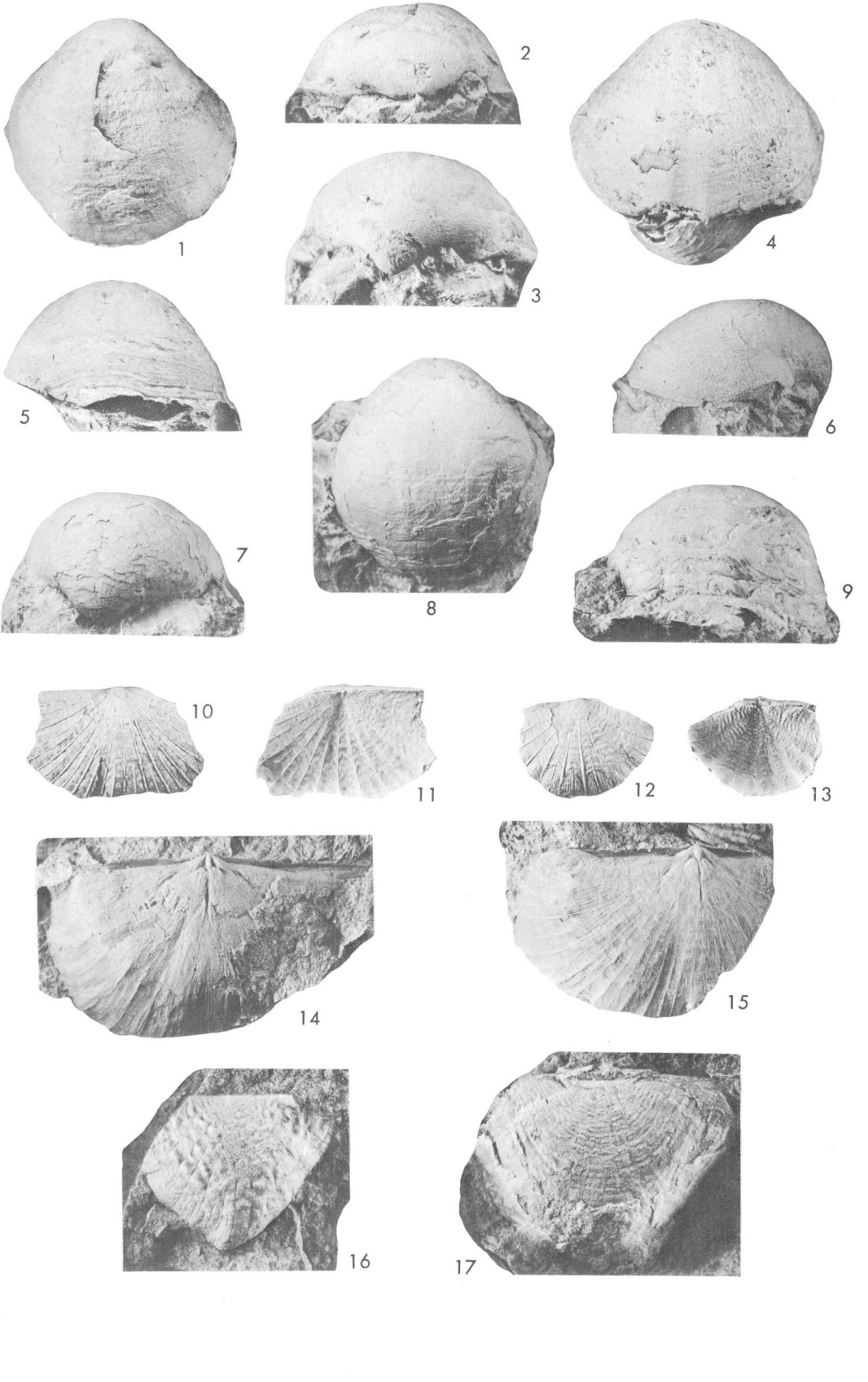
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PLATE VI

Thliborhynchia kerri new species (PAGE 24)

Figures 1–5. Ventral, dorsal, side, posterior, and anterior views of holotype (GSC 31831); GSC locality 67038, Bathurst Island; x1.5.

Figures 6–10. Side, ventral, dorsal, anterior, and posterior views (GSC 31832); same locality; x2.

Figures 11–15. Ventral, side, dorsal, posterior, and anterior views (GSC 31833); same locality; x2.

Figures 16–20. Dorsal, side, ventral, anterior, and posterior views (GSC 31834); same locality; x3. Note this specimen is also illustrated in Textfig. 7.

Figures 21, 22. Internal mould of brachial valve and rubber impression (GSC 31835); GSC locality C-11467, Cornwallis Island; x3.

Figure 23. Internal mould of brachial valve (GSC 31836); same locality; x4.

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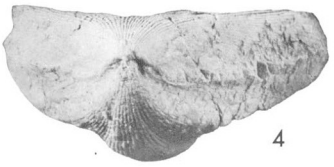
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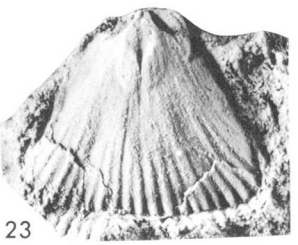
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PLATE VII

Thliborhynchia kerri new species (PAGE 24)

Figure 1. Ventral view of pedicle valve (GSC 31837); GSC locality C-11467, Cornwallis Island; x2.

Figure 2. Partial internal mould of pedicle valve (GSC 31838); same locality; x3.

Figure 3. Exterior of pedicle valve (GSC 31839); same locality; x3.

Ancillotoechia sp. A (PAGE 26)

Figures 4–8. Ventral, dorsal, anterior, posterior, and side views (GSC 31840); GSC locality C-8223, Prince of Wales Island; x3.

Katunia sp. (PAGE 25)

Figures 9–13. Ventral, dorsal, posterior, anterior, and side views (GSC 31841); GSC locality 67141, Bathurst Island; x3.

Figures 14–18. Ventral, dorsal, posterior, anterior, and side views (GSC 31842); same locality; x3.

Ancillotoechia sp. B (PAGE 26)

Figures 19–23. Ventral, dorsal, posterior, anterior, and side views (GSC 31843); GSC locality 67141, Bathurst Island; x1.5.

Figures 24–28. Ventral, dorsal, posterior, anterior, and side views (GSC 31844); same locality; x1.5.

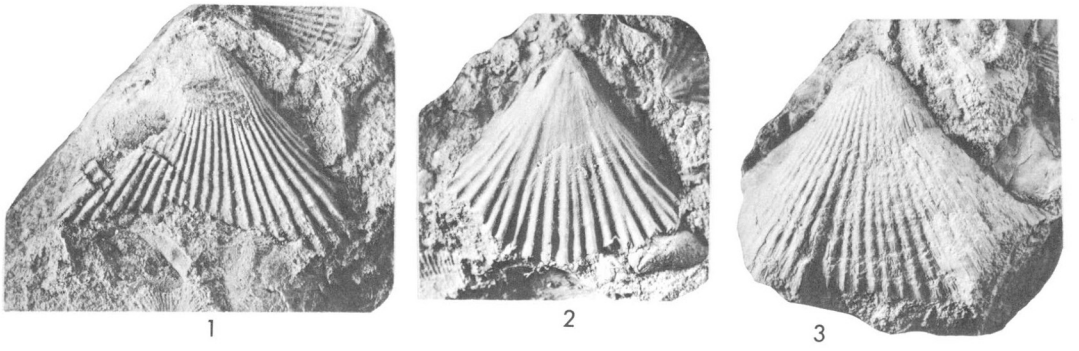
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PLATE VIII

Machaeraria sp. (PAGE 22)

Figures 1–5. Ventral, dorsal, posterior, anterior, and side views (GSC 31845); GSC locality C-8214, Prince of Wales Island; x2.

Figures 6–10. Ventral, dorsal, posterior, anterior, and side views of internal mould (GSC 31846); same locality; x2.

Figures 11, 12. Ventral and dorsal views of internal mould (GSC 31847); GSC locality 67039, Bathurst Island; x3.

Atrypa sp. (PAGE 27)

Figures 13–15. Ventral, dorsal, and side views (GSC 31848); GSC locality C-8216, Prince of Wales Island; x2.

Figures 16–18. Ventral, dorsal, and side views (GSC 31849); GSC locality C-8216, Prince of Wales Island, x2.

Atrypa exquisita new species (PAGE 26)

Figures 19–23. Posterior, anterior, dorsal, ventral, and side views of holotype (GSC 31850); GSC locality 67141, Bathurst Island; x1.5.

Figures 24, 25. Dorsal, and ventral views (GSC 31851); same locality; x1.5.

Figure 26. Dorsal view (GSC 31852); same locality; x2.

Figure 27. Ventral view (GSC 31853); same locality; x2.

Figure 28. Dorsal view (GSC 31854); same locality; x2.

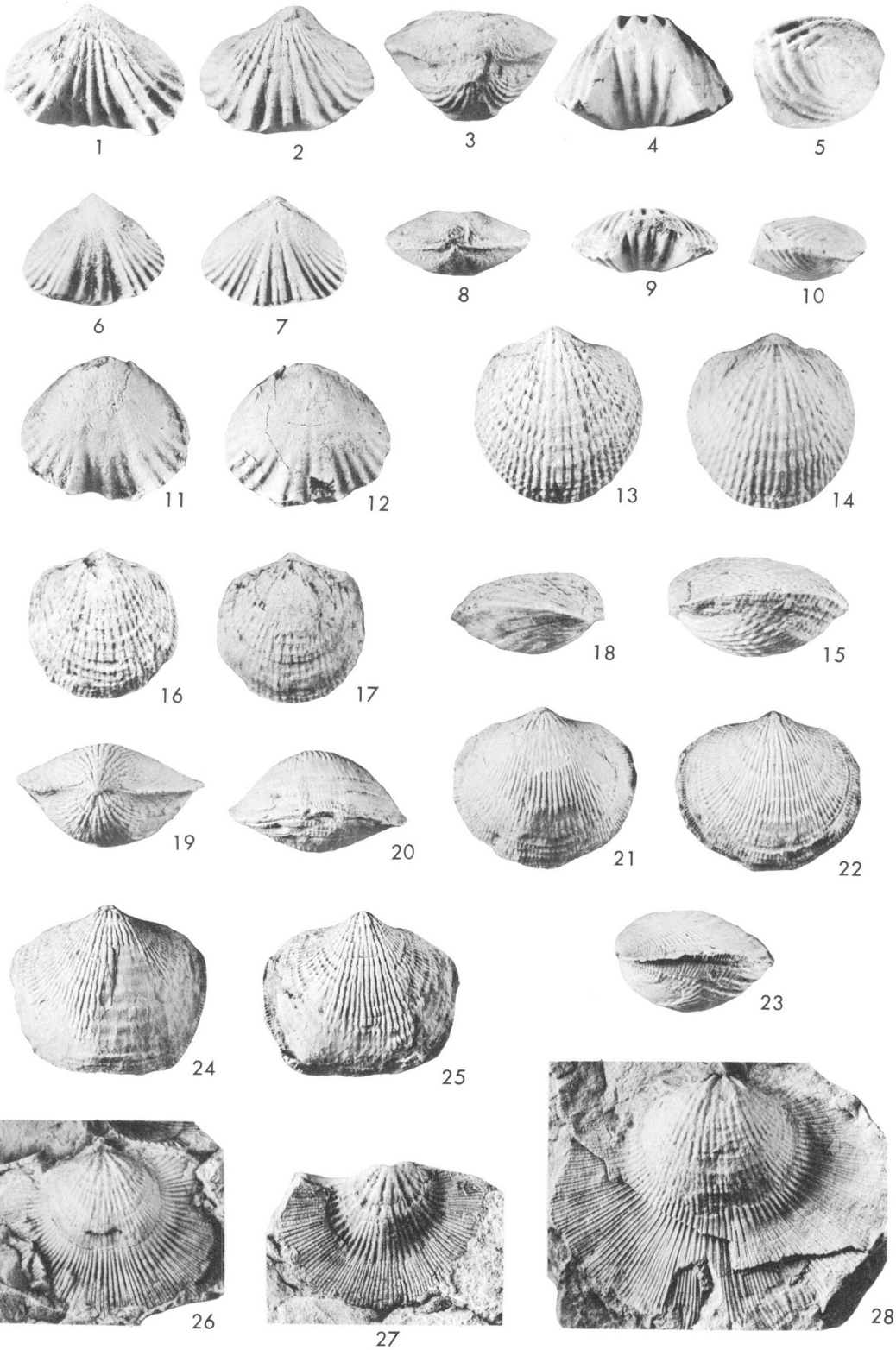
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PLATE IX

Spirigerina supramarginalis (Khalfin) (PAGE 28)

Figures 1–5. Ventral, dorsal, side, posterior, and anterior views (GSC 31855); GSC locality 67038, Bathurst Island; x3.

Figures 6-10. Side, dorsal, ventral, anterior, and posterior views (GSC 31856); same locality; x3.

Figures 11,12. Ventral and dorsal views (GSC 31857); same locality; x3.

Figures 13, 14. Ventral and dorsal views (GSC 31858); same locality; x3.

Figures 15–19. Ventral, anterior, side, dorsal, and posterior views (GSC 31859); GSC locality 67039, Bathurst Island; x2.

Figures 20, 21. Ventral and dorsal views (GSC 31860); same locality; x2.

Figures 22–26. Side, anterior, dorsal, posterior, and ventral views (GSC 31861); same locality; x2.

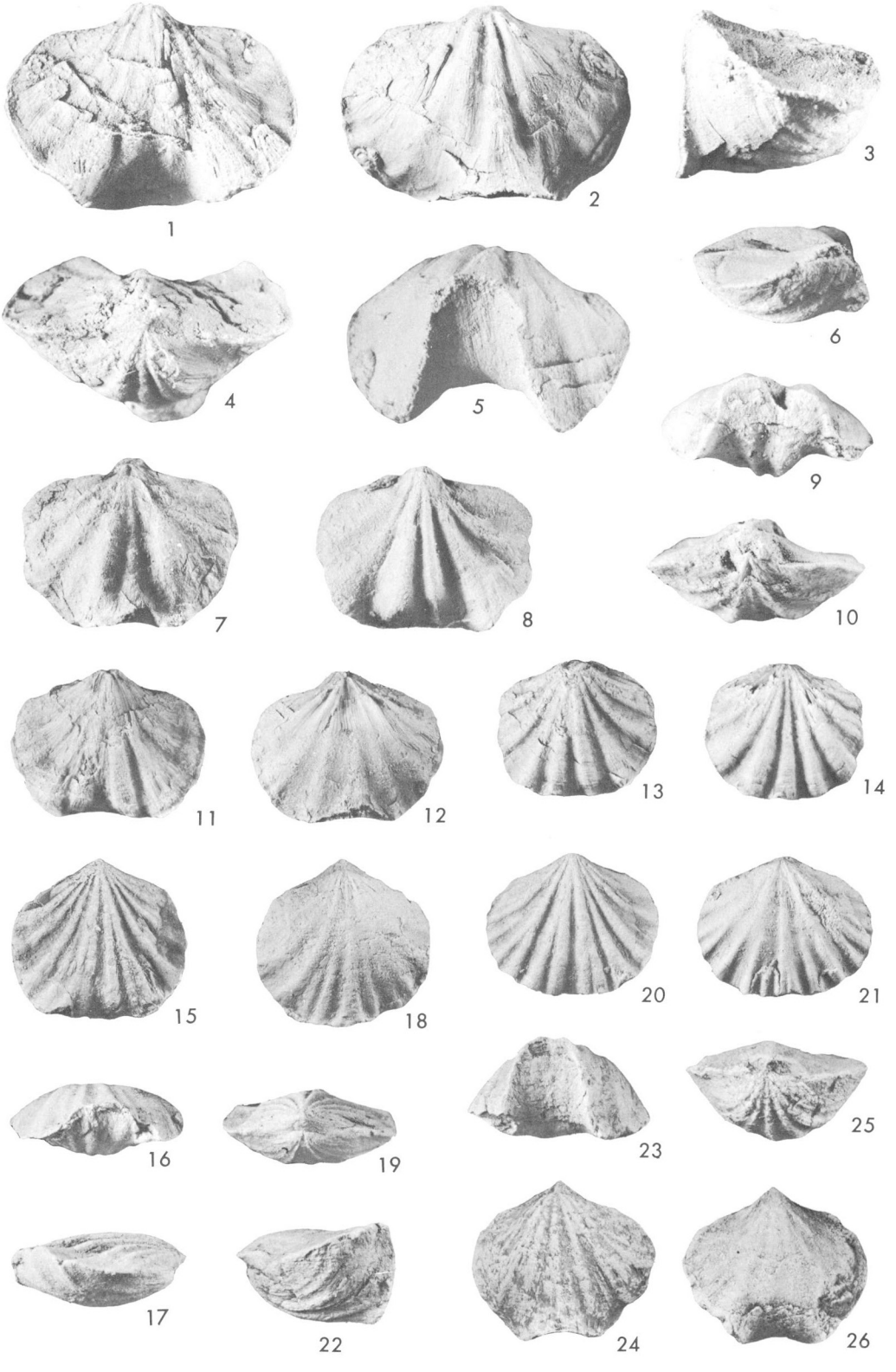
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PLATE X

Dubaria cf. *D. thetis* (Barrande) (PAGE 29)

Figures 1–5. Ventral, dorsal, posterior, anterior, and side views (GSC 31862); GSC locality C-8216, Prince of Wales Island; x3.

Figures 6–10. Side, ventral, dorsal, anterior, and posterior views (GSC 31863); GSC locality 67039, Bathurst Island; x3.

Ogilviella cf. *O. rotunda* Lenz (PAGE 29)

Figures 11–15. Ventral, dorsal, anterior, posterior, and side views (GSC 31864); GSC locality 67038, Bathurst Island; x3.

Figures 16, 19–22. Side, posterior, anterior, ventral, and dorsal views (GSC 31865); same locality; x3.

Figures 17, 18. Ventral and dorsal views (GSC 31866); same locality; x3.

Figures 23, 24. Ventral and dorsal views (GSC 31867); same locality; x3.

Undispirifer? sp. (PAGE 32)

Figures 25–29. Side, anterior, posterior, ventral, and dorsal views of partial internal mould (GSC 31868); GSC locality C-8219, Prince of Wales Island; x2.

Pinguispirifer carlsi new species (PAGE 31)

Figures 30–34. Side, anterior, posterior, ventral, and dorsal views of holotype (GSC 31870); GSC locality 67141, Bathurst Island; x2.

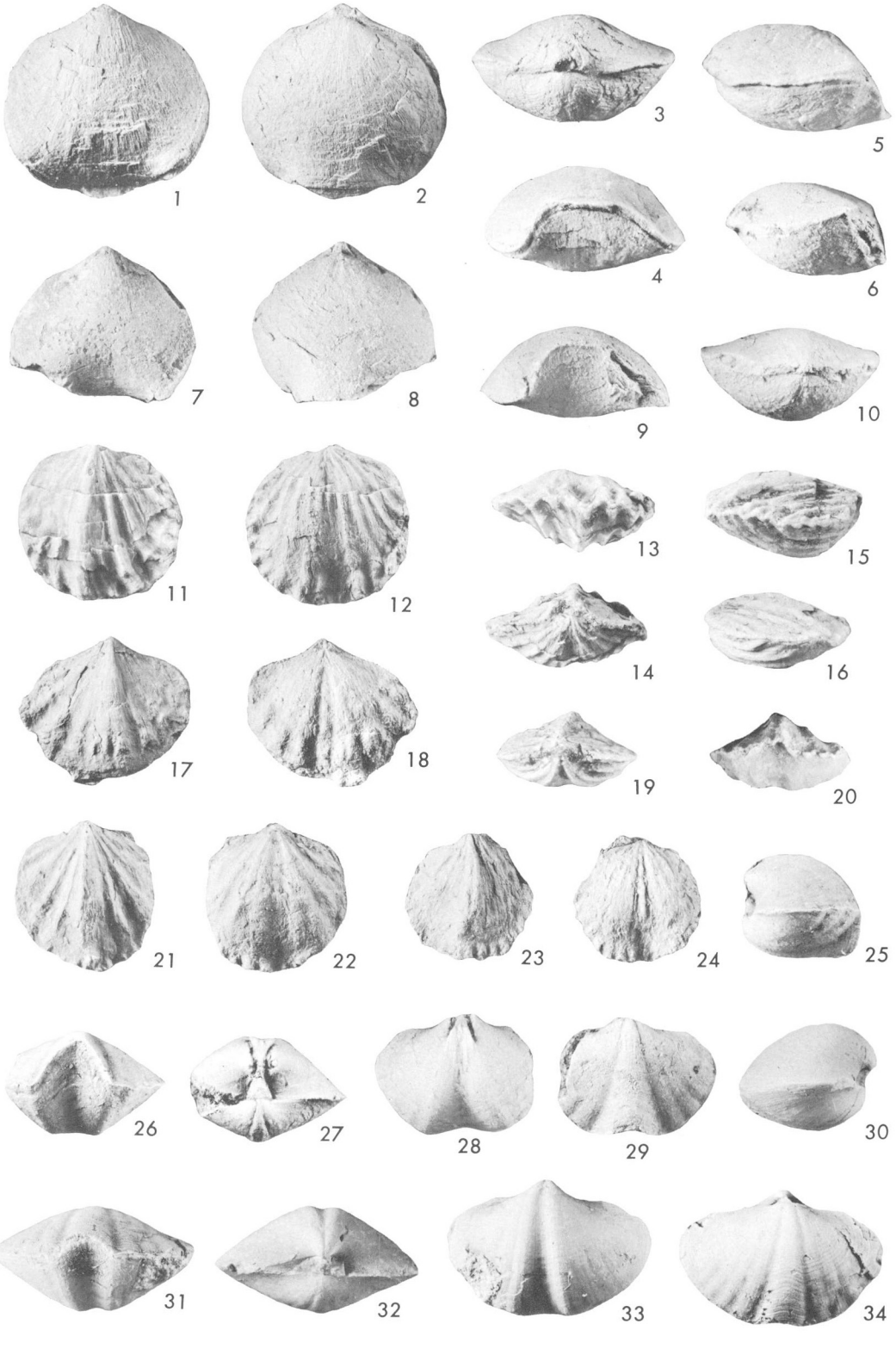
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PLATE XI

Pinguispirifer carlsi new species (PAGE 31

Figures 1, 2. Ventral and posterior views of internal mould of pedicle valve, with posterior and ventral views of an attached specimen (GSC 31871); GSC locality 67141, Bathurst Island; x3.

