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LOWER PERMIAN BRACHIOPODS AND MOLLUSCS FROM THE UPPER JUNGLE CREEK FORMATION, NORTHERN YUKON TERRITORY, CANADA

G.R. Shi and J.B. Waterhouse

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D.K. Norris

Authors' addresses

G.R. Shi
School of Aquatic Science and
Natural Resources Management
Deakin University
Rusden Campus
662 Blackburn Road
Clayton, Victoria 3168
Australia

J.B. Waterhouse
274 Princes Drive
Nelson
New Zealand

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PREFACE

Carboniferous and Permian strata occur at the surface or in the subsurface over most of the northern Yukon and adjacent Northwest Territories. The regional stratigraphy of these rocks has been described over the last 30 years in a series of GSC and other publications. They have been of particular interest for petroleum and Pb/Zn/Ag exploration in Eagle Plain and Ogilvie Mountains.

The geological time framework that has proven essential for understanding this stratigraphic succession is based on zonations provided by several fossil groups, but main emphasis is on the brachiopod zonation. The present publication is one of several that provide documentation not only of the biostratigraphic distribution of the rich brachiopod faunas of the area, but also of their significance for understanding paleogeographic and tectonic patterns, and their taxonomy. This Bulletin will serve as a biostratigraphic standard for further studies throughout the Arctic internationally, and other areas with similar sequences.

The paleontology program of the Geological Survey of Canada provides the essential biostratigraphic framework for accurate mapping and stratigraphic analyses. Publications such as this make public the results of the detailed studies that are necessary to ensure the quality of a wide variety of regional geological studies.

M.D. Everell
Assistant Deputy Minister
Earth Sciences Sector

PRÉFACE

À la surface ou dans le sous-sol de presque tout le nord du Yukon et des Territoires du Nord-Ouest adjacents s'étendent des couches carbonifères et permiennes. Au cours des trente dernières années, la stratigraphie régionale de ces roches ont fait l'objet de descriptions dans une série de publications publiées par la CGC et d'autres organismes. Ces données ont été d'un intérêt particulier pour l'exploration pétrolière et la prospection du plomb, du zinc et de l'argent dans le plaine d'Eagle et les monts Ogilvie.

La géochronologie, qui s'est avérée essentielle pour comprendre cette succession stratigraphique, se base sur les zones établies à partir de plusieurs groupes de fossiles, mais l'accent porte surtout sur la zonation des brachiopodes. La présente publication, à linstar de quelques autres, documente non seulement la répartition biostratigraphique des riches faunes de brachiopodes de la région, mais également leur importance au niveau de la compréhension des configurations paléogéographiques et tectoniques, ainsi que leur taxonomie. On prévoit que le présent bulletin pourra servir de norme biostratigraphique dans les prochaines études internationales dans l'Arctique et les autres régions comportant des séquences semblables.

La programme de paléontologie de la Commission géologique du Canada fournit le cadre biostratigraphique essentiel servant à l'établissement de cartes et aux analyses stratigraphiques. Grâce à ce type de publication, le public a accès aux résultats d'études approfondies qui sont nécessaires pour assurer la qualité d'une vaste gamme d'études géologiques régionales.

M.D. Everell
Sous-ministre adjoint
Secteur des sciences de la Terre

CONTENTS

Figures

Tables

Appendix Figures

Appendix Tables

Plates

LOWER PERMIAN BRACHIOPODS AND MOLLUSCS FROM THE UPPER JUNGLE CREEK FORMATION, NORTHERN YUKON TERRITORY, CANADA

Abstract

The study aims to provide a comprehensive systematic account of Lower Permian brachiopods and molluscs (excluding gastropods) from the upper Jungle Creek Formation in northern Yukon Territory, western Canada, and to assess their biostratigraphic and paleoecological significance.

Sixty-nine brachiopod species belonging to 53 genera, six bivalve species belonging to five genera, and one ammonoid species are described and illustrated. New taxa include *Arctitreta peelensis* n. sp., *Orthotetes canadensis* n. sp., *Liosotella compacta* n. sp., *Anemonaria auriculata* n. sp., *Costispinifera paucispinosa* n. sp., *Rugivestis arctica* n. sp., *Thamnosia spinosa* n. sp., *Globiella costellata* n. sp., *Protoanidanthus umbonatus* n. sp., *Rhynoleichus dorsoconvexa* n. sp., *Septacamera triangulata* n. sp., *Composita bamberi* n. sp., *Ogilviecoelia inflata* n. gen. et sp., *Tumarinia yukonica* n. sp., *Yukonella plana* n. gen. et sp., *Timaniella convexa* n. sp., *Yukonospirifer yukonensis* n. gen. n. sp., *Larispirifer ettrainensis* n. sp., *Domokhotia junglensis* n. sp., *Tiramnia canadica* n. sp., and Retimarginiferinae n. subfam.

The three brachiopod biozones previously recognized within the upper Jungle Creek Formation are revised and substantiated. These are the (in ascending stratigraphic order) *Yakovlevia transversa* Assemblage Zone, *Ogilviecoelia inflata* Assemblage Zone, and *Jakutoproductus verchoyanicus* Assemblage Zone. The distribution of these zones in the study area and their correlation with other major Lower Permian marine sequences in North America and the Arctic are discussed. Close correlation of the Yukon brachiopod faunas with those from the Urals, northeast Russia, and the Canadian Arctic, reinforced by some data from fusulinids and ammonoids, suggests that the *Yakovlevia transversa* Zone is probably Early Sakmarian (Tastubian) in age, the *Ogilviecoelia inflata* Zone is Late Sakmarian (Sterlitamakian), and *Jakutoproductus verchoyanicus* Zone is Early Artinskian (Aktastinian).

A computerized ordination technique (principal components analysis) is used to delineate recurrent paleocommunities. Four fossil communities are recognized: *Rhynchopora magna*, *Fimbrinia–Tubersulculus–Kutorginella*, *Ogilviecoelia inflata*, and *Tityrophoria nelsoni–Septacamera triangulata*. These paleocommunities are analyzed in terms of faunal composition and possible depositional environments. They seem to record positions in an onshore to offshore sequence across a shallow marine shelf, with the *Rhynchopora magna* paleocommunity possibly representing a shallow subtidal restricted zone; the *Fimbrinia–Tubersulculus–Kutorginella* paleocommunity representing probably an open shelf, above wave base zone; the *Ogilviecoelia inflata* paleocommunity possibly an open shelf, near or at wave base zone; and the *Tityrophoria nelsoni–Septacamera triangulata* paleocommunity a low energy position, farther offshore, below wave base.

Résumé

La présente étude vise à dénombrer de facon systématique et globale les brachiopodes et les mollusques (excluant les gastropodes) du Permien inférieur dans la partie supérieure de la Formation de Jungle Creek dans le nord du Yukon (Ouest canadien) et d'évaluer leur valeur biostratigraphique et paléoécologique.

Soixante-neuf espèces de brachiopodes appartenant à 53 genres, six espèces de bivalves appartenant à cinq genres et une espèce d'ammonodés sont décrits et illustrés. Les nouveaux taxons incluent *Arctitreta peelensis* n. sp., *Orthotetes canadensis* n. sp., *Liosotella compacta* n. sp., *Anemonaria auriculata* n. sp., *Costispinifera paucispinosa* n. sp., *Rugivestis arctica* n. sp., *Thamnosia spinosa* n. sp., *Globiella costellata* n. sp., *Protoanidanthus umbonatus* n. sp., *Rhynoleichus dorsoconvexa* n. sp., *Septacamera triangulata* n. sp., *Composita bamberi* n. sp., *Ogilviecoelia inflata* n. gen. et sp., *Tumarinia yukonica* n. sp., *Yukonella plana* n. gen. et sp., *Timaniella convexa* n. sp., *Yukonospirifer yukonensis* n. gen. n. sp., *Larispirifer ettrainensis* n. sp., *Domokhotia junglensis* n. sp., *Tiramnia canadica* n. sp. et Retimarginiferinae n. subfam.