Figures 3–5. Posterior view of internal mould; posterior and ventral views of internal mould (GSC 31872); same locality; fig. 3, x5; figs. 4, 5, x2.

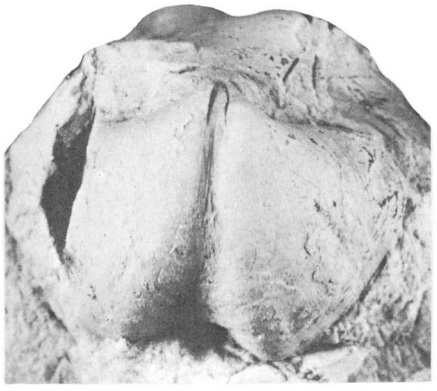
Figures 6, 7. Posterior and dorsal views of internal mould of brachial valve (GSC 31873); same locality; x3.

Undispirifer? sp. (PAGE 32)

Figures 8, 9. Ventral and dorsal views (GSC 31869); GSC locality C-8216, Prince of Wales Island; x2.

"*Camerella*"*?* sp. (PAGE 21)

Figures 10–15. Side, dorsal, ventral, posterior, and two anterior views (GSC 31874); GSC locality 67038, Bathurst Island; x3.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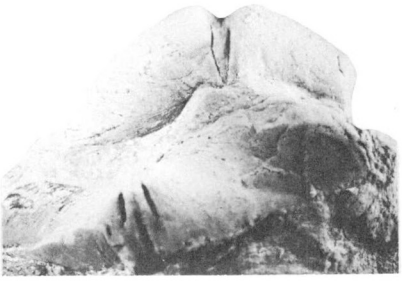
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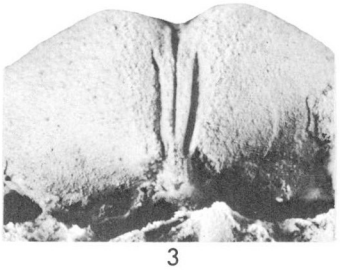
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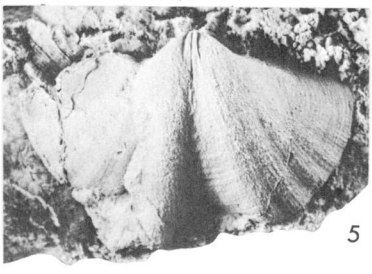
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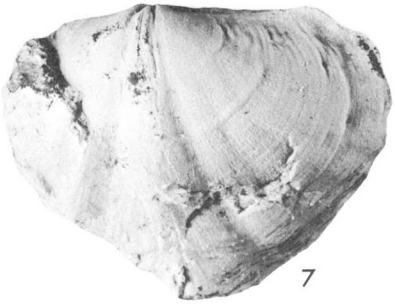
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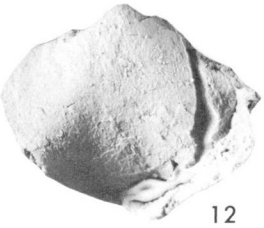
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THE BRACHIOPOD *WARRENELLA* IN THE LOWER AND MIDDLE DEVONIAN FORMATIONS OF NORTHWESTERN CANADA

by Rolf Ludvigsen[1] and D. G. Perry[1]

Abstract

Ten species of the brachiopod *Warrenella* Crickmay, 1953 from Lower and Middle Devonian strata of northern Canada are analyzed from a phylogenetic viewpoint and assigned to two distinct lineages: Occidentalis and Franklinii. These two lineages evolved from a common ancestor occurring in the mid-Lower Devonian of northern Canada, and by the early Middle Devonian, had migrated to other parts of the Old World Province, the Occidentalis Lineage to western Europe and the Franklinii Lineage to Nevada. Close correspondence in age and morphology of taxa of the Franklinii Lineage from northern Canada and Nevada and, to a lesser extent, of taxa of the Occidentalis Lineage from northern Canada and western Europe, demonstrate that a high degree of faunal interchange operated along the Old World Province seaway. The Franklinii Lineage became extinct before late Givetian time and *Warrenella laevis* was the only species of the Occidentalis Lineage to survive its nearly complete extinction at the end of the Givetian. The widespread *Warrenella* plexus in the Frasnian is the terminal development of the Eclectea Lineage which arose from the Occidentalis Lineage during early Givetian(?) time. During the Devonian, *Warrenella* persistently occupied a soft substrate habitat in a low energy and moderately deep water environment. The Occidentalis and Franklinii Lineages may serve as the basis for a refined zonation of the Emsian to Givetian interval in northern Canada. New taxa described are: *W. sekwensis*, *W. transversa*, *W. quadrata*, *W. weigelti meeki*, and *W. crickmayi*.

Résumé

L'analyse phylogénétique de dix espèces du brachiopode *Warrenella* Crickmay, 1953, des étages du Dévonien inférieur et du Dévonien moyen du nord du Canada les a classées dans deux lignées distinctes: l'Occidentalis et le Franklinii. Ces deux lignées, issues d'un ancêtre commun du milieu du Dévonien inférieur du nord du Canada ont émigré, au début du Dévonien moyen vers d'autres parties de la «Old World Province», la lignée Occidentalis allant vers l'Europe occidentale et la lignée Franklinii, au Nevada. L'étroite correspondance d'âge et de morphologie des taxons de la lignée Franklinii du nord du Canada et du Nevada, ainsi que, à un moindre degré, celle des taxons de la lignée Occidentalis du nord du Canada et de l'Europe occidentale, démontre qu'il s'est produit un grand nombre d'échanges dans la faune

[1] Department of Geology, University of Western Ontario, London.

avec la «Old World Province». La lignée Franklinii s'est éteinte avant la fin du Givétien, et le *Warrenella laevis* a été la seule espèce de la lignée Occidentalis à survivre à l'extinction presque totale de la fin du Givétien. Le plexus *Warrenella*, très répandu dans le Frasnien, constitue de développement final de la lignée Eclectea venue de la lignée Occidentalis au début du Givétien (?). Au cours du Dévonien, le *Warrenella* a continuellement occupé une sous-couche tendre comme habitat, dans un milieu plutôt stable et d'une profondeur d'eau moyenne. Les lignées Occidentalis et Franklinii peuvent servir de base à une répartition plus poussée de l'intervalle entre l'Emsien et le Givétien dans le nord du Canada. Les nouveaux taxons sont: *W. sekwensis*, *W. transversa*, *W. quadrata*, *W. weigelti meeki* et *W. crickmayi*.

Introduction

The Devonian strata of western and northern Canada contain an almost bewildering array of the reticulariid brachiopod *Warrenella*. The present investigation was prompted by the discovery of new species and subspecies of *Warrenella* in Lower and early Middle Devonian formations of northwestern Canada. Recent complementary studies of *Warrenella* in Nevada (Johnson, 1966, 1970a, 1971) and Germany (Struve, 1970) encouraged an attempt to place the *Warrenella* species in a phylogenetic framework. The suggested phylogeny has decisive implications in Devonian brachiopod provinciality, the dispersal of this and other taxa, and in correlation of Middle Devonian strata within northern Canada and with Nevada and Germany.

Warrenella is common in many Devonian formations in northern Canada and has good potential for zonation to amplify the existing one based mainly on rhynchonellids. Such biostratigraphic use already has been alluded to in the Givetian (Crickmay, 1960; Johnson, 1970b). The present study attempts zonation spanning the late Early Devonian (Emsian) to the latest Middle Devonian (Givetian) based on two separate lineages of *Warrenella*.

Acknowledgments

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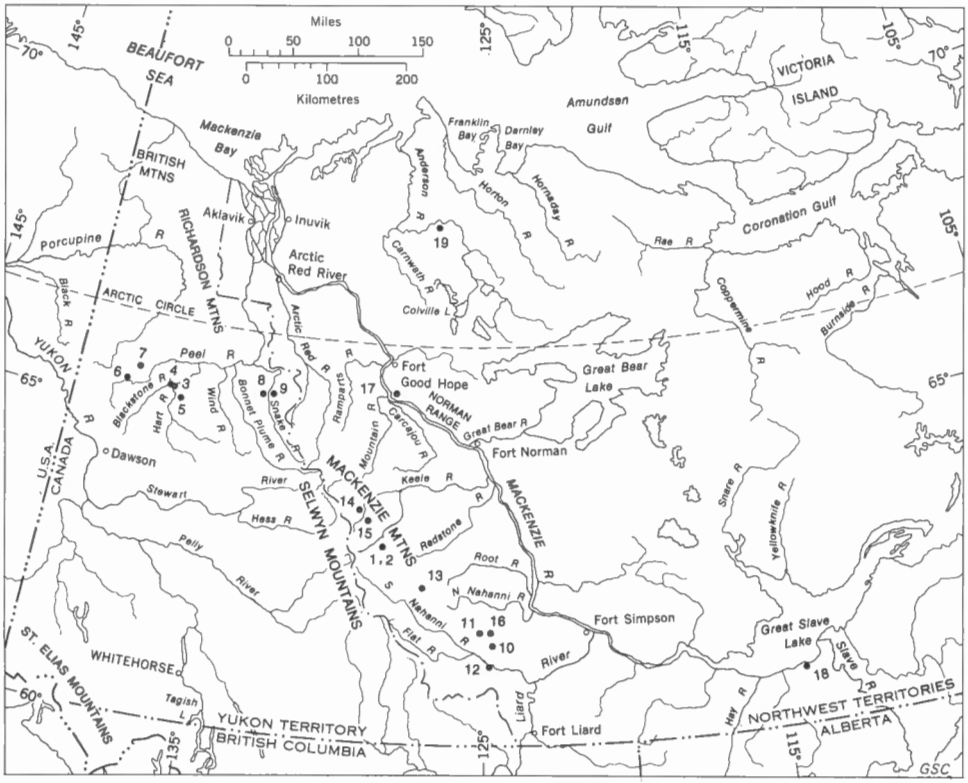
Stratigraphy

The proposed phylogeny of the species of *Warrenella* depends on a number of new age assignments of Lower and Middle Devonian formations in northern Canada.

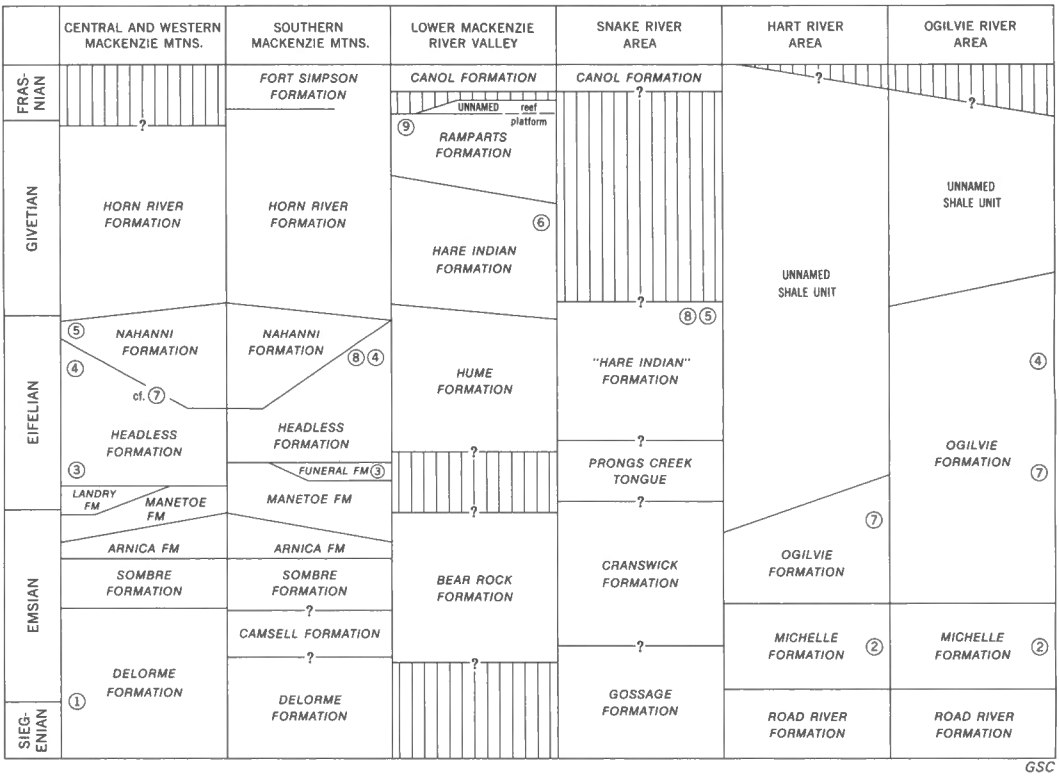
The faunas from the Delorme Formation are under study by Perry and the following tentative conclusions can be made. In the western Mackenzie Mountains, this unit spans the interval from late Ludlow to early Emsian and perhaps younger time. *Warrenella sekwensis* n. sp. is thought to be of late Siegenian or earliest Emsian age, and was collected 70 and 370 feet above an occurrence of *Monograptus yukonensis* Jackson and Lenz in the Delorme Formation.

Brachiopods and trilobites of the Michelle Formation indicate an Emsian age and dacryoconarid tentaculites and conodonts an early Emsian (Pragian) age (Ludvigsen, 1970, 1972; Ormiston, 1971; Fåhraeus, 1971). *Warrenella transversa* n. sp. is considered to be early Emsian.



1. G.S.C. locality C-23536, Delorme Formation, Natla River
2. G.S.C. locality C-23537, Delorme Formation, Natla River
3. G.S.C. locality C-23538, Michelle Formation, Hart River
4. G.S.C. locality C-23539, Michelle Formation, Hart River
5. G.S.C. locality C-23540, Ogilvie Formation, Hart River
6. G.S.C. locality C-23541, Ogilvie Formation, Ogilvie River
7. G.S.C. locality C-23542, Ogilvie Formation, Ogilvie River
8. G.S.C. locality C-23543, "Hare Indian Formation," Snake River
9. G.S.C. locality C-23544, "Hare Indian Formation," Snake River
10. G.S.C. locality C-23545, Headless Formation, Manetoe Range
11. G.S.C. locality C-23546, Headless Formation, Arnica Range
12. G.S.C. locality C-23547, Headless Formation, Headless Range
13. G.S.C. locality C-23548, Headless Formation, Backbone Ranges
14. G.S.C. locality C-23549, Headless Formation, Backbone Ranges
15. G.S.C. locality C-23550, Nahanni/Headless Formation, Backbone Ranges
16. G.S.C. locality C-23551, Funeral Formation, Manetoe Range
17. G.S.C. locality C-23552, Ramparts Formation, Carcajou Ridge
18. G.S.C. locality 19267, Pine Point Formation, Great Slave Lake
19. G.S.C. locality 41319, Hume Formation, Anderson River

TEXTFIGURE 12. Locality map (paper by Ludvigsen and Perry).



TEXTFIGURE 13. Correlation chart of Devonian formations in northern Canada showing occurrences of species of *Warrenella*.

1. *W. sekwensis* n. sp.
2. *W. transversa* n. sp.
3. *W. praekirki* Johnson
4. *W. kirki* (Merriam)
5. *W. crickmayi* n. sp.
6. *W. franklinii* (Meek)
7. *W. quadrata* n. sp.
8. *W. weigelti meeki* n. subsp.
9. *W. occidentalis timetea* Crickmay

Norris (1968a, b) suggested that the top of the Ogilvie Formation was highly diachronous. Perry (1971) demonstrated that the Ogilvie Formation is conformable with the underlying Michelle Formation and that the upper limit varies in age from late Emsian to late Givetian. *Warrenella quadrata* n. sp. is relatively well dated as late Emsian and Eifelian (probably early) based on associated brachiopods, conodonts, and trilobites (*see* locality index). *Warrenella kirki* (Merriam) was collected from near the top of the formation in the Nahoni Range, but without datable associated fauna. This horizon is thought to be of late Eifelian age based on the restricted range of the species in the southern Mackenzie Mountains. *Warrenella collina* (Crickmay) occurs "in the Lower Devonian with two-hole crinoid joints and a fauna of brachiopods" (Crickmay, 1968, p. 6) in the Campbell Lake Uplift south of Inuvik In this area, the interval with two-hole crinoid ossicles is restricted to an interval of less than 40 feet near the base of the Ogilvie Formation (Norris, 1967, p. 245, 258). In the Yukon Territory, the interval with abundant two-hole ossicles locally occurs in the lower

part of the Ogilvie Formation and, based on conodonts (Klapper *in* Perry, 1971), can be dated as late Emsian, or rarely early Eifelian. The Campbell Lake horizon is thought to be the same age.

Norris (1968a) applied the name Hare Indian to approximately 2,000 feet of shale underlying the Canol Formation and overlying the Prongs Creek Tongue in the Snake River area, but suggested that perhaps only the top few hundred feet of this might be correlative with the Hare Indian Formation of the type area. In the present paper, the term "Hare Indian" Formation is used for this thick development of shales to differentiate from the Hare Indian Formation of the Mackenzie Valley. *Warrenella crickmayi* n. sp. and *W. weigelti meeki* n. subsp. are present in a collection (C-23543) from the base of a distinct limestone unit (Units 74 to 76 of Norris, 1968a, Sec. 6) near the top of the "Hare Indian" Formation. *Warrenella crickmayi* is interpreted as the descendant of *W. kirki* (Merriam) in the lineage leading to *W. franklinii* (Meek) and should be restricted to a fairly short time interval in the late Eifelian to early Givetian. Elsewhere, *W. weigelti meeki* occurs in the Eifelian Headless Formation in association with *W. kirki.*

Assignment of the Middle Devonian faunas of the Headless Formation (and its facies equivalent Nahanni and Hume Formations) to the Eifelian or Givetian has long been a source of contention. An occurrence of *Warrenella weigelti meeki* and *W. kirki* high in the Headless Formation at GSC locality C-23546 indicates an Eifelian age for the Headless. In the Eifel region, *W. weigelti weigelti* (Struve) is restricted to the Eifelian. The Nahanni and Hume Formations also are considered to be Eifelian in the present paper, except for their highest beds that contain *Leiorhynchus castanea* (Meek) and are Givetian (House and Pedder, 1963, p. 498; Lenz and Pedder, 1972, p. 7). Eifelian conodonts have been recovered from the Hume Formation at Powell Creek, below the *L. castanea* beds (Lenz and Pedder, 1972). The occurrence of the *L. castanea* fauna slightly above late Eifelian faunal elements and the absence of any evidence of a break in sedimentation indicate an early Givetian age and, consequently, a late Eifelian age can be suggested for the underlying and widespread occurrences of *W. kirki* in the Headless Formation. *Warrenella* aff. *kirki* (Pl. XIV, figs. 18, 19) from *L. castanea* beds of the upper Hume Formation on Anderson River (GSC loc. 41319) differs markedly from *W. kirki* and may be a new species.

The lower part of the Hare Indian Formation contains *Leiorhynchus castanea* at many localities (McLaren, 1962). *Warrenella franklinii* (Meek) occurs higher in the formation, but its exact stratigraphic range is uncertain. Other than the holotype, only one Canadian specimen illustrated in the literature can be assigned with confidence to this species. This came from "about 50 feet below the contact with the overlying Ramparts Formation" (Caldwell, 1971, p. 14). *Warrenella franklinii* occurs in the *L. castanea* Zone in Nevada (Johnson, 1970b), but this association has not yet been demonstrated in Canada, perhaps because of insufficient detailed collecting. *Warrenella franklinii* is thought to be of early to mid-Givetian age, based on its occurrence above, and probable coexistence with, the *L. castanea* fauna and on its stratigraphic position well below the late Givetian *L. hippocastanea* fauna. McLaren (1962) considered *L. hippocastanea* (Crickmay) a junior synonym of *L. castanea*, but Johnson (1970b) emphasized the distinctiveness of these two species and demonstrated that they occupy consistent and discrete positions within the Givetian of western North America.

The Ramparts Formation is used in the sense of Caldwell (1964) and Tassonyi (1969) and consists of a lower platform member and an upper reef member. The *Leiorhynchus hippocastanea* fauna, which generally is reported as occurring at the top of the Ramparts Formation, actually occurs in the upper part of the platform member. This fauna contains the brachiopods *L. hippocastanea* (Crickmay), *Warrenella occidentalis timetea* Crickmay, and *Hadrorhynchia sandersoni* (Warren) and has been assigned a latest Middle Devonian age

(Crickmay, 1960; McLaren, 1962). This correlation is strengthened by the late Givetian age of the other geographic subspecies of *W. occidentalis—occidentalis* (Merriam) from Nevada and *torleyi* (Struve) from Germany (Johnson, 1970b, p. 2093)—and by the presence of conodonts of the *hermanni–cristatus* Zone in strata with *W. occidentalis timetea* at Powell Creek (Lenz and Pedder, 1972, p. 36). Crickmay (1970) suggested that the reef member of the Ramparts Formation (using the name Beavertail) is, at least in part, of Late Devonian age, but his cited fossil evidence is not convincing. A study of the reef margin of the Ramparts Formation on Powell Creek by MacKenzie (1970) shows the thickness of the Ramparts to increase from 100 to 800 feet in about one half mile, presumably due to the build-up of the reef member. MacKenzie identified 18 feet of limestone and shale containing reef debris directly overlying the platform member of the Ramparts Formation. The lower few feet of the reef debris unit contains a conodont fauna assignable to the Lower *Polygnathus asymmetrica* Zone of early Frasnian age (Lenz and Pedder, 1972, p. 37). MacKenzie concluded that the source of the reef debris was the nearby build-up of the reef member. The presence of an early Late Devonian fauna a few feet above *W. occidentalis timetea* further supports the high Givetian position of that species.

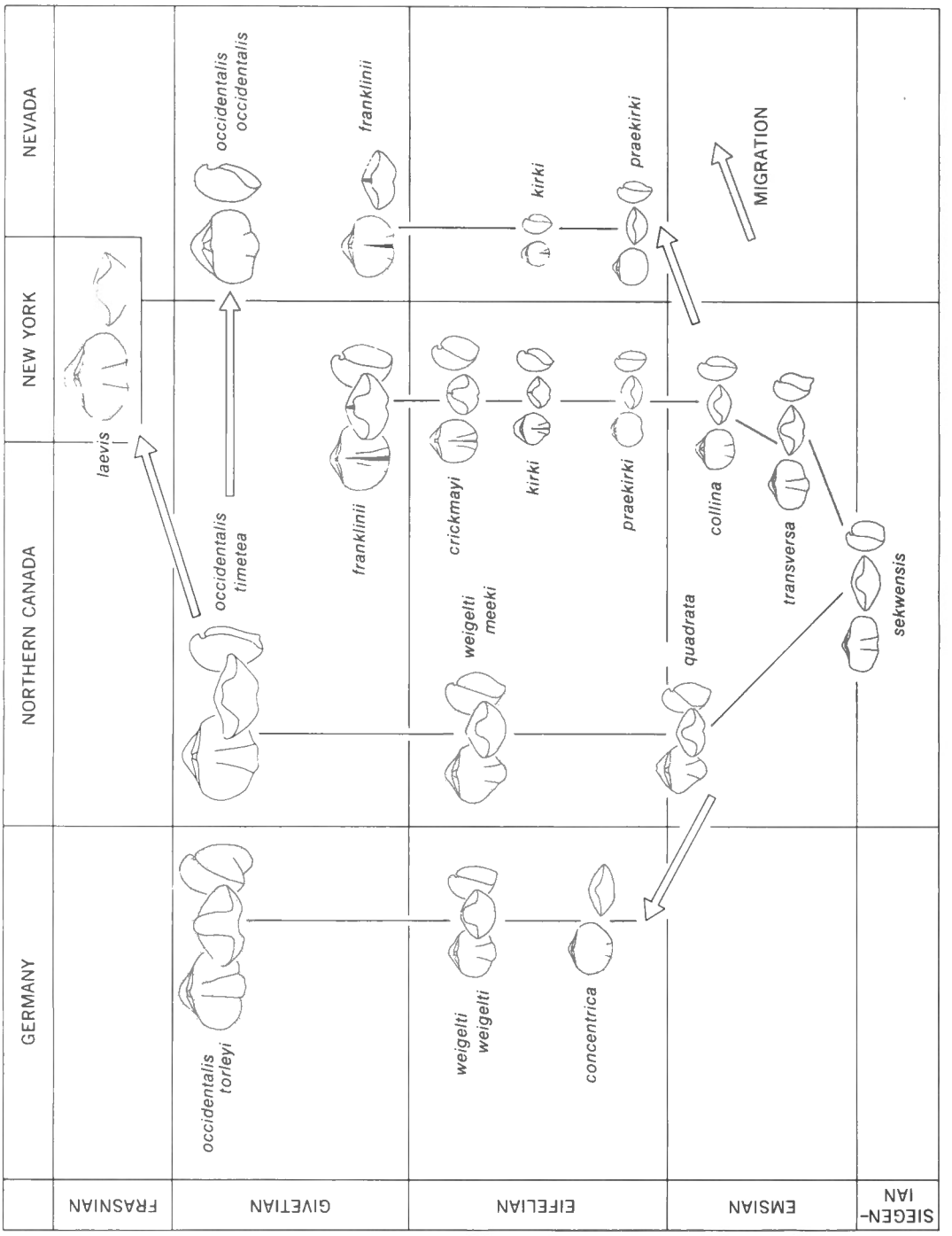
Phylogenetic Lineages of *Warrenella*

General Comments

Although species of *Warrenella* are common in Middle and Upper Devonian strata of western North America, few authors have commented on their temporal and phylogenetic relationship. Crickmay (1963, p. 17) considered *W. franklinii* (Meek) to be the ancestor of *W. timetea* Crickmay while McLaren (1962, p. 10) suggested that *W. timetea* was merely a large form of *W. franklinii*. Johnson (1966, p. 174) discussed the lineage *W. praekirki* Johnson – *W. kirki* (Merriam) from Nevada that was subject to a trend from transverse to elongate specimens and postulated that *W. kirki* was the ancestor to both *W. franklinii* and *W. timetea*.

Struve (1970), using the name *Minatothyris*, recently outlined an important sequence of *Warrenella* from Middle Devonian rocks of the Eifel region. This lineage starts in the mid-Eifelian Ahrdorf-Schichten with *W. concentrica* (Schnur), followed by *W. weigelti* (Struve) in the Junkerberg-Schichten, and culminates in the latest Givetian Massenkalk with the large *W. torleyi* (Struve). Johnson (1962, p. 168) commented on the overall similarity of *W. torleyi* (as *Spirifer maureri* Holzapfel, *in* Torley, 1934, Pl. 7, fig. 32) and *W. occidentalis* and concluded (1970b, p. 2091) that these taxa could be considered end members of one widely distributed species of late Givetian age and that *W. timetea* was a morphologic and geographic intermediate.

A close morphologic similarity between the type species of *Warrenella*, *W. eclectea* Crickmay from the Frasnian of western Canada and the approximately contemporary type species of *Minatothyris* Vandercammen, *M. euryglossus* (Schnur, 1851), from Germany, Poland, and Belgium was implied by Pitrat (1965, p. H721) and Biernat (1971, p. 156) in considering *Minatothyris* a junior synonym of *Warrenella*. These taxa are part of a widely distributed group of closely related species in the early Late Devonian of North America, western Europe, and Australia. This species group is badly in need of restudy, but the western North American species, *W. eclectea* Crickmay, *W. apodecta* Crickmay, *W. labrecquei* Crickmay, and *W. nevadaensis* (Walcott) should be included; also *W. euryglossus* (Schnur) and *W. maureri* (Holzapfel) from Europe; and *W.* cf. *W. eclectea* (*Minatothyris* sp. B, *in* Hill



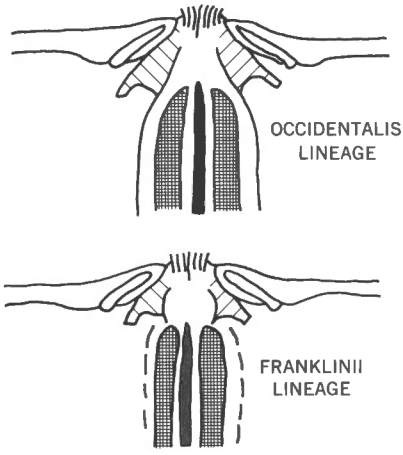
TEXTFIGURE 14. Suggested phylogeny of species of Occidentalis and Franklinii Lineages. Outline drawings are to scale and based on the largest complete specimens available. Placement on chart does not imply exact stratigraphic position.

et al., 1967, Pl. 11, figs. 30-34) from Australia. The only Frasnian species to be excluded from this group is *W. laevis* (Hall) from New York.

At least two distinct lineages of *Warrenella* can be recognized in northern Canada. One of these, the Franklinii Lineage, is present also in the Middle Devonian of Nevada and the other, the Occidentalis Lineage, with slight geographic variation, in the Middle Devonian of western Europe. A third lineage, the Eclectea Lineage, diverged from the Occidentalis Lineage during the Givetian and produced a widespread *Warrenella* plexus in the Frasnian (exclusive of *W. laevis*).

In charting these phylogenies, selected morphological features have been qualitatively analyzed, including entities that remain relatively constant in successive species, those that change gradually, and features that serve to distinguish the lineages. The more important features are shell outline, relative length of hinge line and height of ventral interarea, posterior persistence and shape of sulcus, height and cross-sectional shape of fold (and size and shape of anterior deflection), presence of a median dorsal furrow, and position of crural plates in relation to dorsal adductor field. The acquisition and change of some features is paralleled in both the Occidentalis and Franklinii Lineages. In both lineages the size of the shells increases from the Early to the Middle Devonian, the relative and absolute size of the deltidium and crural plates increase, and there is a tendency to decrease the anterior deflection although this feature is strongly modified in the last three species of the Franklinii Lineage. The articulating mechanisms undergo similar phylogenetic changes in both lineages. The hinge teeth become smaller relative to the size of the shell and the dental plates become thinner.

Some morphological features are useful in discriminating the Occidentalis from the Franklinii Lineage; but these, generally, cannot be used to differentiate the phylogenetic stage within the lineage. A wide hinge line which is only slightly shorter than the maximum width of the shell and a low, triangular ventral interarea characterize shells of the Franklinii Lineage, while a hinge line which is notably shorter than the maximum width and a high, triangular ventral interarea typify shells of the Occidentalis Lineage. An important difference between the two lineages is the relationship of the crural plates to the dorsal adductor field (Textfig. 15). In the Occidentalis Lineage, the anterior part of the crural plates bends slightly laterally to enclose the posterior part of the adductor scars; the lateral bounding ridges of the muscle field are continuous with the bases of the crural plates. In the Franklinii Lineage, the subparallel to slightly convergent crural plates terminate against the posterior edge of the



TEXTFIGURE 15

Schematic diagram showing differences in disposal of crural plates in relation to the dorsal adductor field of the Occidentalis and Franklinii Lineages.

adductor muscle field and are not continuous with the low, lateral bounding ridges. In the late Eifelian and Givetian interval, the presence of a median dorsal furrow and a narrow sulcus which initiates at the ventral beak readily identifies species of the Franklinii Lineage.

The succession of species in each lineage is outlined on stratigraphic position and on a restricted number of external features (shell outline; persistence, shape, amplitude of fold and sulcus; size and shape of the anterior deflection). Textfigure 14 illustrates diagrammatically the change in external morphology of the species of the Occidentalis and Franklinii Lineages. The oldest member of the genus, *Warrenella sekwensis* n. sp., contains both highly transverse and nearly equidimensional individuals and appears to share affinities with both *W. transversa* n. sp. and *W. quadrata* n. sp. and it was probably the ancestor to both lineages.

Franklinii Lineage

The Franklinii Lineage in northern Canada involves at least six species in the early Emsian to mid-Givetian interval: *Warrenella transversa* n. sp., *W. collina* (Crickmay), *W. praekirki* Johnson, *W. kirki* (Merriam), *W. crickmayi* n. sp., and *W. franklinii* (Meek). The most obvious phylogenetic modification in this lineage is the change in outline from transverse to elongate to equidimensional accompanied by an increase in size. Concurrent with this change are, initially, a decrease in the height of the anterior deflection and, subsequently, an increase in the height of the anterior deflection accompanied by progressive development of a dorsal median furrow.

The Middle Devonian part of the Franklinii Lineage is matched closely in Nevada, although *Warrenella crickmayi* has not been recognized. *Warrenella franklinii* is present in the *Leiorhynchus castanea* Zone in faunas being described by J. G. Johnson. Appropriate ancestors to *W. praekirki* have not been recognized in Nevada, although the Early Devonian brachiopods are well known, and it is suggested that a *praekirki* ancestor (*W. collina* or an unknown form) migrated south to Nevada from the Yukon/District of Mackenzie region during the latest Emsian or earliest Eifelian. Judging from the close similarity of brachiopod faunas during parts of the Early Devonian (Lenz, 1968; Johnson *et al.*, 1968; Ludvigsen, 1970; Perry, 1971) and a nearly identical succession of species of the Franklinii Lineage in Nevada and northern Canada, a vital connection between the two areas must have been maintained for most of the Devonian. Johnson (1971) assigned an early Givetian age to the *W. kirki* Zone in Nevada. In view of the previously cited brachiopod and conodont evidence from northern Canada and additional unpublished conodont evidence from Nevada (J. G. Johnson, pers. com., 1972) this age should be revised to late Eifelian.

Occidentalis Lineage

The Occidentalis Lineage in northern Canada includes three species: *Warrenella quadrata* n. sp., *W. weigelti meeki* n. subsp., and *W. occidentalis timetea* Crickmay, from the late Emsian to late Givetian interval, in addition to the common ancestor with the Franklinii Lineage, *W. sekwensis* n. sp. This phylogenetic lineage involves a change in outline from quadrate to subcircular to slightly transverse accompanied by a decrease in the relative length and depth of the sulcus.

The presence of a nearly identical lineage of *Warrenella* in the Middle Devonian of the Eifel region of Germany, *W. concentrica* (Schnur), *W. weigelti weigelti* (Struve), and *W. occidentalis torleyi* (Struve), raises the question of the degree and route of faunal interchange between these two areas. Faunal exchange between western North America and Europe during the Early and Middle Devonian is certain and the route of this exchange generally has been accepted to be via the Arctic Islands and Uralian Seaway. It is suggested that *W.*

quadrata or a related form migrated from northern Canada to Europe during the early Eifelian by the Arctic route and that a high degree of faunal interchange was maintained for the duration of the Middle Devonian. This finds evidence in the two successive pairs of geographic subspecies, *W. weigelti meeki* and *W. occidentalis timetea* from Canada and *W. weigelti weigelti* and *W. occidentalis torleyi* from Germany. It is suggested despite the lack of any record of *Warrenella* in the Middle Devonian of the Arctic Islands. A combination of a restricted paleoenvironment of *Warrenella* and an insufficient detailed knowledge of Devonian biostratigraphy in the Arctic Islands may be a partial explanation for the lack of a *Warrenella* record.

The earliest member of the Occidentalis Lineage in Germany, *Warrenella concentrica*, is less inflate and has a lower anterior deflection than its Canadian ancestor, *W. quadrata*; and, as is implied by the trivial names, their outlines differ. The illustrations in Struve (1970) demonstrate that some specimens of *W. concentrica* approach the morphology of *W. quadrata*: his Plate 13, figure 64 shows a large quadrate specimen with a well-pronounced and moderately deep sulcus and Plate 12, figure 61 an inflate specimen with a moderately high and rounded anterior deflection (the "*torleyi*-Tendenz" of Struve, 1970). In Canada, the *W. quadrata* morphology persists well into the Eifelian based on a single specimen of *W.* cf. *W. quadrata* from the Headless Formation (Pl. XVI, figs. 12–15).

Warrenella weigelti appears in the mid-Eifelian, or slightly later, in Canada and Germany as two subspecies showing minor geographic variation. *W. weigelti meeki* from Canada is more inflate and has a higher ventral interarea than *W. weigelti weigelti* from Germany. Larger specimens of the Canadian subspecies develop a broad, very shallow, and flat-bottomed sulcus while the German subspecies has a moderately deep and rounded sulcus.

The transition to a *Warrenella occidentalis* morphology occurred earlier in Germany than in Canada judging from the transverse specimen with a deep and flat sulcus illustrated by Struve (1970, Pl. 11, figs. 54a, b) from the late Eifelian. A direct comparison of *W. occidentalis* from the late Givetian of Germany and Canada allows a distinction to be made on the height and shape of the anterior deflection. *W. occidentalis torleyi* has a very high, rounded deflection with parallel flanks while *W. occidentalis timetea* has a moderately low, rectangular deflection, typically with flanks slightly divergent ventrally. The height of the anterior deflection of some Canadian specimens (Crickmay, 1963, Pl. 11, figs. 16–18) approaches that of the German subspecies.

Until the latest Givetian, species of the Occidentalis Lineage were confined to northern Canada and western Europe. At this time the Occidentalis Lineage appeared for the first time in Nevada as *Warrenella occidentalis occidentalis*, a geographic subspecies which can be distinguished from the other subspecies by its very shallow sulcus and its low anterior deflection. Based on the morphology of the Nevada subspecies, it is interpreted to be a migrant from northern Canada. *W. laevis* (Hall) from the mid-Frasnian of New York also is interpreted to be a derivative of *W. occidentalis timetea* which migrated eastward across the continental backbone during Taghanic time.

Eclectea Lineage

The type species, *Warrenella eclectea* Crickmay, is part of a widely distributed species group of Frasnian age from western North America, Europe, and Australia. Full consideration of this group is beyond the scope of this paper, but a few comments can be made on its origin. In northern Canada, the only Middle Devonian species that can be assigned to the Eclectea Lineage is *Warrenella* cf. *maureri* (Holzapfel) from the Pine Point Formation. The short hinge line and slightly convex brachial valve, almost completely lacking a fold, de-

monstrate its derivation from the Occidentalis Lineage. The transverse outline and the broad, indistinct anterior deflection ally it to the species of the Frasnian *eclectea* plexus, especially *W. maureri*, suggesting that the Eclectea Lineage split from the Occidentalis Lineage during the early Givetian. Judging from the few poorly preserved *W. maureri* noted by Vandercammen (1957b) in the Middle Devonian of Belgium, this split also can be recognized in Europe.

Paleoecology

One of the more distinctive features of *Warrenella* is the wide discrepancy in the thickness of the brachial and pedicle valves. The posterior part of the pedicle valve has a thick prismatic deposit of secondary shell material under a thin lamellar layer. The shell of the brachial valve and the anterior part of the pedicle valve is composed exclusively of lamellar layer. The older species of *Warrenella* (*W. sekwensis* and *W. transversa*) lack a delthyrial cover or have only an apical deltidium but, by the start of the Middle Devonian, species of both the Occidentalis and Franklinii Lineages had developed extensive deltidia. This means that a functional pedicle became atrophied during an early ontogenetic stage and the adult shells were free lying. The extra weight of the callus in the posterior part of the ventral valve would indicate a living position with the umbo down and the anterior part pointing upward. Rudwick (1970, p. 89) noted that this adaptation for stability in a soft substrate was common in Paleozoic brachiopods and developed independently in a number of diverse groups, including the Athyridacea, Stenoscismatacea, and Pentameracea.

Biernat (1971, p. 159) noted the occurrence of *Warrenella euryglossus* in "nest-like clusters," but did not describe the orientation of the shells within the clusters. This may be consistent with the living position suggested above since the nest-like grouping could be attributed to juvenile brachiopods attached by the pedicle. As the shells grew and the pedicle became atrophied, the nest-like grouping would be maintained even though the shells were free lying.