Les trois biozones de brachiopodes antérieurement établies dans la partie supérieure de la Formation de Jungle Creek sont révisées et étayées. Ce sont, par ordre stratigraphique ascendant, les Zones à *Yakovlevia transversa*, à *Ogilviecoelia inflata* et à *Jakutoproductus verchoyanicus*. La répartition de ces cénozones dans la région à l'étude et leur corrélation avec d'autres séquences marines importantes du Permien inférieur en Amérique du Nord et dans l'Arctique sont traitées. L'étroite corrélation établie entre les faunes de brachiopodes du Yukon et celles de l'Oural, du nord-est de la Russie et de l'Arctique canadien, corroborée par certaines données sur les fusulinidés et les ammonodés, révèle que la Zone à *Yakovlevia transversa* date probablement du Sakmarien précoce (Tastubien), que la Zone à *Ogilviecoelia inflata* remonte au Sakmarien tardif (Sterlitamakien) et que la Zone à *Jakutoproductus verchoyanicus* date de l'Artinskien précoce (Aktastinien).

Une technique d'ordination par ordinateur (analyse des composantes principales) est utilisée pour délimiter les paléocommunautés récurrentes. Quatre communautés de fossiles sont observées : *Rhynchopora magna, Fimbrinia–Tubersulculus–Kutorginella, Ogilviecoelia inflata* et *Tityrophoria nelsoni–Septacamera triangulata*. Ces paléocommunautés sont analysées en fonction de la composition faunistique et des milieux de sédimentation possibles. Elles semblent indiquer des positions dans une séquence littorale à extralittorale à travers une plate-forme marine peu profonde, la paléocommunauté *Rhynchopora magna* représentant peut-être une zone subtidale restreinte peu profonde, la paléocommunauté *Fimbrinia–Tubersulculus–Kutorginella* probablement une plate-forme continentale ouverte au-dessus du niveau de base des vagues, la paléocommunauté *Ogilviecoelia inflata* peut-être une plate-forme continentale ouverte près du niveau de base des vagues ou à ce niveau et la paléocommunauté *Tityrophoria nelsoni–Septacamera triangulata,* un milieu à faible énergie, plus éloignée vers le large, au-dessous du niveau de base des vagues.

INTRODUCTION

Fossils are abundant throughout the Permian strata of northern Yukon Territory. Brachiopods are particularly common, and there are intervals with fusulinids, ammonoids, bivalves, gastropods, corals, and bryozoans. Since Nelson (1961) first illustrated six brachiopods from the northern Ogilvie Mountains, Permian brachiopods have been the basis of several systematic studies (e.g., Nelson and Johnson, 1968; Bamber and Waterhouse, 1971; Sarytcheva and Waterhouse, 1972; Waterhouse and Waddington, 1982), reinforced by several paleoecological and biozonal studies (Waterhouse, 1967, 1975a, b, 1976, 1977a–c, 1979). A succession of brachiopod faunas and zones has been proposed for the Upper Paleozoic of northern Yukon Territory in an attempt to establish a regional biostratigraphic standard (Bamber and Waterhouse, 1971; Waterhouse and Waddington, 1982).

The present study describes the Yukon faunas from the "E" level zones, of approximately Sakmarian–Early Artinskian age (Early Permian). Fossil communities are outlined.

Previous work

Early geological reconnaissances were conducted by Maddren (1912), Cairnes (1914), and Gabrielse (1957). Martin (1959, 1961) was first to outline the general distribution of the Upper Paleozoic rocks in the area, and Nelson (1961) provided an initial stratigraphic framework. General accounts of the Upper Paleozoic sequences were provided by Norris et al. (1963) and Douglas et al. (1963), and generalized paleogeographic maps and stratigraphic columns were presented by Ziegler (1967). The first comprehensive report on the Carboniferous–Permian succession of the area was provided by Bamber and Waterhouse (1971), who established both a stratigraphic and biostratigraphic framework and provided paleogeographic maps. Subsurface studies of the Upper Paleozoic in southern Eagle Plain were provided by Martin (1972), Graham (1973), and Pugh (1983).

Permian brachiopods throughout the area have received limited systematic attention (Table 1). Nelson (1961) reported and illustrated three brachiopods under the names *Waagenoconcha* Chao, "Horridonid brachiopod", and *Neospirifer* Frederiks, that helped to characterize the Permo-Pennsylvanian rocks of northern Yukon Territory. In the same paper, Nelson illustrated specimens from the Tahkandit Formation as *Spiriferella saranae* (Verneuil), *Muirwoodia greenlandica* (Dunbar), and *Leiorhynchus* sp. Later, Nelson (1962a) illustrated two horridonid species as indicators of the Permian Tahkandit Formation in Yukon Territory under the names *Horridonia horrida* (Sowerby) and *H. timanica* (Stuckenberg). The former was said to be typical of the lower Tahkandit Formation and the latter of the upper Tahkandit Formation. Nelson and Johnson (1968) described and figured from the Permian of northern Yukon Territory members of the genera *Horridonia* Chao and *Spiriferella* Chernyshev (Table 1). Waterhouse (*in* Bamber and Waterhouse, 1971) divided the Carboniferous–Permian succession into different faunas and zones, and listed and illustrated for each brachiopod zone the most characteristic forms, most of which were identified only to generic level. In the same paper, Waterhouse also named two new brachiopod genera from the Permian formations: *Tubersulculus* and *Tityrophoria* (Table 1). Material collected from the unnamed sandstone unit (equivalent to Tahkandit Formation) in the northern Richardson Mountains (Fig. 1) was described by Waterhouse (1971b) as a new species, *Terrakea arctica*. Yancey (1978) pointed out the similarity between *Terrakea arctica* and the aulostegid *Costellarina* Muir-Wood and Cooper. However, the similarity is superficial—*Costellarina* differs internally and lacks dorsal spines.

Sarytcheva and Waterhouse (1972) recorded three Arctic species of the family Retariidae Muir-Wood and Cooper under the names *Kutorginella yukonensis, K. triangulata* from the Jungle Creek Formation, and *Thuleproductus arcticus* from the Tahkandit Formation. *Thuleproductus* appears to be a junior synonym of *Svalbardoproductus* Ustritskiy (Lazarev, 1990, p. 105).

Nelson (1975), in his paleontological field guide of northern Canada and Alaska, illustrated several "Permo-Pennsylvanian" brachiopods from northern Yukon Territory under the names *Camerisma*? sp., *Horridonia bullocki* Nelson and Johnson, and *Yakovlevia* sp., and Lower Permian forms under the names *Spiriferella* sp., *Licharewia* Einor, and *Spirifer osborni* Harker. Gorveatt and Nelson (1975) reported a choristitid "*Spirifer*" *nikitini* Chernyshev from the basal Jungle Creek Formation.

Several specimens from the lower Jungle Creek Formation were figured by Waterhouse et al. (1978) as *Spiriferella pseudodraschei* Einor and *S. ordinaria* Einor.

Waterhouse and Waddington (1982) reviewed the Spiriferellinae from northern Canada, and described a number of species of the subfamily from the Permian

Table 1

Brachiopods previously described and figured from the Permian Jungle Creek Formation and the overlying Tahkandit Formation, northern Yukon Territory

Taxa	Reference	Stratigraphic position	Revised here
Horridonia bullocki (Nelson and Johnson)	Nelson and Johnson, 1968	Jungle Creek Fm.	*Sowerbina bullocki*
H. granulifera (Toula)	as above	Tahkandit Fm.	*S. granulifera*
Spiriferella saranae Zavodovskiy	as above	Tahkandit Fm.	*S. vaskovkski* (Verneuil)
S. rajah (Salter)	as above	Jungle Creek Fm. Tahkandit Fm.	*S. keilhavii* (Buch)
S. ordinaria (Einor)	as above	Jungle Creek Fm.	*Alispiriferella ordinaria*
S. editareatus (Einor)	as above	Lower Tahkandit Fm.	
S. keilhavii (Buch)	as above	Upper Tahkandit Fm.	
Tubersulculus maximus Waterhouse	Bamber and Waterhouse, 1971	Jungle Creek Fm.	
Tityrophoria nelsoni Waterhouse	as above	Jungle Creek Fm.	
Timaniella harkeri Waterhouse	as above	Tahkandit Fm.	
Terrakea arctica Waterhouse	Waterhouse, 1971b	Unnamed sandstone unit, Richardson Mtns.	
Kutorginella yukonensis Sarytcheva and Waterhouse	Sarytcheva and Waterhouse, 1972	Jungle Creek Fm.	
K. triangulata Sarytcheva and Waterhouse	as above	Jungle Creek Fm.	*K. yukonensis*
Thuleproductus arcticus Sarytcheva and Waterhouse	as above	Tahkandit Fm.	*Svalbardoproductus? arcticus*
Spirifer nikitini Chernyshev	Gorveatt and Nelson, 1975	Jungle Creek Fm.	*Purdonella nikitini*
Spiriferella pseudodraschei Einor	Waterhouse and Waddington, 1982	Jungle Creek Fm.	
S. saranae Einor	as above	Jungle Creek Fm.	
S.? loveni (Diener)	as above	Tahkandit Fm.	
S. cf. *vojnowskii* Ifanova	as above	Tahkandit Fm.	
S. leviplica Waterhouse and Waddington	as above	Tahkandit Fm.	
S. keilhavii (Buch)	as above	Tahkandit Fm.	
Eridmatus petita Waterhouse and Waddington	as above	Jungle Creek Fm.	
Alispiriferella ordinaria (Einor)	as above	Jungle Creek Fm.	
Timaniella harkeri Waterhouse and Waddington	as above	Tahkandit Fm.	
Elivina cordiformis Waterhouse and Waddington	as above	Tahkandit Fm.	

Jungle Creek and Tahkandit formations (Table 1), including one new genus *Alispiriferella*.

Remains of fossil groups other than brachiopods occur sporadically in the Permian sequences of northern Yukon Territory. Fusulinids were described by Ross (1967a; *in* Bamber and Waterhouse, 1971), ammonoids by Nassichuk et al. (1965) and Nassichuk (1971), corals by Nelson (1962b), and palynomorphs by Bamber and Barss (1969). Permian gastropods and bivalves from the study area are rare and described for the first time in this study. The Carboniferous and Permian biostratigraphy of northern Yukon Territory was recently reviewed by Bamber et al. (1989). They reported reworked Carboniferous conodonts in the Permian age of lower Jungle Creek Formation in the Peel River area, and a rare Asselian conodont species in the Jungle Creek Formation (level not specified) in the northern Ogilvie Mountains. They also reported a striate disaccate assemblage zone of (?)Late Asselian–Sakmarian age from the lower Jungle Creek Formation, locality and level not specified.

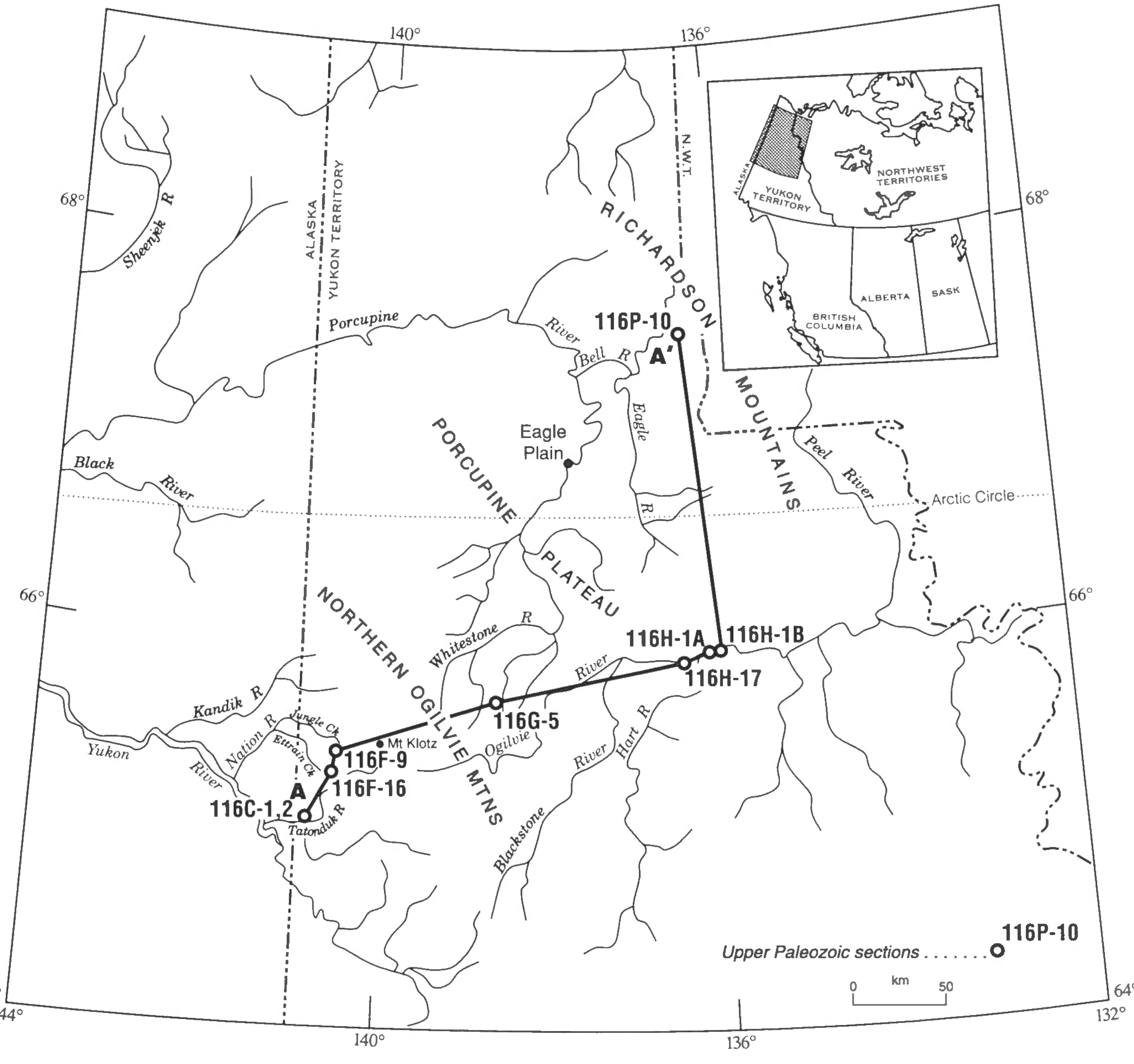


Figure 1. *Index map showing area of study. The cross-section line (A–A') indicates locations of principal upper Paleozoic sections shown in Figure 3.*

Material

Some of the material examined in this report was collected by officers of the Geological Survey of Canada, especially Dr. E.W. Bamber in 1962 and 1963. Fossil localities are registered at the Geological Survey of Canada with the prefix GSC loc. and a five-figure serial number. Some collections were augmented from the same locality by JBW during 1968 to 1972 and given the same locality number. Locations of sections are given in Appendix Table 1. Stratigraphic details of GSC localities are given in Appendix Table 2. Collections were made at other localities by one of us (JBW) and colleagues during expeditions to the area from 1968 to 1972; the localities are numbered serially with the prefix JBW loc. and a one- to three-figure serial number. Stratigraphic details of the JBW localities are given in Appendix Table 3. Most localities examined come from three main areas (Fig. 1): the Peel River (GSC sections 116H-1A, 116H-1B, 116H-17); the Tatonduk River (GSC sections 116C-1, 116C-2); and the Ettrain and Jungle creeks in the northern Ogilvie Mountains (GSC sections 116F-9 and 116F-16). Fossils from a few other localities in GSC section 116G-5, Nahoni Range East, northern Ogilvie Mountains (Fig. 1), and section 116P-10, northern Richardson Mountains, were also examined.