In northern Canada, *Warrenella* occurs in abundance in formations characterized by micrite and biomicrite, often highly argillaceous, and calcareous shale, such as the Michelle, Headless, "Hare Indian," and Delorme Formations, and is commonly absent or rare in units with significant amounts of in situ coralline or stromatoporoidal material, such as the Nahanni, upper part of the Hume, and parts of the Ogilvie and Ramparts Formations. The horizon with abundant *W. occidentalis timetea* in the generally reefoid Ramparts Formation was termed the Carcajou marker by Tassonyi (1969) who noted that it consisted of interbedded dark limestones and shales.

Warrenella very rarely has been reported with *Stringocephalus*. In the Ramparts Formation, *Stringocephalus* occurs in the well-bedded, resistant carbonates of the platform member, stratigraphically lower than the thin-bedded, argillaceous Carcajou marker. *Warrenella* has not been collected from the 700 feet of grey limestone bearing *Stringocephalus* in the upper part of the Ogilvie Formation on Mount Burgess (Norris, 1968a; Perry, 1971). Johnson (1971) noted the absence, or extreme rarity, of *Warrenella* in the *Stringocephalus* Biostrome of Nevada. The environmental significance of *Stringocephalus* is difficult to assess, but it appears to have occupied a shallower water habitat than *Warrenella*. This is underscored by numerous occurrences of *Stringocephalus* in the Givetian Elk Point Basin of Alberta, Saskatchewan, and Manitoba (Boucot *et al.*, 1966). *Warrenella* has not been reported from the cratonic side of the Presqu'ile Barrier, probably because it was unable to invade this shallow-water sea of restricted circulation. *Warrenella* succeeded in crossing the continental backbone during Taghanic time when a sufficiently deep water regime was established.

Johnson (1971) noted the low species diversity and the extreme abundance of a few taxa (*W. kirki* and *Leiorhynchus miriam*) in the upper fauna of the *W. kirki* Zone from Nevada and referred to it as the "*Warrenella* Community." Noble and Ferguson (1971) recognized a similar "*Warrenella* Rhynchonellid Community" from the shale–limestone transition in the Headless/Nahanni Formation of the southern Mackenzie Mountains. They placed this community seaward from communities dominated by tabulate corals and stromatoporoids and landward from the pelagic community. Harrington (1970) placed his low species diversity "*Warrenella* Biotope," from the Upper Devonian Genesee Group of New York, at the edge of the outer neritic zone, landward from the "Naples Biotope" dominated by a pelagic fauna. There appears to be good basis for the recognition of a *Warrenella* Community that persistently maintained a soft substrate habitat, in a low energy and moderately deep water environment from Early to Late Devonian time.

Systematic Paleontology

Prefix GSC refers to specimens in the type collections of the Geological Survey of Canada, Ottawa.

Suborder *SPIRIFEROIDEA*

Superfamily RETICULARIACEA

Family RETICULARIIDAE

Genus *Warrenella* Crickmay, 1953

Type species. *Warrenella eclectea* Crickmay, 1953, p. 596, Figs. 1–5, 16–19, from the Frasnian of Alberta.

Diagnosis. Shells medium to large, equally to ventribiconvex, outline transverse to elongate. Ventral sulcus and dorsal fold of variable strength. Anterior commissure weakly to strongly uniplicate. Hinge line slightly to markedly shorter than maximum width. Ventral interarea broadly triangular, cleft by relatively large delthyrium with variably developed, convex deltidium. Concentric ornament of fine rows of closely spaced spine bases. Pedicle valve interior has short dental plates bounding posterior part of moderately to very deeply impressed muscle field. Shell very thick in posterior part of pedicle valve. Dorsal interior has variably developed crural plates.

Assigned Lower and Middle Devonian species:

Spirifer concentricus Schnur, 1851
Spirifer (Martinia) franklinii Meek, 1867
Spirifer maureri Holzapfel, 1895
Martinia kirki Merriam, 1940
Martinia kirki var. *occidentalis* Merriam, 1940
Warrenella timetea Crickmay, 1960
Warrenella kirki praekirki Johnson, 1966
Spirinella collina Crickmay, 1968
Minatothyris torleyi Struve, 1970
Minatothyris weigelti Struve, 1970
Warrenella sekwensis n. sp.
Warrenella quadrata n. sp.

Warrenella weigelti meeki n. subsp.
Warrenella transversa n. sp.
Warrenella crickmayi n. sp.

Remarks. In the definitive paper, Crickmay (1953) assigned *Martinia franklinii* to *Warrenella* along with two Late Devonian species, *W. apodecta* and the type species *W. eclectea.* Curiously, he did not comment on the relationship of *W. franklinii* to Merriam's (1940) species from Nevada, *Martinia kirki* and *M. kirki* var. *occidentalis*, even though Merriam had stated clearly that he thought these three taxa differed only at the species level. In a later paper, Crickmay (1960), in commenting on the possible conspecificity of *W. timetea* and the specimens illustrated by Warren (1944) and Warren and Stelck (1956) as *M. occidentalis*, stated that he did not consider *W. timetea* to be even generically related to *M. occidentalis.*

Crickmay (1962) assigned *Warrenella franklinii* and *W. timetea* to *Tingella* Grabau (junior synonym of *Reticulariopsis* Fredericks) because both species possess crural plates. Johnson (1971), however, demonstrated that crural development in *W. kirki* from Nevada is highly variable and that specimens with well-developed crural plates occur in the same populations as specimens completely lacking crural plates; this suggests that presence or absence of crural plates in these species is of less than generic importance.

Warrenella collina (Crickmay, 1968) from the late Emsian (?) of the Campbell Lake Uplift area was assigned originally to *Spirinella* Johnston. This assignment does not stand because *Spirinella* possesses long subparallel dental plates and a ventral muscle field that is not noticeably impressed. These features stand in sharp contrast to the short dental plates and the deeply impressed ventral muscle field of *W. collina.*

The specimens identified as *Warrenella* sp. by Johnson (*in* Ormiston, 1969) from the upper Siegenian Drake Bay Beds on Prince of Wales Island can best be assigned to *Cingulodermis* Havlíček, 1971. It seems worthwhile to separate these small shells with open delthyria and only very minor thickening of the posterior part of the ventral valve from the more robust *Warrenella.*

Vandercammen (1957a) described a new genus, *Minatothyris*, with the type species, *Spirifer euryglossus* Schnur, 1851. He diagnosed his genus as "Reticulariids with single spines, without costae, with a ventral sulcus and a smooth dorsal fold, with dental plates and umbonal callus." This diagnosis is virtually identical to the one presented for *Warrenella* by Crickmay four years earlier. Recently, Struve (1970) applied the name *Minatothyris* to the group of robust shells from the German Middle Devonian previously known as *Spirifer concentricus* Schnur, 1851 and *S. maureri* Holzapfel (Torley, 1934, Pl. 7, fig. 32); that is, *M. concentrica* (Schnur), *M. weigelti* Struve, and *M. torleyi* Struve. That these species are congeneric with *Warrenella* is well demonstrated by the recognition of a nearly identical group from the Middle Devonian of northern Canada. The same conclusion for Frasnian species was reached by Pitrat (1965, p. H721) and Biernat (1971, p. 156) who placed *M. euryglossus* in *Warrenella.*

Delthyris laevis Hall, 1843 from the Upper Devonian of New York has been assigned recently to *Warrenella* (Harrington, 1970). Serial sectioning and preparation of internal moulds of material from the top of the Sherburne Formation at Ithaca (*Ponticeras perlatum* Zone, mid-Frasnian) confirms the assignment to *Warrenella.* The presence of the genus in the Frasnian of New York is of interest because *W. laevis* is morphologically distinct from the species of the *eclectea* plexus and appears to be related to *W. occidentalis timetea.* It is suggested that *W. laevis* is the only member of the Occidentalis Lineage to survive its otherwise complete extinction at the end of the Middle Devonian and that the species is a migrant from the *W. occidentalis* group in western North America.

Warrenella sekwensis new species

Plate XII, figures 1–15

Material (silicified). Holotype (GSC 32053), paratypes (GSC 31314, 31315) GSC loc. C-23536; (GSC 31316, 31337–31339) GSC loc. C-23537; all from Delorme Formation.

Description. Exterior. Shell equally biconvex, outline subrectangular. Hinge line slightly less than maximum width which is attained slightly anterior to midlength. Cardinal angles subrounded, obtuse. Pedicle valve bears distinct, rounded, relatively deep, sharply bounded sulcus which widens and deepens anteriorly. Brachial fold moderately high, subrounded. Ventral interarea high, triangular, apsacline, divided by wide, open delthyrium with short apical deltidium. Dorsal interarea low, triangular, slightly anacline. Anterior commissure uniplicate, deflection subrounded. Concentric ornament of fine growth lines near anterior margin.

Pedicle valve interior. Hinge teeth weak, dorsally directed knob-like projections which diverge slightly anteriorly; supported by short medially bowed dental plates which diverge markedly basally. Ventral muscle scar broadly subpyriform, deeply impressed, divided by low myophragm, covered by coarse radial striae; anterior part slightly raised. Thick posterior callus. Highly pustulose areas flank muscle field.

Brachial valve interior. Sockets strong, deep, widely divergent; socket ridges extend laterally for about one-third length of hinge line. Thin crura project dorsomedially from inner edges of socket ridges, remaining free of valve floor. Diductor muscles attached to deeply striate, slightly flaring, comb-like process which fills apical part of notothyrial cavity. Pair of very elongate, subelliptical, deeply impressed adductor muscle scars divided medially by distinct myophragm. Remainder of interior smooth.

Discussion. The subtransverse shell, subrounded anterior deflection, high triangular ventral interarea with small apical deltidium distinguish *Warrenella sekwensis* from other *Warrenella* species. *Warrenella sekwensis* has features common to both Franklinii and Occidentalis Lineages. The high triangular ventral interarea and sharply defined sulcus ally it to the Occidentalis Lineage while the relatively deeply impressed adductor scars and transverse outline of many shells indicate affinity to *W. transversa* of the Franklinii Lineage.

The species name is after Sekwi Mountain in the western Mackenzie Mountains.

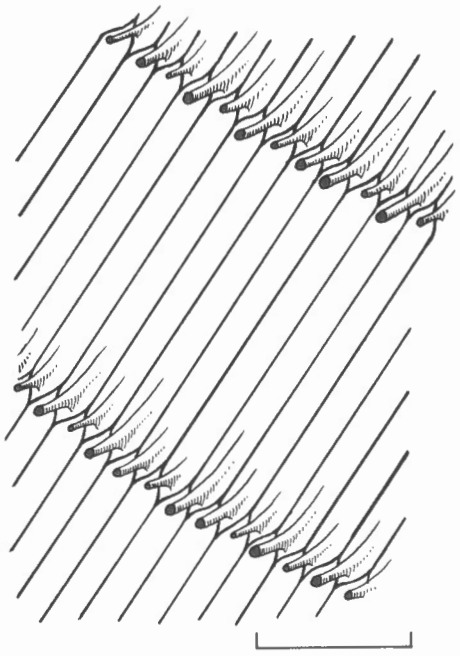
Warrenella transversa new species

Plate XIII, figures 1–26; Textfigures 16, 17

Warrenella n. sp., Ludvigsen, 1970, Pl. 2, figs. 23–27.
Reticulariopsis sp. cf. *R. reticularioides* (Grabau), Ludvigsen, 1970, Pl. 2, figs. 13–15.

Material (calcareous). Holotype (GSC 31287); paratypes (GSC 31288–31297, 31333), GSC loc. C-23538; (GSC 26645, 26646), GSC loc. C-23539; serial sectioned paratypes (GSC 31325, 31326), GSC loc. C-23538; all from Michelle Formation.

Description. Exterior. Shell ventribiconvex, outline transversely suboval to subcircular. Hinge line slightly shorter than maximum width. Pedicle valve bears distinct, relatively deep, evenly concave sulcus beginning at moderately incurved beak, becoming flat-bottomed anteriorly. Narrow, steep-sided fold initiates at brachial beak, becoming slightly wider anteriorly; near anterior margin fold flares slightly. Anterior deflection steep-sided, with



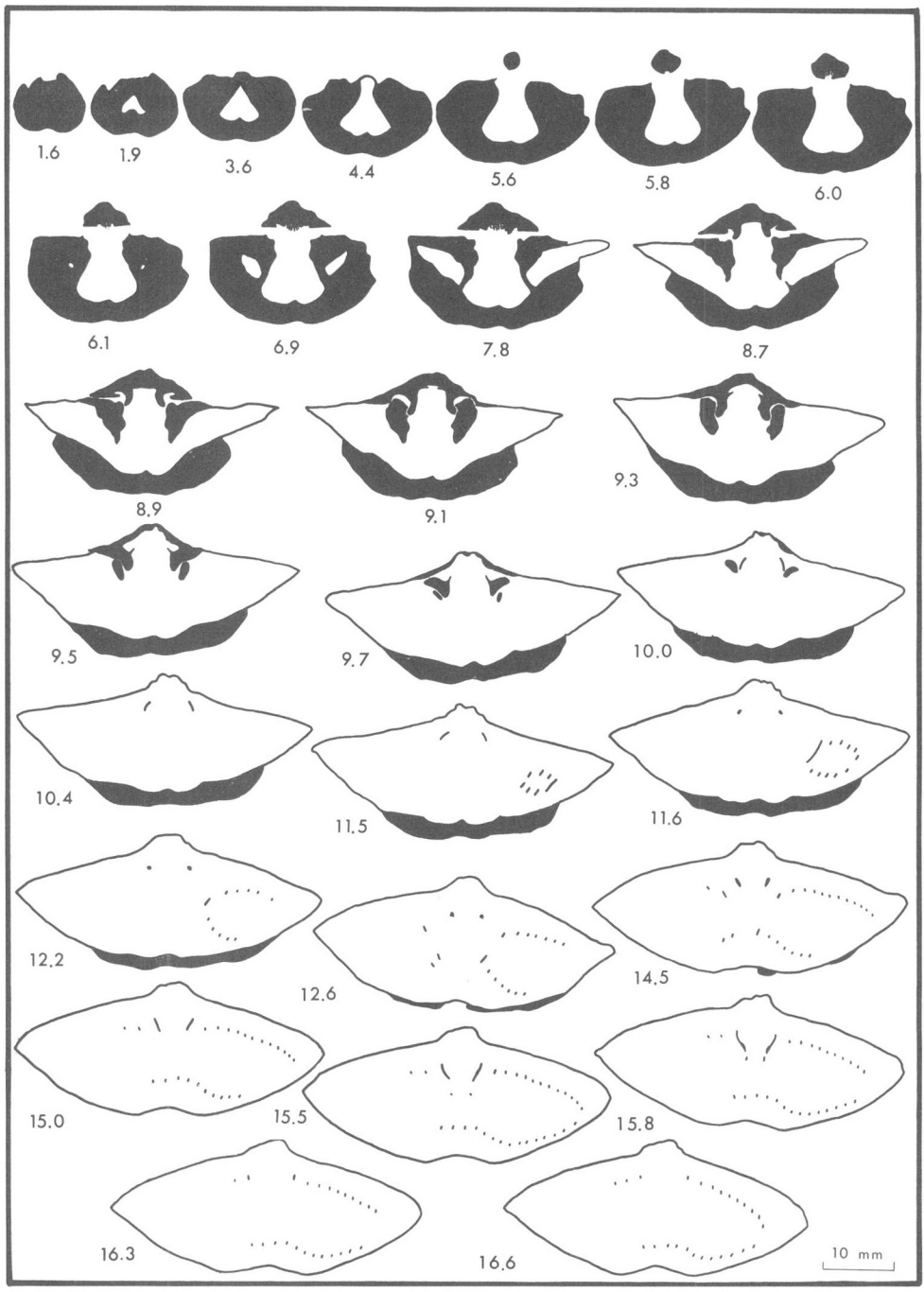
TEXTFIGURE 16

Schematic diagram showing microsculpture of concentric ornament of closely spaced spine bases and radial ornament of fine fila from pedicle valve of *Warrenella transversa* n. sp. Bar represents $\frac{1}{2}$ mm.

subparallel flanks at anterior margin. Ventral interarea moderately high, broad, apsacline; divided by relatively broad delthyrium carrying a thin apical deltidium. Dorsal interarea low, linear, orthocline. Lateral slopes of large specimens bear low, rounded plicae, about three on either flank. Concentric ornament of very closely spaced spine bases arranged in rows, 1 to 2 mm apart. Radial ornament of extremely fine fila interrupted and offset by rows of spine bases (Textfig. 16).

Pedicle valve interior. Large stubby hinge teeth supported by short, straight, basally divergent dental plates. In large specimens, dental plates lodged in very thick callus filling most of lateral chambers. Dental plates enclose posterior part of moderately impressed, subpyriform muscle field divided by low myophragm. Anterior edges of muscle field slightly elevated. Valve interior smooth except for impress of shallow plicae.

Brachial valve interior. Sockets widely divergent, bounded by moderately stout, recurved socket ridges whose anterior rims rise above valve floor. Socket ridges extend laterally one-third to one-half length of hinge line. Diductors attach to comb-like process filling posterior part of notothyrial cavity (Textfig. 17, 6.0 to 7.8 mm). Medially disposed, thin crura attached to inner edges of socket ridges. In large specimens, posterior part of crura lodged in callus, appearing to rise from valve floor anterior to comb-like process. In small specimens, dorsal edge of crura connect to valve floor for short distance. Thin, triangular, ventromedially directed cura become subcylindrical anteriorly, then become thin ventrally convergent plates which divide; ventral part terminates as thin jugal process, dorsal part thins becoming innermost of minimum of 13 whorls of spiralia (Textfig. 17, 10.0 to 15.8 mm). Moderately impressed, elongate, rectangular adductor scars divided by sharp myophragm. Muscle field confined to posterior half of fold impress. Remainder of interior smooth.



TEXTFIGURE 17. Camera lucida drawings of serial sections of *Warrenella transversa* n. sp. Paratype, GSC 31325.

Discussion. The transverse shell and high, often rectangular, anterior deflection readily distinguish *Warrenella transversa.* Features common with *Elythyna* sp. A of Johnson (1970a) from the Emsian *Eurekaspirifer pinyonensis* Zone of Nevada (transverse outline, narrow fold, long hinge line, low lateral plicae) suggest that *Elythyna* was derived from an early Emsian member of the Franklinii Lineage, probably *W. transversa.*

Warrenella praekirki Johnson, 1966

Plate XIV, figures 1–10

Warrenella kirki praekirki Johnson, 1966, p. 173–175, Pl. 27, figs. 10–25; Johnson, 1971, p. 319, Pl. 41, figs. 15–23.

Material (calcareous). Hypotypes (GSC 31321, 31323) Funeral Formation, GSC loc. C-23551; (GSC 31324) Headless Formation, GSC loc. C-23548.

Discussion. The material available is limited and does not allow amplification of the description by Johnson (1966). *Warrenella praekirki* is similar in many respects to *W. kirki,* but lacks elongate individuals. The dorsal fold of *W. praekirki* is less well defined than on *W. kirki* and the median furrow on the dorsal valve is usually absent.

Warrenella kirki (Merriam, 1940)

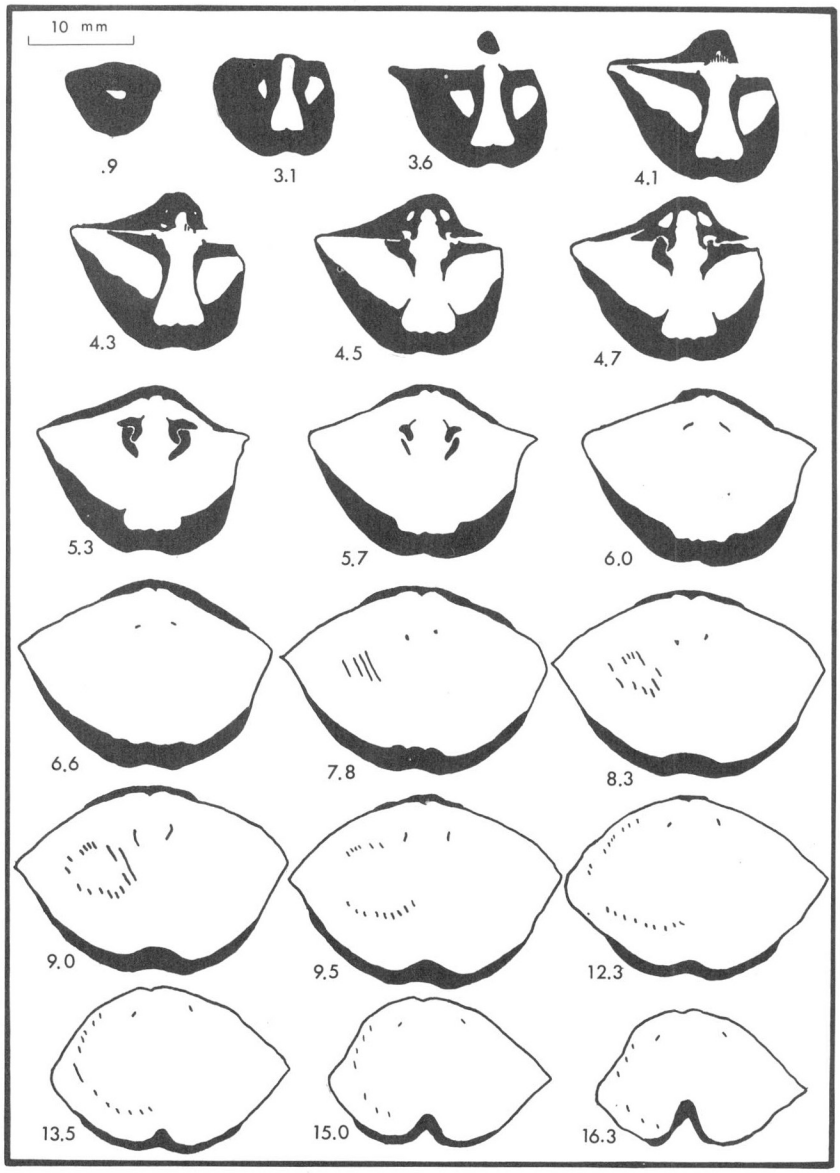
Plate XII, figures 16–27; Plate XIV, figures 11–17, 20–25;
Plate XV, figures 1–9; Textfigures 18, 19

Martinia kirki Merriam, 1940, p. 85, Pl. 8, figs. 26–29.
"*Martiniopsis*"*? kirki* (Merriam), Cooper, 1944, p. 329, Pl. 126, figs. 36, 37.
? Martinia? kirki (Merriam), Warren and Stelck, 1956, Pl. 4, figs. 25–27.
Warrenella kirki (Merriam), Caldwell, 1971, Pl. 2, figs. 7a–d.
Warrenella kirki kirki (Merriam), Johnson, 1971, p. 318, Pl. 45, figs. 1–22, Pl. 46, figs. 1–8, Textfigs. 3a, b.