Acknowledgments

Most of this study was done by G.R. Shi as partial requirement for a Ph.D. degree at the University of Queensland. Revisions were completed at Deakin University, Rusden Campus, Melbourne.

This study, in terms of collections, stratigraphic and regional framework, is based on work by the officers of the Geological Survey of Canada, especially Dr. E.W. Bamber, Institute of Sedimentary and Petroleum Geology, Geological Survey of Canada, Calgary. The authors particularly wish to acknowledge the loan of the collections and provision of stratigraphic information facilitated by Dr. E.W. Bamber. We are especially grateful to Drs. J.S. Jell of the University of Queensland, Brisbane, E.W. Bamber and D.K. Norris, Geological Survey of Canada, Calgary, and J. Thomas Dutro, Jr. of the U.S. Geological Survey, for critically reading various parts of the manuscript and providing constructive suggestions on various aspects of the work. Special thanks must be extended to Dr. N.W. Archbold, Deakin University, Rusden Campus, Melbourne, who read parts of the text and greatly assisted in completing the work.

STRATIGRAPHIC FRAMEWORK

The study area (Fig. 1) is situated in the northern Canadian Cordillera near its junction with the northeast-trending Innuitian structural province. The Carboniferous–Permian succession in the area, which ranges in age from (?)Tournaisian to Late Permian (Kazanian), forms part of the thick, shallow, marine sequence of the Western Canada Sedimentary Basin (cf. Henderson, 1989, Fig. 10.2) and consists mainly of highly fossiliferous carbonates, siltstone, and shale. An early attempt to bring order to the upper Paleozoic rocks was made by Nelson (1961), who recognized four mappable units (Table 2). The lower two (Calico Bluff Formation and Lower Limestone Unit) were assigned to the Carboniferous, and the upper two (the Middle Recessive Unit and Tahkandit Formation) to the Wolfcampian (Asselian–Sakmarian) and Leonardian (Artinskian–Ufimian). The units were not formally defined. Bamber (*in* Bamber and Waterhouse, 1971) formally subdivided and named the succession, and recognized five lithostratigraphic units (Table 2). These were shown in the 1:250 000 geological map of the Ogilvie River area (Map No. 1526A) by Norris (1982). Virtually the entire upper Carboniferous was placed in one formation (Ettrain Formation), divided into two unnamed informal members, and the uppermost Carboniferous and most of the lower Permian was allocated to one formation only (Jungle Creek Formation), with two unnamed informal members. Comparable sequences of about the same age, and showing a comparable range of lithologies and thickness, such as those in the southern Rockies, and in the Canadian Arctic Archipelago and Siberia, are generally allocated to several formations. In particular, each formation includes clearly defined consistent units characterized by distinct lithologies and bedding, that under the International Guide for Stratigraphic Nomenclature (Hedberg, 1976) should be assigned formation status. In addition, there are substantial paraconformities within both the Ettrain and Jungle Creek formations. Detailed studies of outcrops and faunules by the writers strongly suggest that the two formations are each made up of packages of tongues of sediment, separated by paraconformities, with complex facies changes. Waterhouse and Waddington (1982) recognized an unnamed "new formation" between the Upper Carboniferous Ettrain Formation and the Lower Permian Jungle Creek Formation (Table 2). Pugh (1983) reviewed the stratigraphic subdivisions of the Peel River area and proposed a new unit, the Blackie Formation, between the Hart River and Ettrain formations (Table 2).

Ford Lake Formation

Brabb (1969, p. 12) proposed the name "Ford Lake Shale" as a formation for exposures near Ford Lake in east-central Alaska, which consists "predominantly of greyish-black silicious shale and laminated greyish-black chert that splits with slabby parting". The type section is located at about 64°55′N latitude, 141°12′W longitude. Bamber (*in* Bamber and Waterhouse, 1971, Table 1, p. 42) correlated the Ford Lake Shale with his "Unit 1" shale directly underlying the Hart River Formation in the Peel River area. Pugh (1983, p. 45) formally extended the use of the name Ford Lake eastward into northern Yukon Territory "as a thick sequence of very dark shales, previously known informally as 'Unit 1', underlying the Hart River Formation and overlying the Imperial Formation".

The age of the Ford Lake Shale was indicated to be Late Devonian to Late Mississippian in east-central Alaska by Brabb (1969, p. 17). In northern Yukon Territory, a late Viséan age was determined for the

Table 2

Correlation of Carboniferous and Permian stratigraphic subdivisions proposed by different authors in the northern Ogilvie Mountains and southern Eagle Plain

<table>
<tr><th>SYSTEM</th><th>FAUNAS AND ZONES</th><th>AGE</th><th>Nelson, 1961</th><th>Bamber and Waterhouse, 1971</th><th colspan="2">Norris, 1982</th><th>Waterhouse and Waddington, 1982</th><th>Pugh, 1983</th></tr>
<tr><td rowspan="2">PERMIAN</td><td>F, G Faunas</td><td rowspan="2">ASSELIAN to KAZANIAN</td><td>TAHKANDIT FORMATION</td><td>TAHKANDIT FORMATION</td><td colspan="2">TAHKANDIT FORMATION</td><td>TAHKANDIT FORMATION</td><td>TAHKANDIT FORMATION</td></tr>
<tr><td>E Fauna: Eka, Eo, Eta, Ey, Eog, Ej</td><td rowspan="2">Middle Recessive Unit</td><td rowspan="2">JUNGLE CREEK FORMATION</td><td rowspan="2">JUNGLE CREEK FORMATION</td><td>Upper Member</td><td>JUNGLE CREEK FORMATION</td><td rowspan="2">JUNGLE CREEK FORMATION</td></tr>
<tr><td rowspan="5">CARBONIFEROUS</td><td>D Fauna</td><td rowspan="5">VISEAN to GZHELIAN</td><td>Lower Member</td><td>NEW FORMATION</td></tr>
<tr><td>C Fauna</td><td rowspan="2">Lower Limestone Unit</td><td rowspan="2">ETTRAIN FORMATION</td><td colspan="2" rowspan="2">ETTRAIN FORMATION</td><td rowspan="2">ETTRAIN FORMATION</td><td>ETTRAIN FORMATION</td></tr>
<tr><td>B Fauna</td><td>BLACKIE FORMATION</td></tr>
<tr><td>A Fauna</td><td rowspan="2">CALICO BLUFF FORMATION</td><td>HART RIVER FORMATION</td><td colspan="2">HART RIVER FORMATION</td><td>HART RIVER FORMATION</td><td>HART RIVER FORMATION</td></tr>
<tr><td></td><td>Unit 1</td><td colspan="2">FORD LAKE FORMATION</td><td>Unit 1</td><td>FORD LAKE FORMATION</td></tr>
</table>

palynomorph *Murospora aurita–Rotaspora fracta* Assemblage Zone reported to be present in the upper part of the Ford Lake Formation and overlying Hart River Formation (except for its uppermost part) (Bamber et al., 1989).