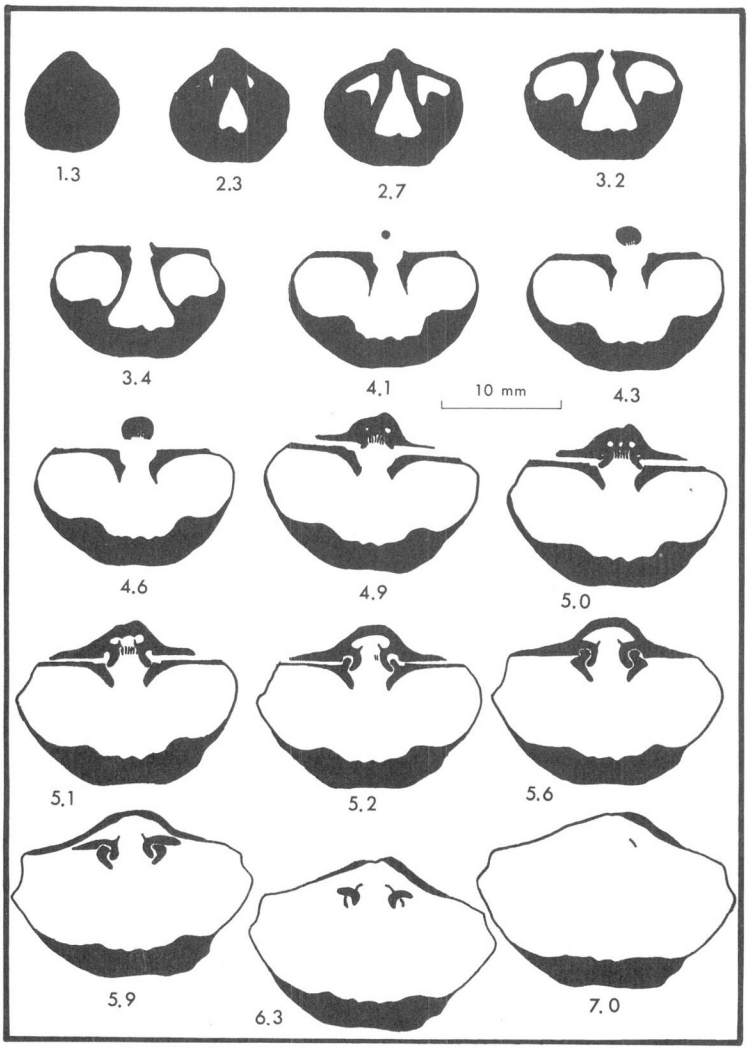
Material (calcareous). Hypotypes (GSC 31317–31319, 31340–31343, 31346–31350) Headless Formation, GSC loc. C-23545; (GSC 31344, 31345) Ogilvie Formation, GSC loc. C-23542. Serial sectioned hypotypes (GSC 31328, 31330) Headless Formation, GSC loc. C-23545; (GSC 31329) Headless Formation, GSC loc. C-23547.

Description. Exterior. Shells medium to large, outline subcircular to markedly elongate, profile ventribiconvex. Pedicle valve bears narrow U-shaped sulcus beginning anterior to beak, becoming deeper, wider anteriorly. Broad fold developed on anterior one-third of brachial valve, most specimens bear distinct U-shaped furrow in anterior two-thirds. Hinge line slightly shorter than maximum width. Ventral interarea low, triangular, apsacline. Ventral beak moderately to highly incurved over broad delthyrium closed apically by convex deltidium. Dorsal interarea low, flatly triangular, narrow, orthocline. Anterior commissure of small specimens rectimarginate, sometimes slightly re-entrant where ventral sulcus and dorsal furrow meet. On larger specimens, anterior commissure markedly uniplicate, generally flat-crested due to influence of median furrow. Flanks of deflection straight, diverge at approximately 90 degrees. Concentric ornament of closely spaced lines, on exceptionally well preserved specimens, seen to be rows of fine, triangular-shaped spine bases.

Pedicle valve interior. Hinge teeth relatively stout, bent medially, supported posteriorly by short, moderately stout, basally divergent dental plates. Ventral muscle field pear-shaped,



TEXTFIGURE 18. Camera lucida drawings of serial transverse sections of *Warrenella kirki* (Merriam). Hypotype, GSC 31330.



TEXTFIGURE 19

Camera lucida drawings of serial transverse sections of *Warrenella kirki* (Merriam). Hypotype, GSC 31329.

usually divided by distinct myophragm. Muscle field moderately to deeply impressed, anterior margin sharp, slightly elevated over valve floor, bounded posteriorly by dental plates. Remainder of interior smooth.

Brachial valve interior. Sockets moderately shallow, trough-shaped, widely divergent. Socket ridges overhang interior cavity, extend laterally over one-half length of hinge line. Moderately short crural plates, basally convergent, attach to inner recurved edge of socket plates, project anteriorly for short distance along parallel to slightly convergent tracks, abutt against posterior margin of adductor field. Crura arise from inner, ventral part of crural plates as dorsally-convergent triangular plates. Farther anteriorly crura become rod-shaped and then flare, becoming dorsally divergent plates before thinning to innermost of a minimum of 10 whorls of the spiralia. Diductor muscles attached to slightly flaring comb-like process in apex of notothyrial cavity. Adductor muscle field composed of two very

elongate, elliptical scars separated by distinct myophragm. Scars weakly to moderately impressed, bounded laterally by low ridges. Remainder of interior smooth.

Discussion. A significant proportion of a *Warrenella kirki* population is markedly elongate. The length of the dorsal furrow of *W. kirki* is intermediate between its ancestor *W. praekirki* and its descendant *W. crickmayi.* The *W. kirki* anterior deflection is broadly triangular opposed to the high steep-sided deflection of *W. crickmayi.*

Warrenella aff. *W. kirki* (Pl. XIV, figs. 18, 19) from *Leiorhynchus castanea*-bearing beds of the upper Hume Formation differs from *W. kirki* in being more globose and in almost completely lacking a fold and sulcus. The dorsal median furrow is low and poorly defined and the hinge line is notably shorter than the maximum width.

Warrenella crickmayi new species

Plate XV, figures 10–32; Textfigure 20

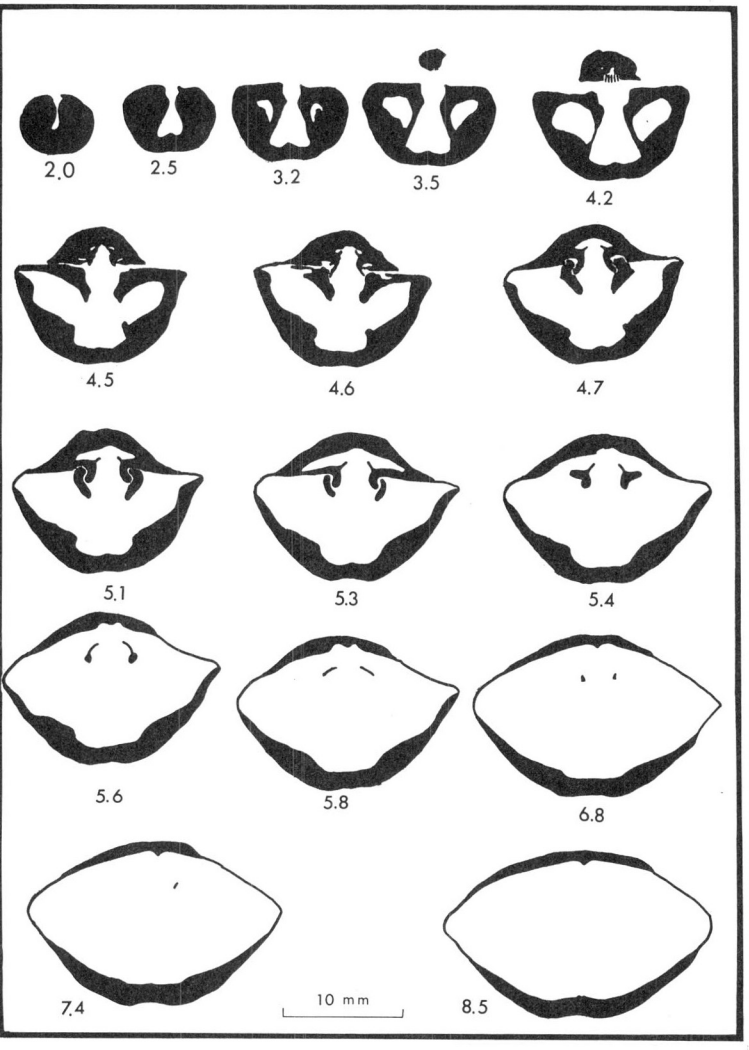
Material (calcareous). Holotype (GSC 32044), paratypes (GSC 32046–32048, 32050) "Hare Indian" Formation, GSC loc. C-23543; (GSC 32045, 32049) Headless Formation, GSC loc. C-23549; serial sectioned paratype (GSC 31331) "Hare Indian" Formation, GSC loc. C-23543.

Description. Exterior. Shell ventribiconvex to evenly biconvex, medium to large, outline variably transverse to elongate. Pedicle valve bears sharp, narrow, V-shaped sulcus initiating at beak, becoming broad, U-shaped near anterior commissure. Anterior half of brachial valve bears low, poorly defined fold divided by sharp, narrow furrow in anterior three-quarters of valve. Hinge line only slightly less than maximum width. Ventral interarea moderately high, broadly triangular, apsacline. Ventral beak moderately to highly incurved over broad delthyrium, apical half covered by convex deltidium. Dorsal interarea very low, triangular, orthocline to slightly anacline. Anterior commissure markedly uniplicate with flat-crested, steep-sided fold, flanks parallel to slightly divergent. Ornament of fine concentric growth lines.

Pedicle valve interior. Hinge teeth relatively large, sharply bent medially to accommodate curved socket ridges. Teeth supported by thin, short, basally divergent dental plates delimiting posterior part of broad pear-shaped adductor scars. Scars moderately to deeply impressed posteriorly, anterior part slightly elevated over valve floor. Faint pustules on posterior part of valve.

Brachial valve interior. Sockets moderately deep, trough-shaped, widely divergent. Inner edges of socket ridges strongly recurved. Socket ridges extend laterally for almost full length of hinge line. Diductors attach to slightly flaring comb-like process occupying apex of notothyrial cavity. Moderately short, subparallel to basally convergent cural plates join inner edge of socket ridge to valve floor. Anteriorly, crural plates elevated above valve floor forming thin, plate-like, dorsally convergent crura. Farther anteriorly, crura assume rod-like proportions (Textfig. 20, 6.8 mm). Adductor field elongate, moderately impressed, composed of two narrow scars separated by sharp, triangular myophragm. Near midlength muscle field merges imperceptively into shell floor. In large specimens, myophragm is impress of dorsal furrow. Interior smooth except for impress of coarse growth lines near anterior margin.

Discussion. Warrenella crickmayi is distinguished from its ancestor, *W. kirki*, by its larger size, long dorsal furrow, and high steep-sided anterior deflection. It can be separated from its descendant, *W. franklinii*, by its smaller size and its equidimensional to transverse outline.



TEXTFIGURE 20

Camera lucida drawings of serial transverse sections of *Warrenella crickmayi* n. sp. Paratype, GSC 31331.

The species name is for C. H. Crickmay whose numerous contributions have helped to elucidate Devonian paleontology of northwestern Canada.

Warrenella franklinii (Meek, 1867)

Plate XIV, figures 26–30

Spirifer (*Martinia*) *franklinii* Meek, 1867, p. 107, Pl. 14, figs. 12a–c.
Martinia franklinii Meek, Merriam, 1940, Pl. 8, fig. 24.
Warrenella franklinii (Meek), Caldwell, 1971, Pl. 2, figs. 6a–d.

Material (calcareous). Hypotype (USNM 14021) from 40 miles below Ramparts of Mackenzie River.

Discussion. Little can be added to the excellent description given by Meek (1867). Due to the scarcity of material from Canada it is difficult to characterize this species; however, the following features appear to be diagnostic: the large size, subcircular to slightly transverse outline, wide hinge line, flatly triangular ventral interarea, long furrow on the dorsal fold, and the narrow ventral sulcus. Additional specimens of *Warrenella franklinii* from Nevada (courtesy of J. G. Johnson) uphold these generalizations.

Warrenella franklinii is distinguished from its immediate ancestors, *W. crickmayi* and *W. kirki*, by its larger size and its subcircular to slightly transverse outline. Generally, it is quite similar to some specimens of *W. weigelti*, but it can be recognized readily in that it never develops the flat-bottomed sulcus and always possesses the furrow on the fold. *Warrenella weigelti* is characterized by a high triangular interarea while *W. franklinii* has a wide, flatly triangular interarea.

Warrenella quadrata new species

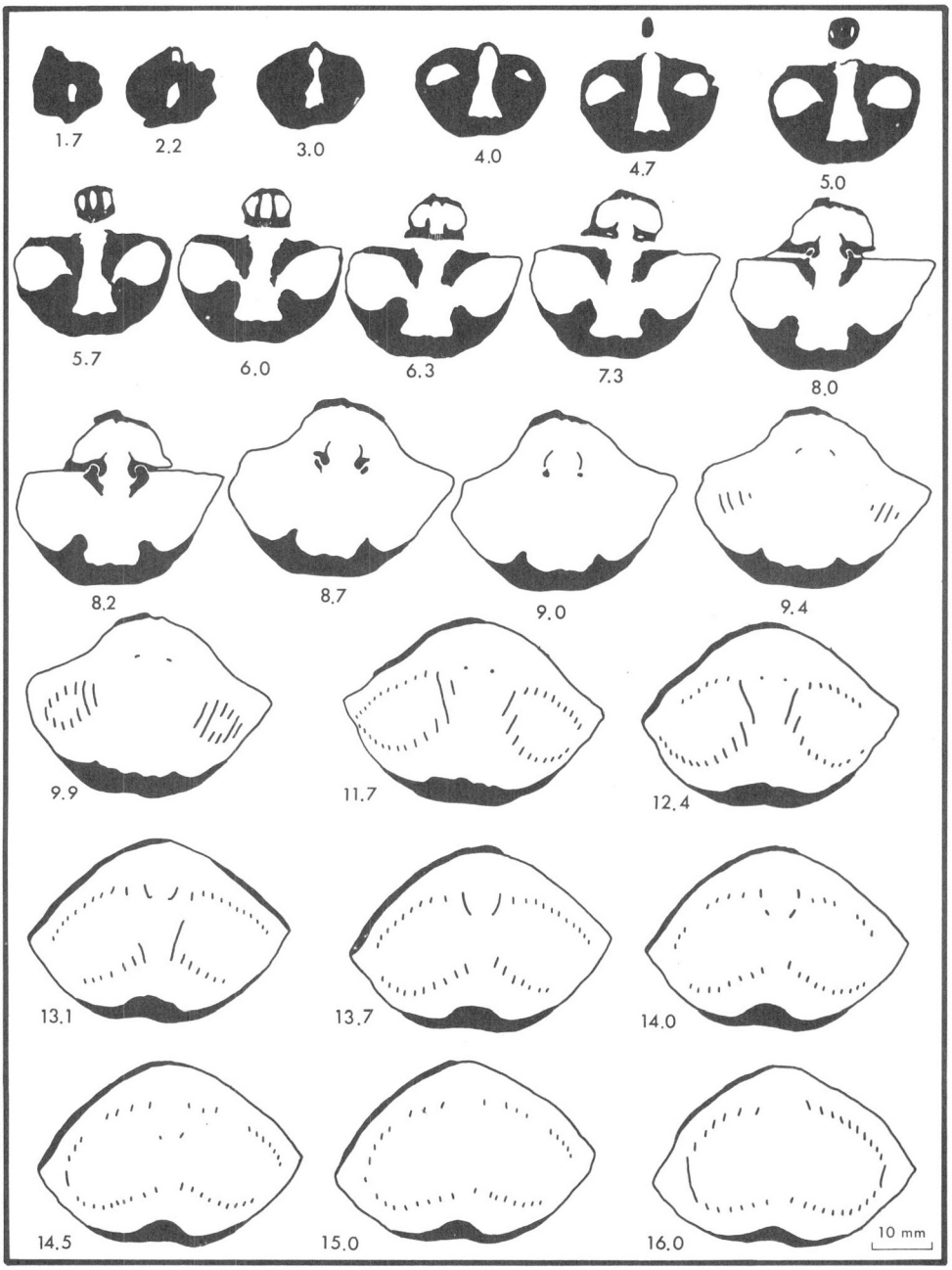
Plate XVI, figures 1–11; Plate XVII, figures 11–24; Textfigure 21

Material (calcareous and silicified). Holotype (GSC 31298); paratypes (GSC 31299–31306, 31334–31336); serial sectioned paratype (GSC 31332); all from Ogilvie Formation, GSC loc. C-23541.

Description. Exterior. Shell ventribiconvex, outline subrhombic. Pedicle valve bears distinct sulcus initiating slightly anterior to beak. Sulcus moderately sharp, V-shaped posteriorly, becoming evenly concave to flat-bottomed near anterior margin. Brachial fold high, rounded, distinct anterior to midlength. In large specimens, anterior part of fold flat-crested. Hinge line straight, notably shorter than maximum width. Ventral interarea steeply apsacline, high, and triangular. Ventral beak highly incurved over large delthyrium covered by slightly convex, apical deltidium. Dorsal interarea low, steeply apsacline to orthocline. Anterior commissure uniplicate. Anterior deflection changes during ontogeny from nearly triangular to broad, flat-crested. Concentric ornament of closely spaced rows of fine notches, interpreted as remains of spine bases.

Pedicle valve interior. Hinge teeth small, supported by short, straight dental plates which thicken considerably along their dorsolateral edges. Dental plates define posterior part of very deeply impressed, diamond-shaped muscle scar divided by low myophragm. Muscle field distinctly defined by sharp flanking ridges along its anterolateral margin. Shell interior smooth except for indistinct pustules in posterior part.

Brachial valve interior. Strongly recurved inner part of socket plates defines widely divergent, trough-shaped sockets. Socket ridges overhang shell cavity, extending about one-third distance along hinge line. Diductors attached to slightly flaring comb-like process situated at apex of notothyrial cavity. Moderately stout, parallel crural plates connect inner edges of socket ridges to valve floor. Crural plates partly enclose posterolateral ends of adductor scars. Crura develop as medially convex plates from ventral part of crural plates. Farther anteriorly, crura assume rod-like proportions, then flare becoming thin, dorsally divergent plates. Crura then split medially, ventral part terminates as thin jugal process near centre of valves and dorsal part becomes first of 13 whorls of spiralia (Textfig. 21, 8.7–12.4 mm). Adductors attached to weakly impressed muscle field of two elongate scars separated by thin myophragm, bounded laterally by low ridges, extending for about one-third length of valve. Muscle field open anteriorly, posteriorly continuous with notothyrial cavity.



TEXTFIGURE 21. Camera lucida drawings of serial transverse sections of *Warrenella quadrata* n. sp. Paratype, GSC 31332.