Hart River Formation

The Hart River Formation (Bamber *in* Bamber and Waterhouse, 1971, p. 45) consists mainly of limestone and chert. In its type locality at section 116H-1B on the Peel River (Figs. 2, 3), this formation is estimated to be 242 m thick. In northern Ogilvie Mountains, fine grained, silty, dolomitic, skeletal-micritic limestone separated by covered intervals underlying the type Ettrain Formation at section 116 F-9 (Figs. 3, 4) was originally equated with the Hart River Formation by Bamber (*in* Bamber and Waterhouse, 1971, p. 49). E.W. Bamber (pers. comm., 1992) suggested that this should be the Blackie Formation of Pugh (1983), with the Hart River Formation in this section being represented only by a thin rib much lower in the section.

On the basis of data from brachiopod (brachiopod Aq zone of Waterhouse *in* Bamber and Waterhouse, 1971), goniatites, and foraminifers, Bamber and Waterhouse (1971) assigned the Hart River Formation to an age of mainly late Viséan to Early Namurian. However, outcrops that are deemed comparable in the southeast Eagle Plains have Moscovian brachiopods.

Blackie Formation

This formation was defined by Pugh (1983, p. 47) as a sequence of "shale, siltstone and subordinate limestone and sandstone, overlying the Hart River Formation". It was proposed for the basinal facies equivalents of "Unit 2" of Bamber (*in* Bamber and Waterhouse, 1971, p. 51), Ettrain and Jungle Creek formations. The subsurface type section was designated at the Socony Blackie Y.T. M-59 well, located in southern Eagle Plain at 65°58′55″N latitude, 137°11′11″W longitude. Two "units" are present. The type Blackie is made up of "a lower 294 m of black, bituminous shale, in part silty or sandy, with rare argillaceous limestone, and an upper 388 m of dark, brown-grey, argillaceous, slightly calcareous or dolomitic thin beds of argillaceous limestone" (Pugh, 1983, p. 47). In the type section, the unit is overlain (?)unconformably by the Jungle Creek Formation.

The Blackie Formation is poorly exposed in northern Yukon Territory and is represented in three sections of the present study. In section 116F-9 of the Jungle Creek area, northern Ogilvie Mountains (Figs. 3, 4), an incompletely exposed sequence (417 m thick) beneath the type Ettrain Formation, consisting mainly of dark, brownish-grey-weathering, skeletal-micritic limestone ribs, was originally assigned to the Hart River Formation by Bamber (*in* Bamber and Waterhouse, 1971, p. 49) and is now deemed Blackie Formation by Bamber (pers. comm., 1992). A similar but thinner unit is also present in section 116G-5, Nahoni Range East, northern Ogilvie Mountains (Fig. 3). To the east, the Blackie Formation is represented by the "Unit 2" of Bamber (*in* Bamber and Waterhouse, 1971, p. 51) in section 116H-1B, lying between the type Hart River Formation below and the "Unnamed Ettrain Equivalents" above (Fig. 3). "Unit 2" was defined as a sequence of "resistant, brownish grey- and orange-brown-weathering, dolomitic and calcareous sandstone and conglomerate, and sandy, skeletal limestone, with some interbedded micritic-skeletal limestone" (ibid., p. 51). Pugh (1983) recognized "Unit 2" as a tongue of the Blackie Formation.

Palynomorphs, brachiopods, conodonts, and foraminifers have been found in the Blackie Formation (Bamber et al., 1989), indicating an age range from Serpukhovian to Kasimovian, possibly as young as Early Permian according to Pugh (1983, p. 48). The wide range of fossils from Blackie-like lithotypes could reflect either a massive, central basin, deep-water shale sequence, with tongues of various ages, as assumed by Pugh (1983), or a number of discrete tongues, not all necessarily joined. This underlines the need for much more sophisticated analysis of facies changes, better fossil control, and delineation of paraconformities and structural deformation, before the question can be properly resolved. But this lies beyond the scope of this study.

Ettrain Formation

The Ettrain Formation (Bamber *in* Bamber and Waterhouse, 1971, p. 53) is a light grey- and brownish grey-weathering sequence of skeletal, skeletal-micritic, and micritic limestone with dark grey chert beds and minor intervals of dolomite, and shale bands and conglomerates toward the top. The unit forms a resistant cliff-forming interval between the relatively recessive Blackie Formation below and the Jungle Creek Formation above.

The Ettrain Formation is found extensively in northern Yukon Territory. In the type section (section 116 F-9) at Ettrain Creek in northern Ogilvie

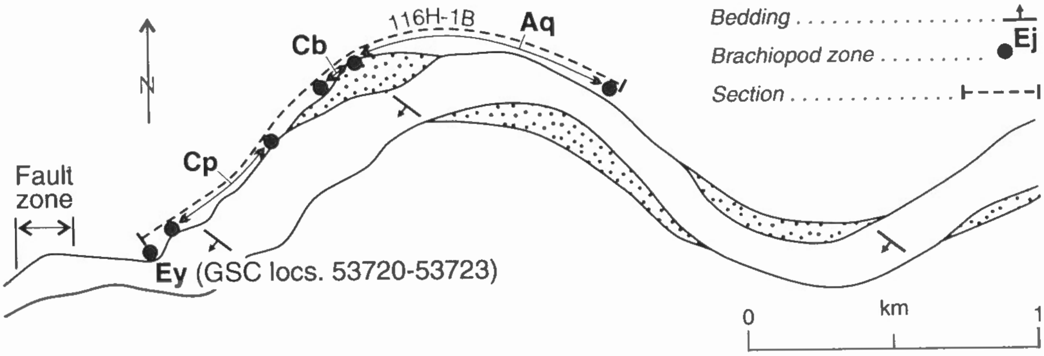


Figure 2. Fossil localities and brachiopod biozones along the Peel River (GSC section 116H-1B) (modified from Bamber and Waterhouse, 1971, Fig. 5).

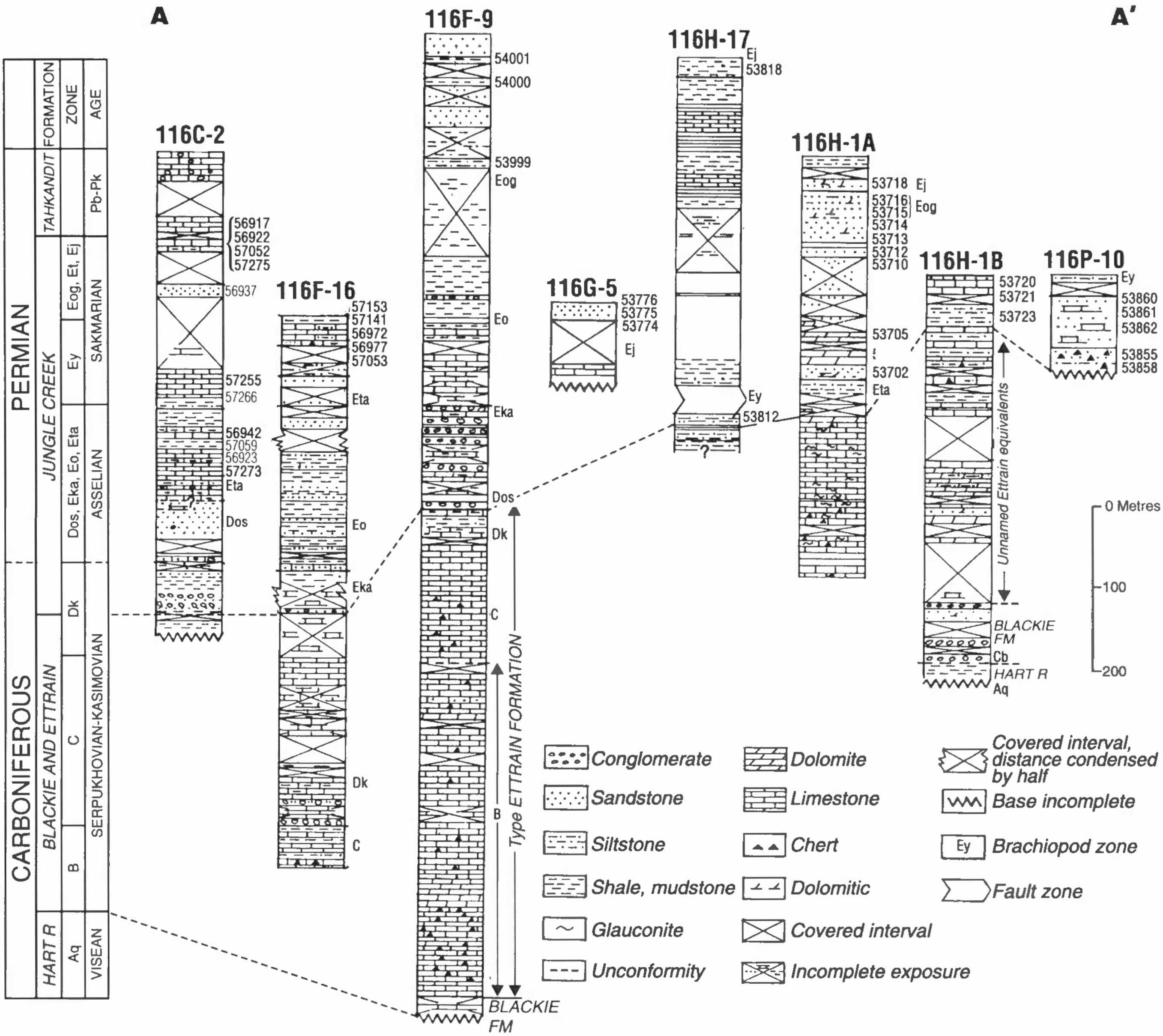


Figure 3. Stratigraphic columns of Carboniferous and Permian strata at cross-section A–A′ (see Fig. 1), with sequences of brachiopod biozones and localities. Stratigraphic data are from Bamber (1972).

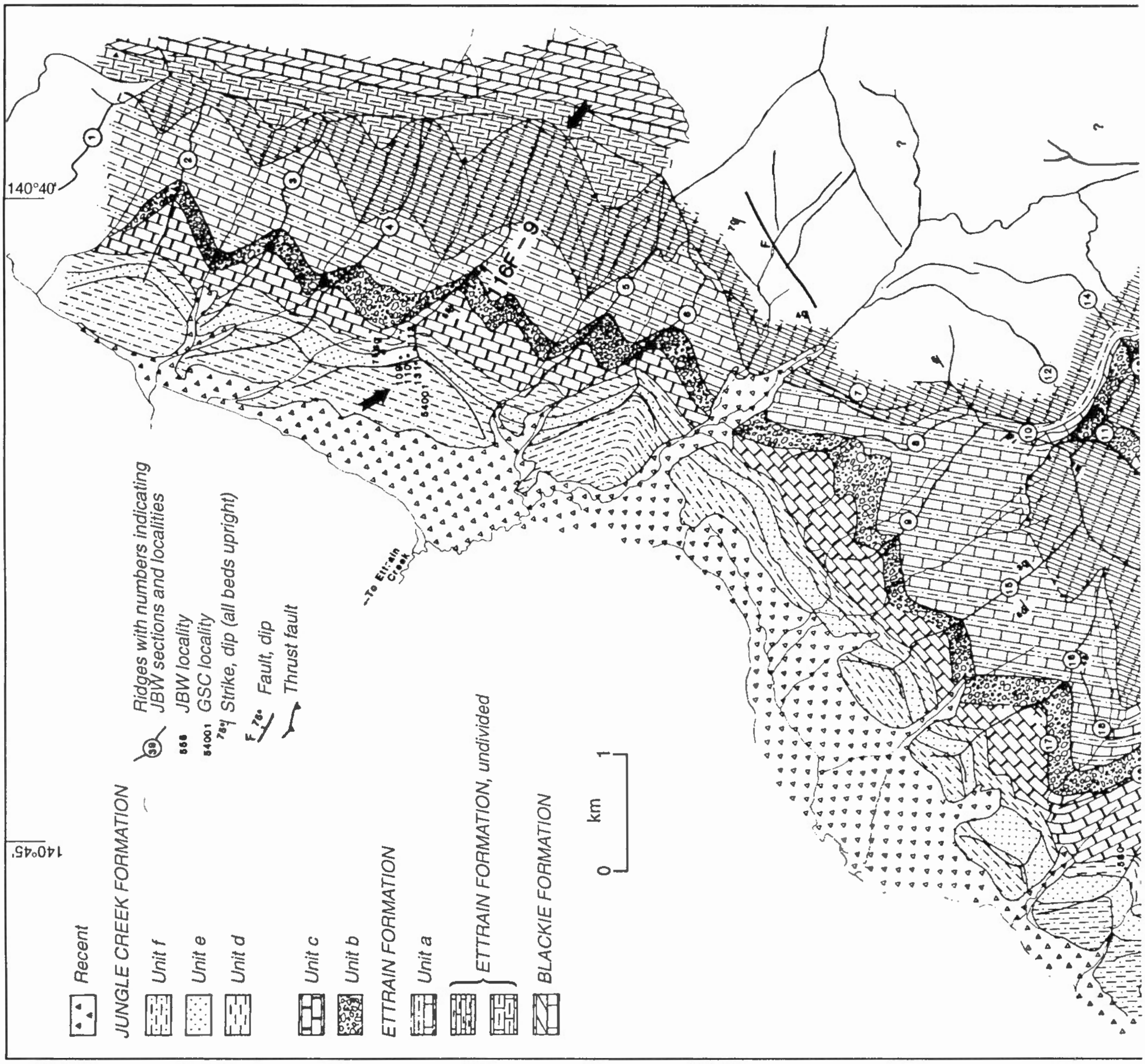


Figure 4. *Geological map of the Ettrain Creek area, with fossil localities (JBW localities) and localities of GSC sections 116F-9 and 116F-16. (Ridge numbers are used to refer to locations of localities and sections in Appendix Table 3.)*

Mountains (Figs. 3, 4), this formation was measured at 548 m thick and includes two informal members recognized by Bamber and Waterhouse (1971): a lower member, estimated to be 391 m thick, dominated by light grey-weathering dense skeletal limestone with dark grey-weathering irregular lenses and beds of chert, with dolomitic limestone in the lower part of the formation, and quartz beds appearing higher; and an upper member, of the order of 57 m thick, characterized by yellowish brown-weathering, skeletal-micritic limestone interbedded with minor medium to coarse grained skeletal limestone and calcareous siltstone. Approximately 48 km southwest of the type Ettrain, a succession approximately 645 m thick, just beneath the type Jungle Creek Formation at section 116C-2 on the Tatonduk River (Figs. 3, 5), has been considered an Ettrain equivalent (Bamber *in* Bamber and Waterhouse, 1971, p. 57), although the basal part of the succession may be in part equivalent to the Hart River Formation or the Blackie Formation discussed above. Bamber and Barss (1969) subdivided this succession into a lower unit (their Rock Unit A) consisting mainly of shale with interbedded siltstone, and an upper unit (their Rock Unit B), consisting of