Discussion. The quadrate, equidimensional shell, with a high rounded anterior deflection and a hinge line markedly shorter than maximum width characterizes *Warrenella quadrata.* The long, distinct, evenly concave sulcus readily distinguishes *W. quadrata* from its descendant *W. weigelti.* The quadrate outline, short hinge line and the correspondingly short ventral interarea readily separate *W. quadrata* from its predecessor *W. sekwensis.*

Warrenella weigelti (Struve, 1970)

Warrenella weigelti meeki new subspecies

Plate XVI, figures 16–20; Plate XVII, figure 25; Plate XVIII, figures 1–12; Textfigure 22

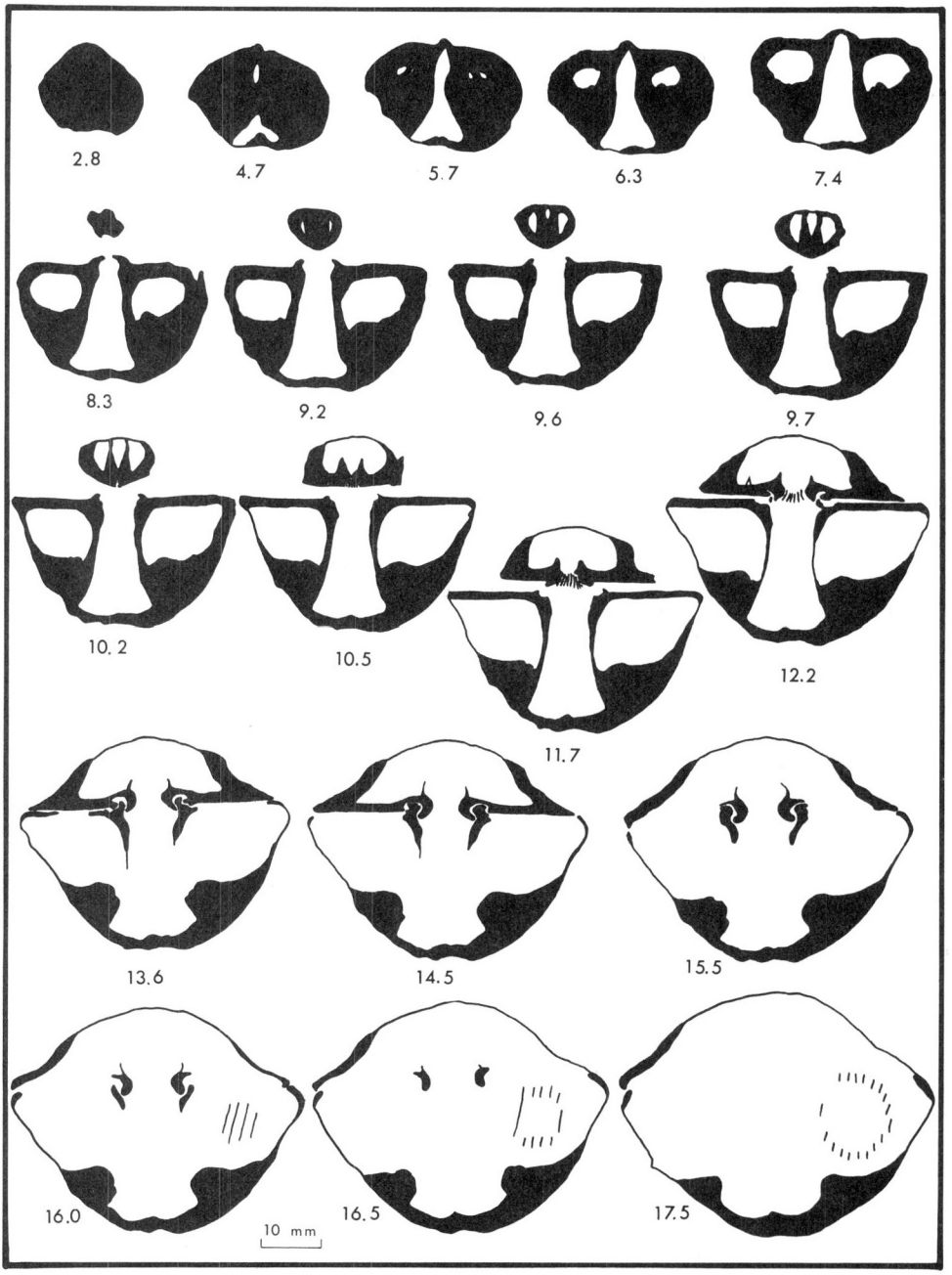
Material (calcareous). Holotype (GSC 32052); paratype (GSC 32051), both from "Hare Indian" Formation, GSC loc. C-23543; paratypes (GSC 31307, 31309, 31310) and paratype (GSC 31308) Headless Formation, GSC loc. C-23546; serial sectioned paratype (GSC 31327) "Hare Indian" Formation, GSC loc. C-23544.

Description. Exterior. Shell large, equally biconvex. Outline subrhombic to subcircular. Hinge line extends about two-thirds maximum width. Pedicle valve bears variably developed sulcus, generally low, poorly defined, outlined on evenly concave pedicle valve by sharp deflection of growth lines. In a few specimens, sulcus low, evenly concave. Dorsal fold lodged posteriorly in central umbonal inflation, becoming moderately high, evenly rounded to slightly rectangular anteriorly. Ventral interarea high, broadly triangular, apsacline, transversely striate. Ventral beak highly incurved over broad delthyrium covered almost completely by convex deltidium. Dorsal interarea low, steeply anacline to orthocline. Concentric ornament of relatively coarse growth lines.

Pedicle valve interior. Hinge teeth moderately small, supported by thin, straight, basally divergent dental plates. Posterior part of dental plates lodged in thick umbonal deposits. Dental plates define V-shaped posterior part of elongate, subelliptical, deeply impressed ventral muscle field, divided by low myophragm. Anterior part of muscle field indistinct. Posterolateral flanks of interior pustulate, occasionally pustules elongate, arranged in radial rows centred about apex.

Brachial valve interior. Sockets moderately deep, widely divergent. Interior edge of sockets highly incurved confining hinge teeth. Laterally, socket ridges extend two-thirds length of hinge line. Diductors attached to slightly flaring comb-like process filling apex of notothyrial cavity. Stout, parallel crural plates attached to medial rim of socket plates, extend anteriorly for about 3 mm, decrease in height and join low posterolateral bounding ridges of adductor muscle field. Crural plates blunt, triangular extensions of dorsomedial part of socket ridges, rapidly attenuate to form thin, slightly dorsally divergent crura (Textfig. 22, 10.5–17.5 mm). Farther anteriorly, crura assume rod-like shape and expand into thin plates which split, dorsal part becoming first whorl of a minimum of 10 in spiralia, ventral part terminating as thin jugal process. Adductor muscle field weakly impressed, flask-shaped, bounded laterally by low ridges divided by myophragm. Valve interior covered by low pustules.

Discussion. The larger size, and weaker fold and sulcus of *Warrenella weigelti meeki* distinguish it from its ancestor, *W. quadrata.* The equally biconvex shell separates it from its descendant *W. occidentalis timetea* which is ventribiconvex and has a high, rectangular fold. *Warrenella weigelti meeki* is more inflate, has a higher ventral interarea and shallower sulcus than *W. weigelti weigelti* (Struve).



TEXTFIGURE 22. Camera lucida drawings of serial transverse sections of *Warrenella weigelti meeki* n. subsp. Paratype, GSC 31327.

The subspecies name is for F. B. Meek who, in 1867, completed the first extensive study of Devonian faunas from northern Canada.

Warrenella occidentalis (Merriam, 1940)

Warrenella occidentalis timetea Crickmay, 1960

Plate XVIII, figures 13–15; Plate XIX, figures 1–15

Martinia? occidentalis Merriam, Warren, 1944, p. 127, Pl. 2, figs. 1, 2; Warren and Stelck, 1956, Pl. 9, figs. 25–27.

Martinia? franklinii Meek, Warren, 1944, p. 126, Pl. 2, figs. 3, 4.

Warrenella timetea Crickmay, 1960, p. 16, Pl. 10, figs. 1–9.

Warrenella occidentalis (Merriam), Caldwell, 1971, Pl. 3, figs. 3, 4.

Tingella timetea (Crickmay), Crickmay, 1962, p. 10, Pl. 1, figs. 8, 9; Crickmay 1963, p. 17, Pl. 3, figs. 21–26, Pl. 11, figs. 14–18.

Material (calcareous). Hypotype (GSC 25669); illustrated material (GSC 31311–31313, 31320) GSC loc. C-23552; (UA 890, 891); all from Ramparts Formation, Carcajou Ridge.

Description. Exterior. Shell ventribiconvex, medium to very large, outline transversely suboval. Ventral sulcus flat-bottomed, steep-sided, initiating anterior to ventral beak, becoming deeper, wider anteriorly. Brachial valve only slightly convex, modified posteromedially by umbonal inflation developing into flat-crested to slightly medially concave fold. Posterior profile unequally lens-shaped. In large specimens pedicle valve with humped appearance due to thickening lateral to sulcus. Hinge line straight, markedly shorter than maximum width. Ventral interarea high, triangular, steeply apsacline. Ventral beak highly incurved over broad delthyrium one-half to two-thirds covered by convex deltidium. Dorsal interarea low, linear, approximately orthocline. Anterior commissure very markedly uniplicate. In large specimens, steep-sided anterior deflection accentuated by ventral deflection lateral to flanks. Concentric ornament of fine growth lines.

Pedicle valve interior. Hinge teeth small, supported by thin, short, basally divergent dental plates. Muscle field divided by distinct myophragm. In small specimens, field elongate, elliptical moderately impressed; in large specimens, field diamond-shaped, deeply impressed, anterior half elevated over valve floor. V-shaped posterior half of muscle field defined by thin dental plates. Flat-bottomed sulcus distinctly impressed on interior of valve. Umbonal callus very thick. Valve interior smooth.

Brachial valve interior. Sockets moderately deep, trough-shaped, widely divergent. Socket ridges moderately stout, inner edges slightly recurved, extending laterally for one-half to two-thirds length of hinge line. Diductors attached to flaring comb-like process filling apex of notothyrial cavity. Stout, parallel, moderately long crural plates attached to inner edge of socket ridges. In large specimens crural plates obscured by shell material filling notothyrial cavity. Bases of crural plates continuous anteriorly with lateral bounding ridges of adductor field. Muscle field composed of two elongate and moderately impressed scars separated by low myophragm. Muscle field open anteriorly, occupying posterior half of interior impress of fold. Remainder of interior smooth.

Discussion. Warrenella occidentalis timetea can be distinguished readily from other *Warrenella* species by its broad, flat-bottomed sulcus and its low rectangular fold. From other subspecies of *W. occidentalis* it can be separated by the nature of the sulcus and the shape and height of the anterior deflection. *Warrenella occidentalis torleyi* (Struve) has a narrow sulcus and a

very high, rounded anterior deflection and *W. occidentalis occidentalis* (Merriam) has a very broad, shallow sulcus. *Warrenella laevis* (Hall) bears a marked similarity to *W. occidentalis timetea;* however, it is typically more transverse and lacks the sharply bounded fold and sulcus. In addition, the anterior part of the sulcus of *W. laevis* shows a sharp dorsal deflection.

Warrenella cf. *W. maureri* (Holzapfel, 1895)

Plates XVII, figures 1–10

Martinia? kirki var. *occidentalis* Merriam?, Warren and Stelck, 1956, Pl. 4, figs. 9–12.
? Martinia? franklinii Meek, Warren and Stelck, 1956, Pl. 2, figs. 1–3.
Warrenella cf. *W. franklinii* (Meek), McLaren *et al.*, 1962, Pl. 9, figs. 23–25.

Material (calcareous). Illustrated material (GSC 16702) GSC loc. 19267, (UA 1346), both from Pine Point Formation at Pine Point, Great Slave Lake.

Description. Exterior. Shell slightly ventribiconvex, medium size, outline transversely suboval. Cardinal angles obtuse, rounded. Pedicle valve sulcus narrow posteriorly, gradually widens, deepens anteriorly. Hinge line markedly shorter than maximum width. Brachial valve evenly convex with only faint trace of low rounded fold. Ventral beak highly incurved over low, triangular, steeply apsacline to almost orthocline ventral interarea. Dorsal interarea low, linear, orthocline to slightly anacline. Near anterior margin, fold flanks sharply deflected dorsally, almost perpendicular to plane of commissure. Anterior commissure uniplicate with low, rounded deflection. Concentric ornament of thin ridges spaced at 1 mm or less. Interior not investigated due to insufficient material.

Discussion. The short hinge line of *Warrenella* cf. *W. maureri* suggests its derivation from the Occidentalis Lineage. The very low ventral interarea, the transverse outline, and the indistinct fold separate it from other Middle Devonian species. The specimen illustrated as *Martinia? franklinii* from lower Hare Indian Shale by Warren and Stelck (1956, Pl. 2, figs. 1-3) is similar to the Pine Point species in possessing a short hinge line and a low ventral interarea. Although the specimen is deformed, it appears to have a flat-crested fold and a subrectangular anterior deflection, reminiscent of shells from the Occidentalis Lineage.

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Locality Index

The prefix C denotes GSC collections registered at the Institute of Sedimentary and Petroleum Geology, Calgary. Fossil identifications, unless otherwise noted, are by the writers. Number in parentheses following a *Warrenella* denotes the number of specimens in the collection. Textfigure 12 shows the following localities:

1. Delorme Formation, 70 ft. above strata bearing *Monograptus yukonensis* Jackson and Lenz, 2 miles northwest of Natla River; 63°17′N, 128°33′W. Collected by D. G. Perry, 1971 (C-23536).

   Warrenella sekwensis Ludvigsen and Perry (63)
   Cortezorthis sp.
   Leptostrophia sp.
   Atrypa sp.
   Desquamatia sp.
   Pelekysgnathus furnishi? Klapper
   corals

   age: late Siegenian or early Emsian

2. Delorme Formation, same section and collector as C-23536, 370 ft. above *Monograptus yukonensis* (C-23537).

   Warrenella sekwensis Ludvigsen and Perry (41)
   Cortezorthis sp.
   Leptostrophia sp.
   Atrypa sp.
   Desquamatia sp.
   Phragmostrophia sp.
   corals

   age: late Siegenian or early Emsian

3. Michelle Formation, upper 50 ft., 6 miles northwest of Hart River, at mountain front; 65°40′30″N, 136°57′W. Collected by Rolf Ludvigsen, 1971 (C-23538).

   Warrenella transversa Ludvigsen and Perry (35)
   Cortezorthis cf. *cortezensis* Johnson and Talent
   Megastrophia iddingsi (Merriam)
   Desquamatia sp.
   Leptaena sp.
   Turkestanella acuaria (Richter)
   conodonts of *Polygnathus dehiscens* Zone
   corals

   age: early Emsian

4. Michelle Formation, 125–135 ft. below top, 8 miles northwest of Hart River, at Mountain front; 65°41′N, 137°01′W. Collected by Rolf Ludvigsen, 1968 (C-23539).

   Warrenella transversa Ludvigsen and Perry (8)
   Cortezorthis cf. *cortezensis* Johnson and Talent
   Desquamatia sp.
   Megastrophia iddingsi
   Schizophoria cf. *nevadaensis* Merriam
   Turkestanella acuaria (Richter)
   Ceratolichas sp.
   Lacunoporaspis norrisi Ormiston
   Otarion sp.
   Proetus cf. *nerudai* Přibyl
   Schizoproetoides sp.
   (trilobite identifications by A. R. Ormiston)
   conodonts of *Polygnathus dehiscens* Zone

   age: early Emsian

5. Ogilvie Formation, 960 ft. above top of Michelle Formation, 2 miles east of Hart River; 65°25′N, 137° 02′ W. Collected by D. G. Perry, 1970 (C-23540).

   Warrenella quadrata Ludvigsen and Perry (76)
   Phragmostrophia aff. *merriami* Harper, Johnson and Boucot
   Linguopugnoides glaberrhynchus Perry, Klapper, and Lenz
   Cyrtina sp.
   Ambocoelia sp.
   Schizophoria sp.
   Atrypa sp.
   Bifida ogilviensis Perry, Klapper, and Lenz
   Megastrophia sp.
   Cortezorthis sp.
   Muriferella aff. *masurskyi* Johnson and Talent
   Gypidula sp.
   Koneprusia cf. *pennata* Lutke
   Acanthopyge (*Nitidulopyge*) *nitidula* (Barrande)
   Otarion cf. *O. druida* Erben
   Leonaspis sp.
   (trilobite identifications by A. R. Ormiston)
   abundant 2- and 4-hole crinoid ossicles
   Polygnathus perbonus n. subsp. (P element)
   Polygnathus linguiformis linguiformis α morphotype Bultynck (P element)
   Pandorinellina exigua n. subsp. (P element; unassigned O_1, A_1, A_3, elements)
   (conodont multielement identifications by G. Klapper)

   age: late Emsian

6. Ogilvie Formation, 1,515 ft. above top of Michelle Formation, 1/2 mile north of Ogilvie River; 65°21′N, 138°26′W. Collected by D. G. Perry, 1971 (C-23541).

   Warrenella quadrata Ludvigsen and Perry (18)
   Schizophoria sp.
   Pholidostrophia sp.
   Dechenella aff. *D. valentini* Stumm and *Ancyropyge arctica* Ormiston occur 200 ft. higher in section
   (trilobite identifications by A. R. Ormiston)
   Polygnathus costatus costatus (P element)
   Polygnathus linguiformis linguiformis (P element)
   Icriodus nodosus group (I element)
   Pelekysgnathus sp. (I element)
   Eognathodus bipennatus (P element)
   Ozarkodina sp. (P element)
   (conodont multielement identifications by G. Klapper)

   age: Eifelian (probably early Eifelian)

7. Ogilvie Formation, near top, 19 miles west of Ogilvie River; 65°36′N, 138°40′W. Collected by A. C. Lenz, 1958 (C-23542).

   Warrenella kirki (Merriam) (6)

   age: late Eifelian

8. "Hare Indian" Formation, 200 ft. below top, 4 miles west of Snake River; 65°26′N, 133°35′W. Collected by D. G. Perry, 1971 (C-23543).

   Warrenella crickmayi Ludvigsen and Perry (13)
   Warrenella weigelti meeki Ludvigsen and Perry (6)

   age: late Eifelian or early Givetian.

9. "Hare Indian" Formation, near top, 7 miles east of Snake River; 65°25′N, 133°09′W. Collected by Keith Williams, 1953 (C-23544).

   Warrenella weigelti meeki Ludvigsen and Perry (4)

   age: late Eifelian or early Givetian

10. Headless Formation, 460-515 ft. below base of Nahanni Formation, 16 miles north of South Nahanni River, Manetoe Range. Headless Formation, 800 ft. thick, overlies Funeral Formation; 61°42′N, 125°05′30″W. Collected by B. D. E. Chatterton, 1971 (C-23545).

    Warrenella kirki (Merriam) (173)
    Desquamatia arctia (Warren) and *Leiorhynchus manetoe* McLaren occur 40 ft. lower in section

    age: late Eifelian.

11. Headless Formation, 355 ft. below base of thin Nahanni Formation, 20 miles north of South Nahanni River, Arnica Range; 60°48′N, 125°15′W. Collected by J. W. Harrington, 1971, (C-23546).

    Warrenella weigelti meeki Ludvigsen and Perry (2)
    Warrenella kirki (Merriam) (1)

    age: late Eifelian

12. Headless Formation, 95 ft. above Manetoe Formation, 370 ft. below base of Nahanni Formation, Second Canyon South Nahanni River, Headless Range; 61°18′N, 124°39′W. Collected by Rolf Ludvigsen, 1971 (C-23547).

    Warrenella kirki (Merriam) (5)
    Leiorhynchus manetoe and *Cassidirostrum* sp. occur 50 ft. lower in section

    age: late Eifelian

13. Headless Formation, 15 miles east of Broken Skull River, Backbone Ranges, Mackenzie Mountains; 62°24′N, 127°18′W. Collected by A. C. Lenz, 1963 (C-23548).

    Warrenella praekirki Johnson (6)

    age: Eifelian (probably early Eifelian)

14. Headless Formation, 20 miles northwest of Caribou Pass, Backbone Ranges, Mackenzie Mountains; 63°44′N, 129°38′W. Collected by J. Harper, 1963 (C-23549).

    Warrenella crickmayi Ludvigsen and Perry (6)

    age: late Eifelian or early Givetian.

15. Nahanni/Headless Formation, 7 miles northwest of Caribou Pass, Backbone Ranges, Mackenzie Mountains; 63°35′N, 129°25′W. Collected by J. Jones, 1963 (C-23550).

    Warrenella cf. *W. quadrata* Ludvigsen and Perry (1)
    ?Warrenella sp.

    age: Eifelian

16. Funeral Formation, basal, 6 in. from top of Manetoe Formation, 22 miles north of South Nahanni River, Manetoe Range; 61°47′N, 125°08′W. Collected by Rolf Ludvigsen, 1971 (C-23551).

    Warrenella praekirki Johnson (22)
    Schizophoria sp.
    Megastrophia sp.
    Vallomyonia sp.
    Spinatrypa sp.

    age: Eifelian (probably early Eifelian)

17. Ramparts Formation, upper part of platform member, Carcajou Ridge, 46.6 miles northwest of Norman Wells; 64°42′N, 128°45′W. Collected by Texaco Exploration Co., 1969 (C-23552).

    Warrenella occidentalis timetea Crickmay (3)
    Leiorhynchus hippocastanea (Crickmay)

    age: late Givetian

18. Pine Point Formation, brown limestone member, 1.7 miles south of Dawson Landing Wharf, Pine Point, Great Slave Lake. Collected by R. de Wit, 1951 (19267).

    Warrenella cf. *maureri* (Holzapfel) (2)

    age: Givetian

19. Hume Formation, 0–15 ft. below top of *Leiorhynchus castanea*-bearing beds, Anderson River; 68°31′40″N, 127°15′W. Collected by A. E. H. Pedder, 1959 (41319).

Warrenella aff. *W. kirki* (Merriam) (33)
"*Spinulicosta*" *stainbrooki* Crickmay
Leiorhynchus castanea (Meek)
Cassidirostrum pedderi McLaren
Spinatrypa sp.
(identifications by A. E. H. Pedder)

age: early Givetian

PLATE XII

Warrenella sekwensis new species (PAGE 72)

Figures 1–4. Dorsal, ventral, side, and posterior views of holotype (GSC 32053); GSC locality C-23536, Delorme Formation; x1.1.

Figures 5–7. Exterior and interior views of pedicle valve and oblique interior views of paratype (GSC 31314); same locality, Delorme Formation, figs. 5, 6, x1; fig. 7, x1.4.

Figures 8, 9. Interior and exterior views of pedicle valve of paratype (GSC 31316); GSC locality C-23537, Delorme Formation; x1.

Figure 10. Interior view of pedicle valve of paratype (GSC 31337); same locality, Delorme Formation; x1.1.

Figures 11–13. Exterior, interior, and posterior views of pedicle valve of paratype (GSC 31339); same locality, Delorme Formation; x1.

Figure 14. Oblique interior view of fragmentary brachial valve of paratype (GSC 31315); GSC locality C-23536, Delorme Formation; x1.5.

Figure 15. Interior view of brachial valve of paratype (GSC 31338); GSC locality C-23537, Delorme Formation; x1.

Warrenella kirki (Merriam) (PAGE 75)

Figures 16–18. Ventral, dorsal, and posterior views of internal mould of hypotype (GSC 31317); GSC locality C-23545, Headless Formation; x1.4.

Figures 19–21. Dorsal, side, and posterior views of hypotype (GSC 31342); same locality, Headless Formation; x1.

Figures 22–25. Dorsal, posterior, side, and ventral views of hypotype (GSC 31319); same locality, Headless Formation; x1.

Figure 26. Posterior view of internal mould of brachial valve of hypotype (GSC 31318); same locality, Headless Formation; x1.4.

Figure 27. Detail of microsculpture on pedicle valve of hypotype (GSC 31341); same locality, Headless Formation; x10.

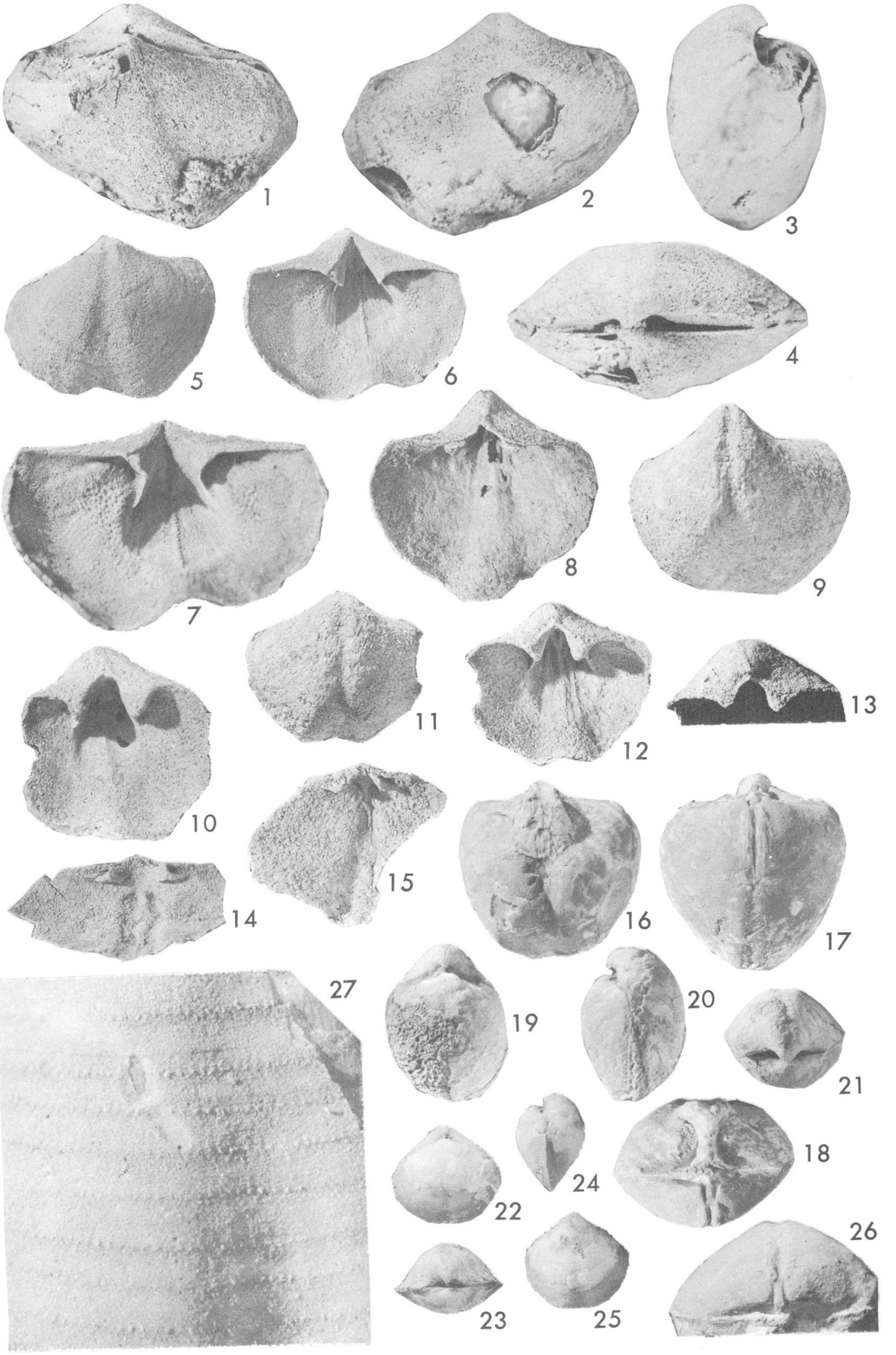
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PLATE XIII

Warrenella transversa new species (PAGE 72)

Figures 1–4. Dorsal, ventral, posterior, and anterior views of internal mould of holotype(GSC 31287); GSC locality C-23538, Michelle Formation; x1.2.

Figures 5–9. Dorsal, ventral, anterior, posterior, and side views of paratype (GSC 31288); same locality, Michelle Formation; x1.

Figures 10–13. Dorsal, posterior, and ventral views and detail of interarea of paratype (GSC 31297); same locality, Michelle Formation; figs. 10, 11, 12, x1; fig. 13, x2.

Figure 14. Ventral view of internal mould of pedicle valve of paratype (GSC 31291); same locality, Michelle Formation; x1.2.

Figure 15. Ventral view of internal mould of pedicle valve of paratype (GSC 26645); GSC locality C-23539, Michelle Formation; x1.

Figures 16, 17. Oblique posterior and dorsal views of internal mould of brachial valve of paratype (GSC 31292); GSC locality C-23538, Michelle Formation; x1.4.

Figures 18, 19. Dorsal and anterior views of paratype (GSC 31296); same locality, Michelle Formation; x1.

Figure 20. Dorsal view of internal mould of brachial valve of paratype (GSC 26646); GSC locality C-23539, Michelle Formation; x1.2.

Figures 21–23. Dorsal, ventral, and anterior views of paratype (GSC 31293); GSC locality C-23538, Michelle Formation; x1.

Figures 24, 25. Dorsal and ventral views of paratype (GSC 31333); same locality, Michelle, Formation; x1.4.

Figure 26. Detail of microsculpture on pedicle valve of paratype (GSC 31290); same locality Michelle Formation; x8.

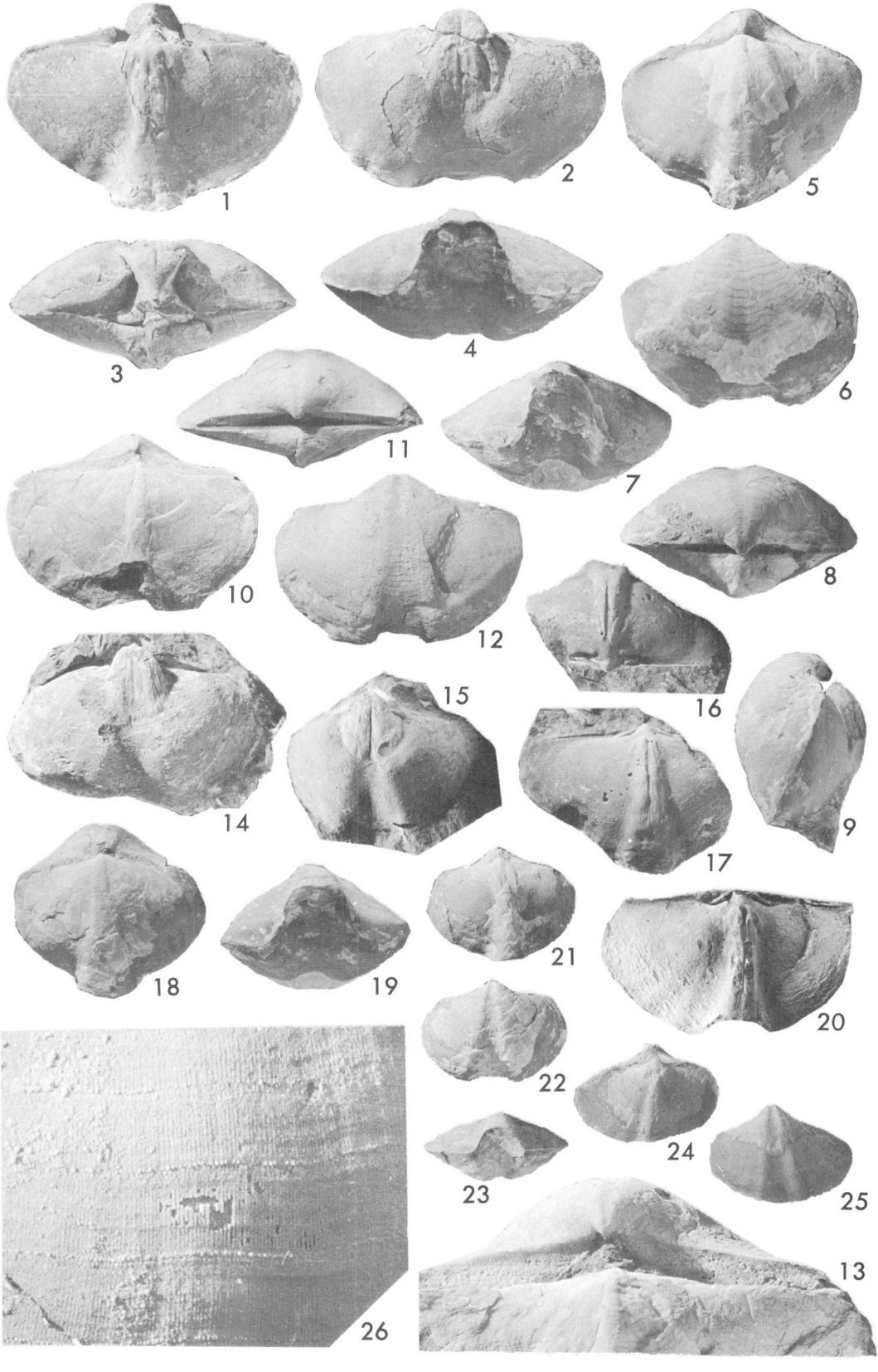
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PLATE XIV

Warrenella praekirki Johnson (PAGE 75)

Figures 1–5. Dorsal, ventral, side, posterior, and anterior views of hypotype (GSC 31321); GSC locality C-23551, Funeral Formation; x1.

Figures 6–8. Dorsal, ventral, and anterior views of hypotype (GSC 31324); GSC locality C-23548, Headless Formation; x1.

Figures 9, 10. Posterior and interior views of pedicle valve of hypotype (GSC 31323); GSC locality C-23551, Funeral Formation; x1.5.

Warrenella kirki (Merriam) (PAGE 75)

Figures 11–14. Dorsal, side, ventral, and anterior views of hypotype (GSC 31344); GSC locality C-23542, Ogilvie Formation; x1.

Figure 15. Posterior view of internal mould of hypotype (GSC 31345); same locality, Ogilvie Formation; x1.4.

Figures 16, 17. Dorsal and posterior views of internal mould of hypotype (GSC 31346); GSC locality C-23545, Headless Formation; x1.3.

Figures 20, 21. Dorsal and side views of hypotype (GSC 31349); same locality, Headless Formation; x1.

Figures 22–24. Dorsal, ventral, and posterior views of hypotype (GSC 31343); same locality, Headless Formation; x1.

Figure 25. Dorsal view of hypotype (GSC 31340); same locality, Headless Formation; x1.

Warrenella aff. *W. kirki* (Merriam) (PAGE 78)

Figures 18, 19. Dorsal and ventral views of hypotype (GSC 16697); GSC locality 41319, Hume Formation; x1.

Warrenella franklinii (Meek) (PAGE 79)

Figures 26–30. Dorsal, posterior, side, anterior, and ventral views of hypotype (USNM 14021); from 40 miles below the Ramparts of Mackenzie River; x1.1.

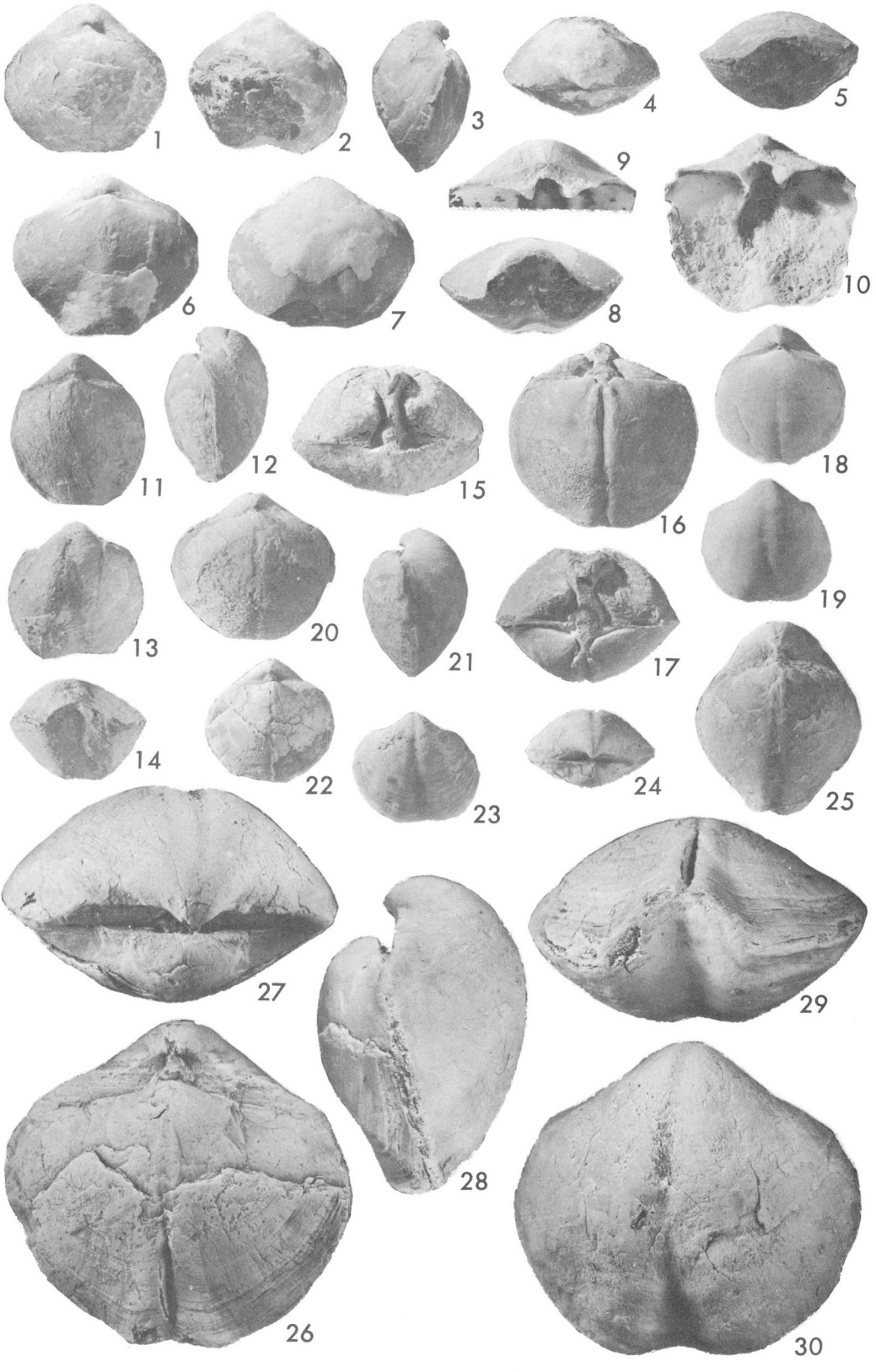
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PLATE XV

Warrenella kirki (Merriam) (PAGE 75)

Figures 1–4. Side, anterior, ventral, and dorsal views of hypotype (GSC 31347); GSC locality C-23545, Headless Formation; x1.

Figures 5–9. Dorsal, side, ventral, anterior, and posterior views of hypotype (GSC 31348); same locality, Headless Formation; x1.

Warrenella crickmayi new species (PAGE 78)

Figures 10–15. Dorsal, ventral, side, posterior, and anterior views and detail of interarea of holotype (GSC 32044); GSC locality C-23543, "Hare Indian" Formation; figs. 10, 11, 12, 13, 14, x1.1; fig. 15, x2.

Figures 16–18. Dorsal, ventral, and posterior views of internal mould of paratype (GSC 32045); GSC locality C-23549, Headless Formation; x1.

Figures 19–22. Dorsal, ventral, anterior, and posterior views of internal mould of paratype (GSC 32047); GSC locality C-23543, "Hare Indian" Formation; x1.4.

Figures 23, 24. Dorsal and side views of paratype (GSC 32046); same locality, "Hare Indian" Formation; x1.

Figures 25–29. Dorsal, ventral, posterior, side, and anterior views of paratype (GSC 32048); same locality, "Hare Indian" Formation; x1.

Figure 30. Anterior view of paratype (GSC 32049); GSC locality C-23549, Headless Formation; x1.

Figures 31, 32. Dorsal and ventral views of paratype (GSC 32050); GSC locality C-23543, "Hare Indian" Formation; x1.