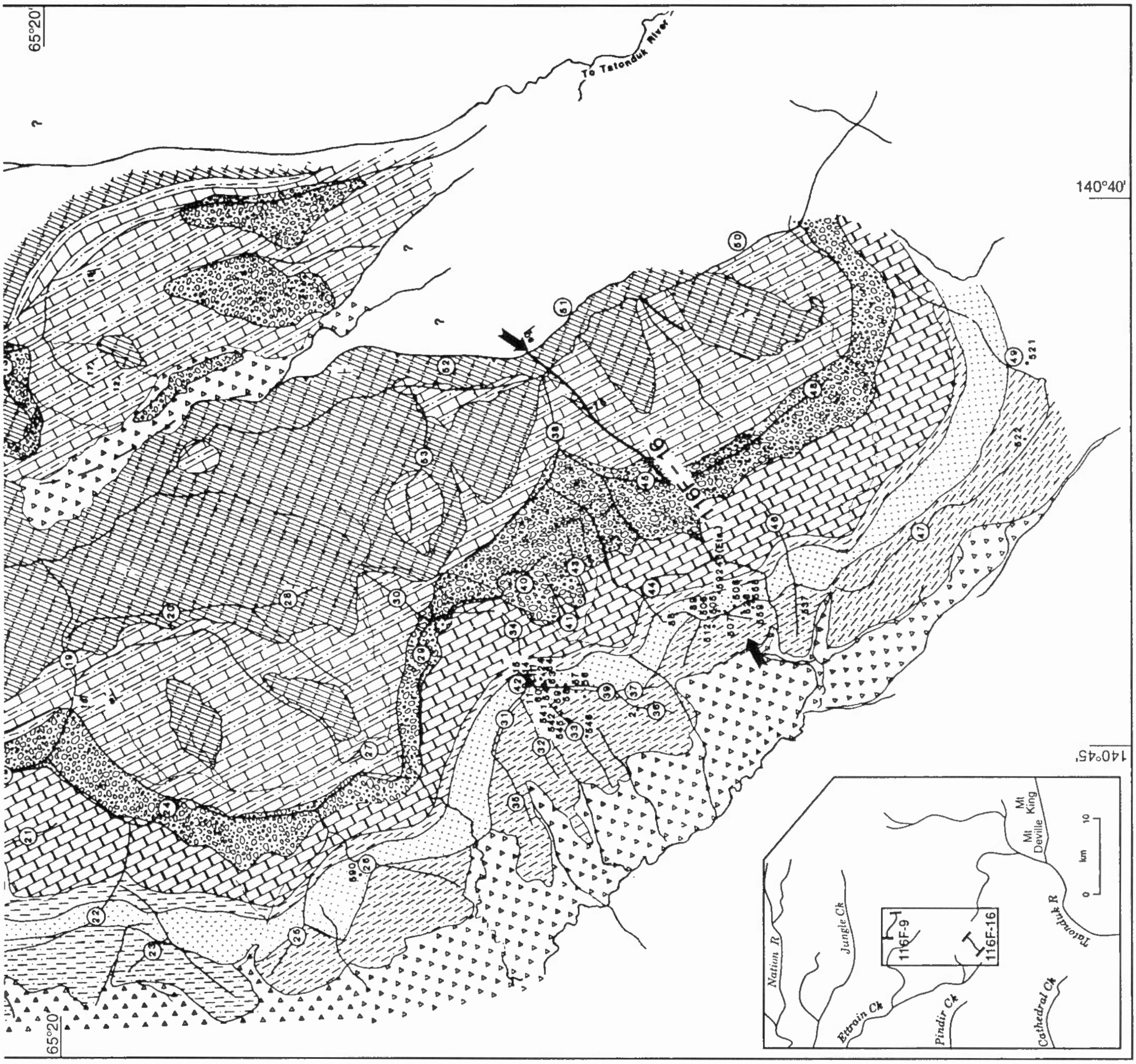


Figure 4 *(cont'd.)*

alternating shale and fine grained limestone. Both of these units differ from the type Ettrain Formation, which is characterized by skeletal and skeletal-micritic limestone. To the northeast and east of the type Ettrain section, the thickness of the Ettrain Formation is markedly reduced; it is estimated to be (?)193 m at section 116G-5, Nahoni Range East (Bamber, 1972), and reported to be approximately 213 m at section 116H-1A on the Peel River in southern Eagle Plain (Figs. 3, 6) (Bamber *in* Bamber and Waterhouse, 1971). Facies equivalents of the Ettrain Formation (called "Unnamed Ettrain Equivalents" by Bamber and Waterhouse, 1971, Fig. 3, p. 40, 41) are present in section 116H-1B on the north bank of the Peel River, immediately downstream (east) from section 116H-1B (Fig. 2). They lack skeletal limestone that is typical of the Ettrain Formation and consist mainly of silty, calcareous, microcrystalline to finely crystalline dolomite, which grades upward to dolomitic, calcareous siltstone in the sequence (see Fig. 3).

Brachiopods are numerous throughout the Ettrain Formation and have been subdivided into three faunas (B, C, and part of D faunas) and nine zones (Table 2) by Waterhouse (*in* Bamber and Waterhouse, 1971) and Waterhouse and Waddington (1982). Apart from the Spiriferellinae species, most of the brachiopods are yet to be described. The age of the faunas may range from Bashkirian to Early Kasimovian. This age assignment appears to agree with age determinations from foraminifers and conodonts as summarized in Bamber et al. (1989, Fig. 2).

Jungle Creek Formation

The Jungle Creek Formation was named by Bamber (*in* Bamber and Waterhouse, 1971, p. 60) for a medium to dark grey-weathering sequence of variable lithology, including skeletal, partly conglomeratic limestone, micritic-skeletal and spicular limestone, calcareous sandstone, chert pebble conglomerate, calcareous shale, silicious mudstone, and siltstone. Its type section (section 116C-2) is located on the north bank of the Tatonduk River (64°58′N latitude, 140°54′W longitude) (Fig. 5) and was described by Bamber (*in* Bamber and Waterhouse, 1971, p. 233–240) and Bamber (1972, p. 10–25). Two "members" were informally recognized at the type section: the lower, moderately resistant member, estimated to be 137 m thick, with conglomerate, calcareous sandstone and silty shale with minor micritic skeletal limestone; and an upper member, estimated at 288 m thick, of chert pebble mudstone with intervals of chert-pebble conglomerate and silty micritic-cherty and micritic-spicular limestone with rare calcareous siltstone and other lithotypes (see Fig. 3). The lower contact with the Ettrain Formation at the type Jungle Creek is unconformable and marked by a conglomerate bed at the base of the Jungle Creek Formation, and its upper contact with the Tahkandit Formation at the type section is covered.

The lower member, or basal Jungle Creek Formation of Bamber, overlaps and is largely equivalent to and correlative with the uppermost beds of the type Ettrain Formation, at the top of the so-called upper member of that formation. In the type Ettrain and many nearby extensively exposed outcrops, there are prominent bands of carbonate, 1–3 m thick, separated by silty shale, and minor conglomerate. In the type lower Jungle Creek, outcrops are more obscure, and differently weathered, but include similar thick carbonates, some shale, and more conglomerate. Both share a characteristic suite of brachiopods, dominated by *Orthotichia* and *Kozlowskia*. They are thought to be of Late Carboniferous, probably Kasimovian, perhaps Gshelian age, but have not been systematically studied. No other faunal elements have yet been evaluated. The overlap between the Jungle Creek and Ettrain formations is clearly significant, and requires one or other of the formations to be amended.