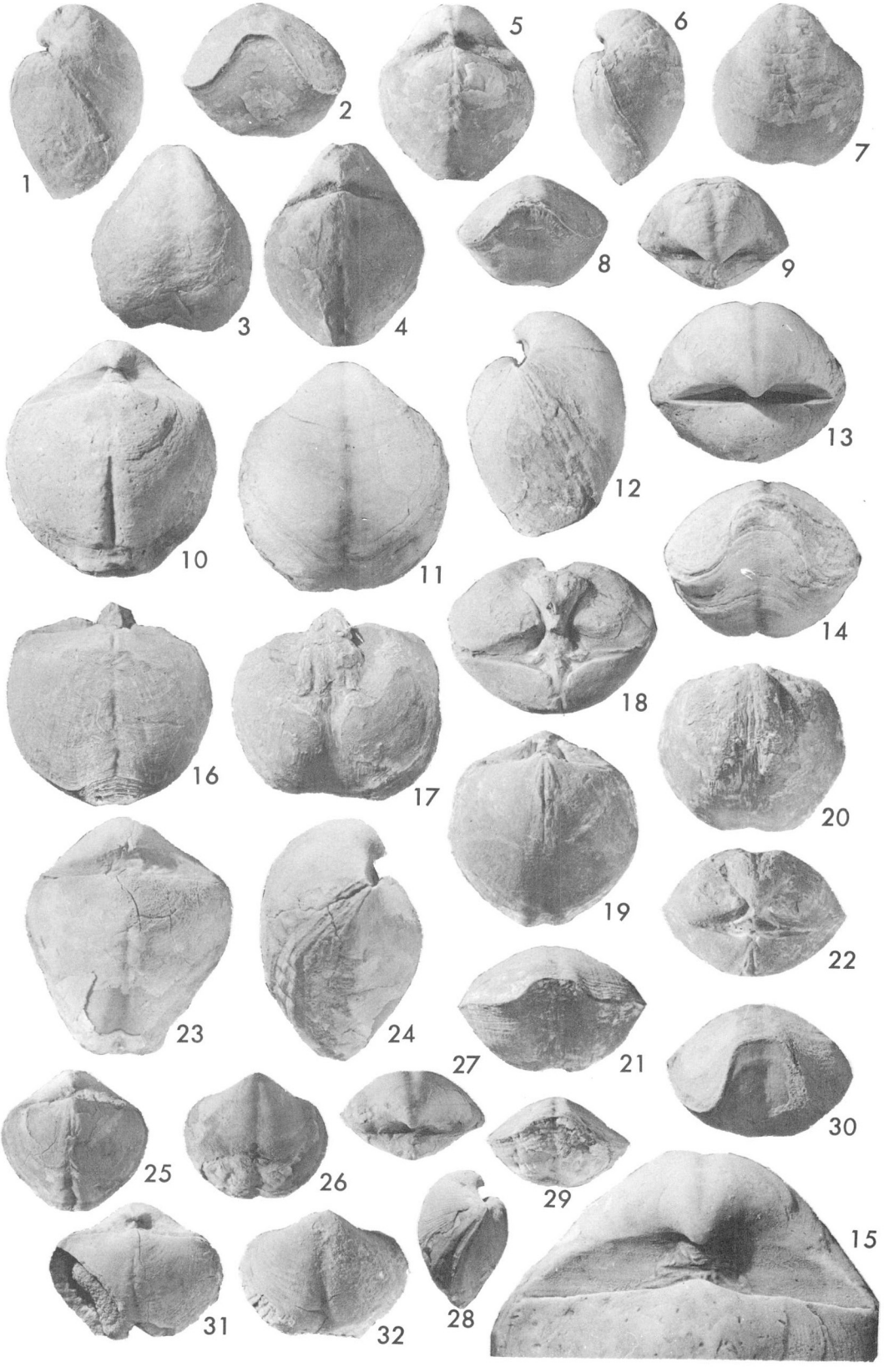
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PLATE XVI

Warrenella quadrata new species (PAGE 80)

Figures 1–5. Dorsal, posterior, anterior, ventral, and side views of holotype (GSC 31298); GSC locality C-23541, Ogilvie Formation; x1.2.

Figures 6, 7. Posterior view and detail of interarea of paratype (GSC 31299); same locality, Ogilvie Formation; fig. 6, x1; fig. 7, x1.5.

Figures 8, 9. Dorsal and posterior views of paratype (GSC 31306); same locality, Ogilvie Formation; x1.1.

Figures 10, 11. Ventral and posterior view of internal mould of pedicle valve of paratype (GSC 31334); same locality, Ogilvie Formation; x1.

Warrenella cf. *W. quadrata* new species (PAGE 68)

Figures 12–15. Dorsal, ventral, posterior, and side views of hypotype (GSC 32054); GSC locality C-23550, Headless Formation; x1.

Warrenella weigelti meeki new subspecies (PAGE 82)

Figure 16. Posterior view of internal mould of paratype (GSC 31309); GSC locality C-23544, "Hare Indian" Formation; x1.

Figures 17–20. Dorsal, side, anterior, and ventral views of paratype (GSC 31308); GSC locality C-23546, Headless Formation; x1.

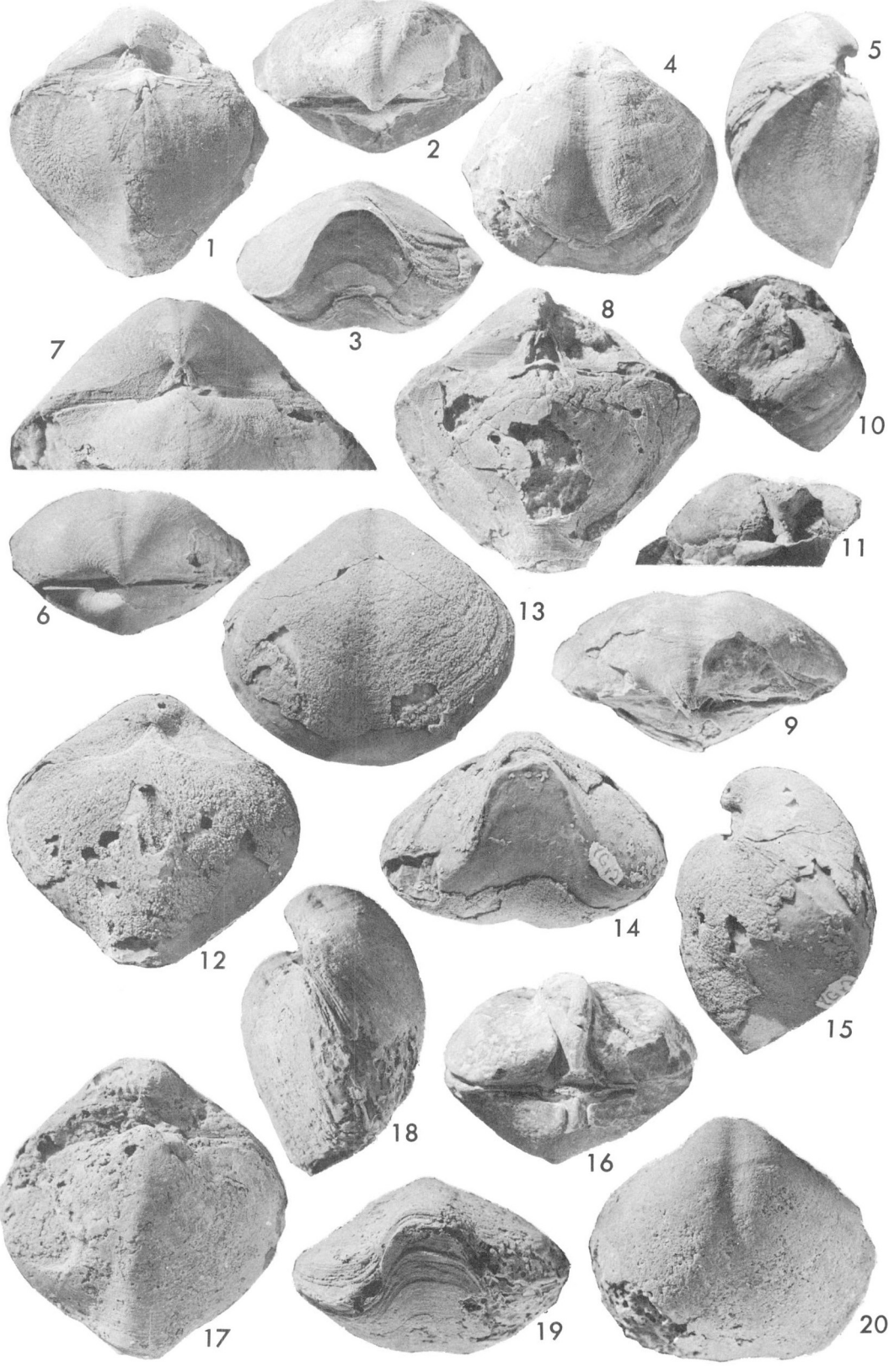
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PLATE XVII

Warrenella cf. *W. maureri* (Holzapfel) (PAGE 85)

Figures 1–5. Dorsal, ventral, posterior, anterior, and side views of hypotype (GSC 16702); GSC locality 19267, Pine Point Formation; x1.

Figures 6–10. Dorsal, ventral, posterior, anterior, and side views of hypotype (UA 1346); Pine Point Formation at Pine Point, Great Slave Lake; x1.

Warrenella quadrata new species (PAGE 80)

Figures 11–13. Dorsal, side, and ventral views of paratype (GSC 31335); GSC locality C-23541, Ogilvie Formation; x1.4.

Figure 14. Anterior view of paratype (GSC 31336); same locality, Ogilvie Formation; x1.

Figure 15. Dorsal view of paratype (GSC 31299); same locality, Ogilvie Formation; x1.

Figure 16. Posterior view of internal mould of brachial valve of paratype (GSC 31305); same locality, Ogilvie Formation; x1.4.

Figures 17–20. External and internal views of brachial valve, posterior and oblique interior views of hinge area of paratype (GSC 31300); same locality, Ogilvie Formation; figs. 17, 18, x1.2; figs. 19, 20, x2.5.

Figure 21. Exterior view of anterior fragment of pedicle valve of paratype (GSC 31303); same locality, Ogilvie Formation; x1.

Figure 22. Oblique interior view of posterior part of brachial valve of paratype, showing attached hinge teeth and dental plates (GSC 31302); same locality, Ogilvie Formation; x2.

Figure 23. Interior view of posterior part of brachial valve of paratype (GSC 31301); same locality, Ogilvie Formation; x3.5.

Figure 24. Detail of microsculpture on pedicle valve of paratype (GSC 31299); same locality, Ogilvie Formation; x8.

Warrenella weigelti meeki new subspecies (PAGE 82)

Figure 25. Ventral view showing shallow and flat sulcus of paratype (GSC 31310); GSC locality C-23544, "Hare Indian" Formation; x1.

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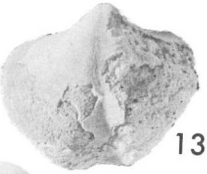
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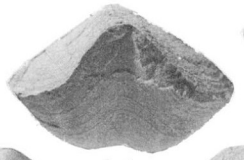
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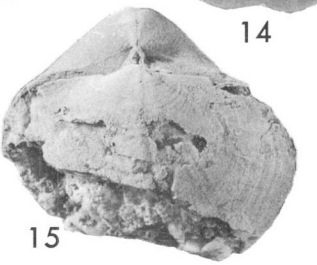
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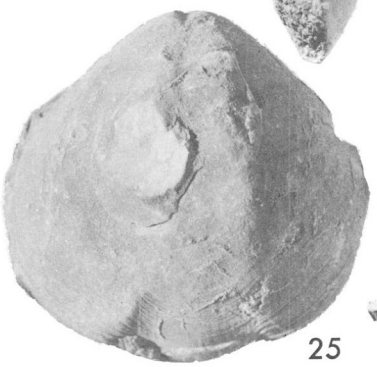
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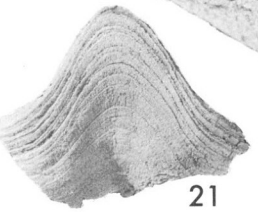
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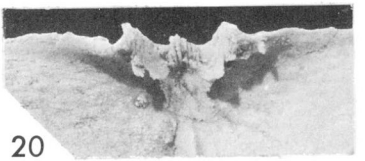
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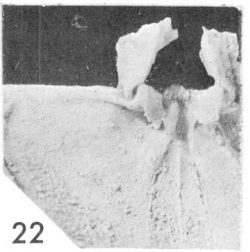
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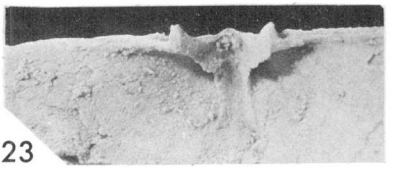
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PLATE XVIII

Warrenella weigelti meeki new subspecies (PAGE 82)

Figures 1–5. Dorsal, ventral, posterior, anterior, and side views of holotype (GSC 32052); GSC locality C-23543, "Hare Indian" Formation; x1.

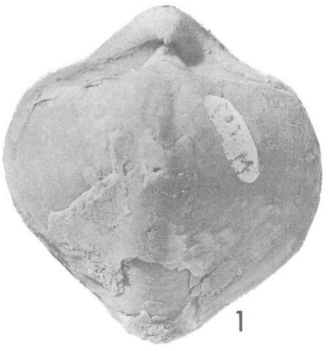
Figure 6. Dorsal view of rubber impression of fragmentary interior of paratype (GSC 32051); same locality, "Hare Indian" Formation; x1.4.

Figures 7–12. Posterior, side, dorsal, ventral, and anterior views, and oblique detail of hinge of paratype (GSC 31307); GSC locality C-23544, "Hare Indian" Formation; figs. 7, 8, 9, 10, 11, x1; fig. 12, x2.

Warrenella occidentalis timetea Crickmay (PAGE 84)

Figure 13. Dorsal view of hypotype (UA 891); "Beavertail Limestone" (Ramparts Formation); x1.

Figures 14, 15. Ventral and anterior views of hypotypes (UA 890); "Beavertail Limestone" (Ramparts Formation); x1.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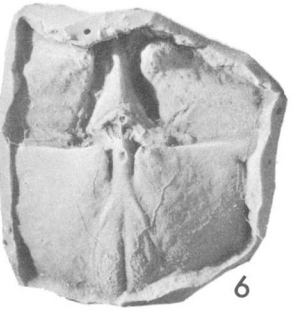
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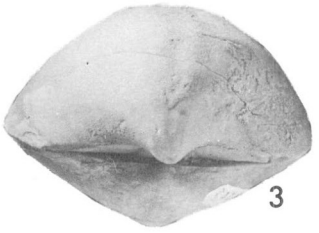
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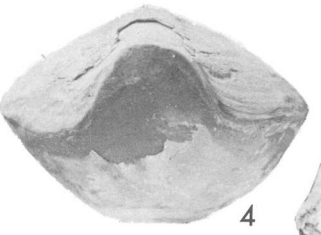
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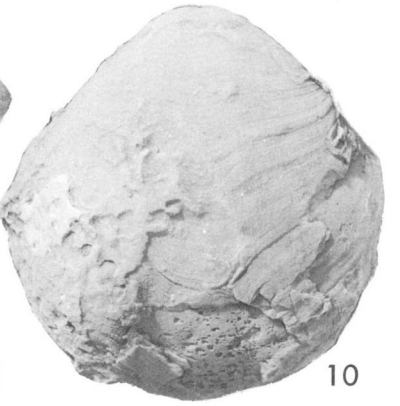
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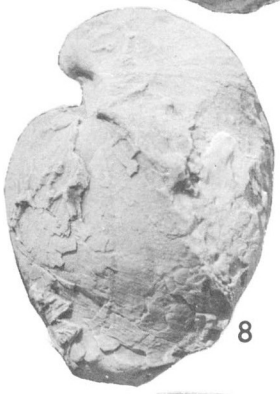
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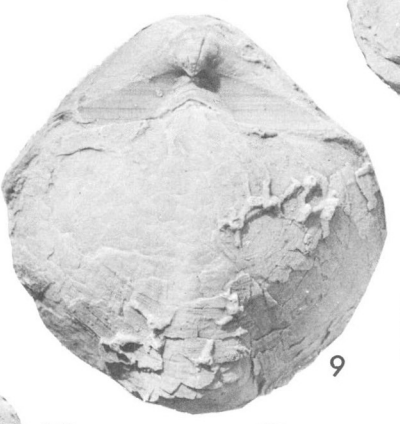
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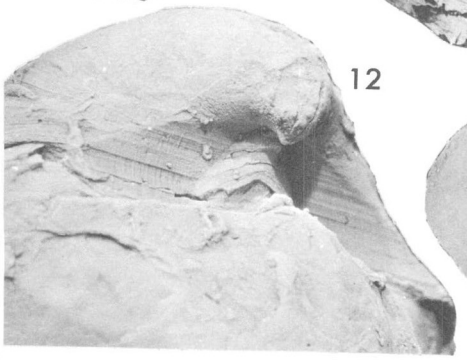
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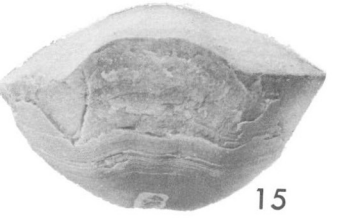
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PLATE XIX

Warrenella occidentalis timetea Crickmay (PAGE 84)

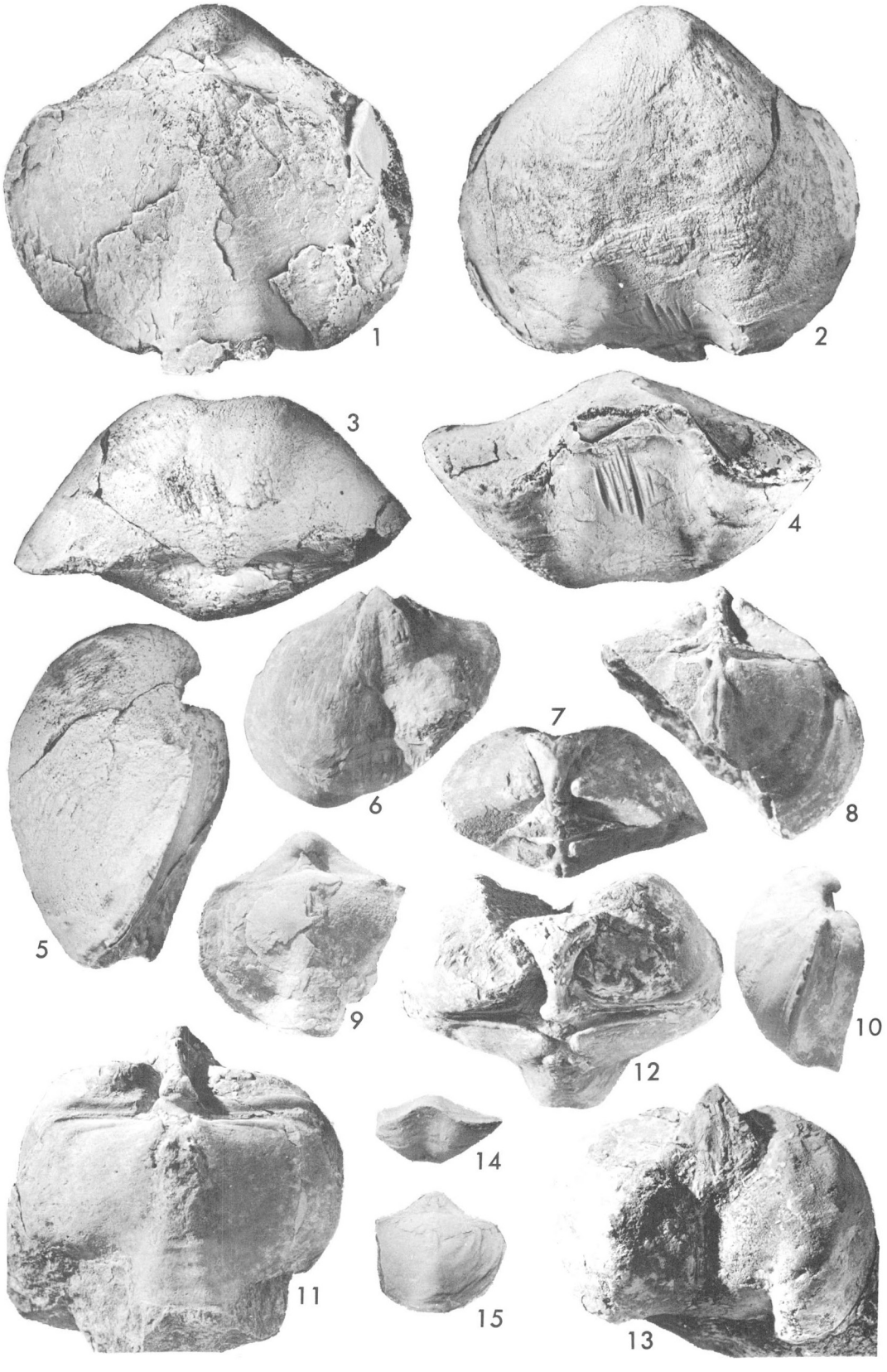
Figures 1–5. Dorsal, ventral, posterior, anterior, and side views of hypotype (GSC 25669); GSC locality C-23552, upper Ramparts Formation at Carcajou Ridge; x1.

Figures 6–8. Ventral, posterior, and dorsal views of internal mould of hypotype (GSC 31320); GSC locality C-23552, Ramparts Formation; x1.4.

Figures 9, 10. Dorsal and side views of hypotype (GSC 31311); same locality, Ramparts Formation; x1.

Figures 11–13. Dorsal, posterior, and ventral views of internal mould of hypotype (GSC 31313); same locality, Ramparts Formation; x1.

Figures 14, 15. Anterior and dorsal views of hypotype (GSC 31312); same locality, Ramparts Formation; x1.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