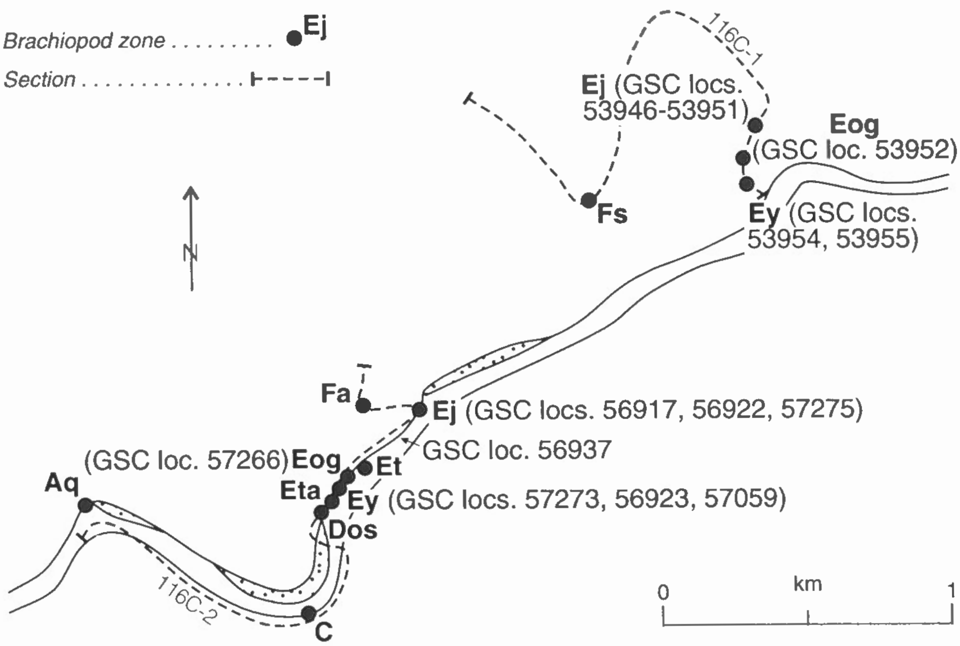


Figure 5. Fossil localities and brachiopod biozones along the Tatonduk River (GSC sections 116C-1 and 116C-2) (drawn from Bamber and Waterhouse, 1971, Fig. 7, based on airphoto A13784-39, National Airphoto Library, Department of Energy, Mines and Resources).

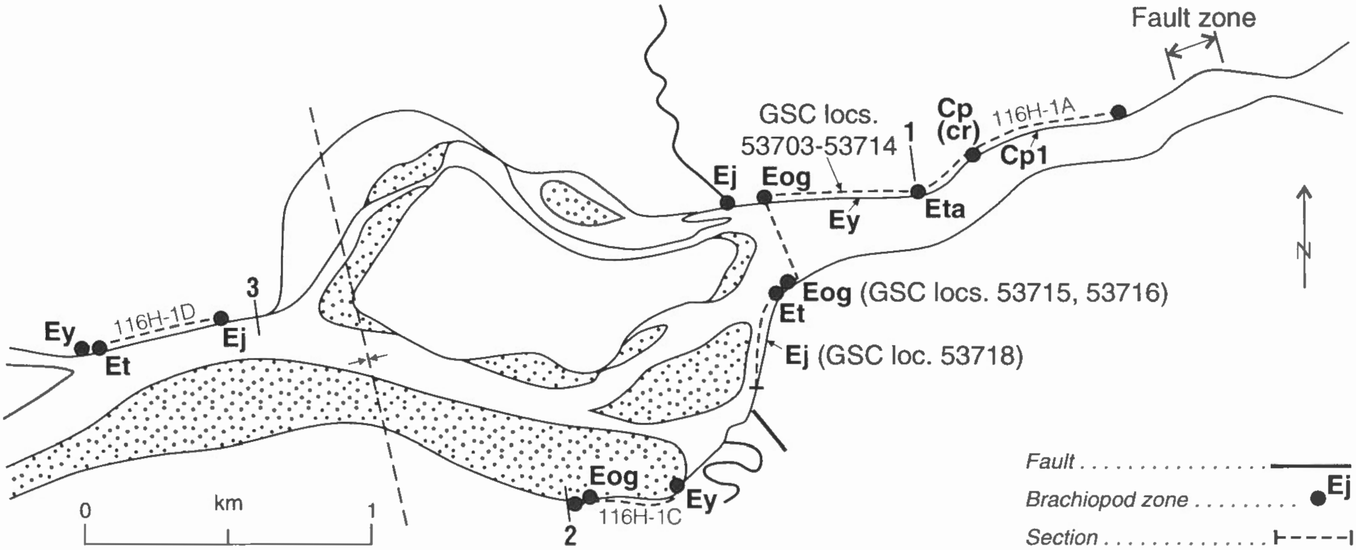


Figure 6. *Fossil localities and brachiopod biozones along the Peel River (GSC section 116H-1A, 116H-1C, and 116H-1D) (modified from Bamber and Waterhouse, 1971, Fig. 4).*

The International Guide to Stratigraphic Nomenclature (Hedberg, 1976), endorsed by the new edition (Salvador, 1994), strongly recommends that in the case of such changes the amended unit, or units, be renamed. We prefer to retain the names, although admitting that some emendation is required for the sake of accuracy. On the 1:250 000 geological map of the Tatonduk headwaters and Jungle and Ettrain creeks by Norris (1982), there are beds designated as lower Jungle Creek member beds that are younger than — and different from — the type lower Jungle Creek member. The true lower Jungle Creek member is largely incorporated into the topmost Ettrain in Norris' map, although details are not consistent. On our map (Fig. 4), this is shown as Unit a.

Overlying beds, best exposed in the headwaters of Jungle and Ettrain creeks, are a complex and variable association of conglomerates and carbonate bands, with other lithotypes, totalling about 230 m in thickness at section 116F-9 (type Ettrain section), but thinning south and westward. The faunules from this level escaped attention in Bamber and Waterhouse (1971) and show strong transitional aspects between Carboniferous and Permian, judging from preliminary informal evaluation. Waterhouse and Waddington (1982) called these beds a new formation (Unit b in Fig. 4), because they outcrop above the type Ettrain, and are completely missing from the type Jungle Creek Formation. Stratigraphically and faunally, they come closest to the underlying overlap beds of the basal Jungle Creek and uppermost Ettrain formations. These beds are entirely missing from the type Jungle Creek Formation, but were mapped by Norris (1982) as the lower member of the Jungle Creek Formation.

Further beds and faunules are missing from the type Jungle Creek section, between the lower and upper members. These are exposed some 48 km to the north in the headwaters of Ettrain Creek, as shale, dolomite, limestone and conglomerate with minor sandstone, becoming conglomeratic to the east toward the headwaters of Jungle Creek (Unit c in Fig. 4). These were incorporated in the basal Jungle Creek Formation, as restricted by Waterhouse and Waddington (1982) and were mapped, as far as can be ascertained from the coarse scale of the 1:250 000 map, largely, but not entirely, as the upper member of the Jungle Creek Formation by Norris (1982). The beds include zones Eka and Eo of Sarytcheva and Waterhouse (1972) and Waterhouse and Waddington (1982), and are regarded as Asselian. Substantial brachiopod faunules are now being studied from this level.

It is thus clear that the Jungle Creek type section is very incomplete. Outcrops along both measured sections in the Tatonduk River are restricted, and with dips comparatively steep, it would be impossible to rule out the presence of faults. Facies changes within the Jungle Creek–Ettrain headwaters also suggest the likelihood of paraconformities within the sequences, which progressively become larger and longer toward the Tatonduk River, involving principally Late Carboniferous and basal Permian strata, and pointing to a substantial chronological break between the Carboniferous and Permian.

Still farther east in the Eagle Plains, the equivalents of upper Ettrain, and lower member of the Jungle Creek Formation, are entirely missing along the Peel River at least on the surface. As Nassichuk (1971) cautioned, there is also faulting and thrusting in this region, which may have removed units, but so far there seems to have been a Carboniferous–Permian unconformity in this region. This unconformity occurs in part close to the lower–upper Jungle Creek boundary described in Norris (1982), and elsewhere within beds he mapped as lower Jungle Creek Formation.

The upper member of the Jungle Creek Formation as delineated along the Tatonduk River is more complete along the Peel River, and there is no evidence for paraconformable breaks of any magnitude. The fresh river-cut outcrops have been studied, largely through thin sections, by Bamber (1972) and in Bamber and Waterhouse (1971), with brachiopod content evaluated by Waterhouse (*in* Bamber and Waterhouse, 1971) and elaborated herein. To the north and east, in the Ettrain–Jungle creeks area and Eagle Plains (Fig. 3), outcrops are much more favourable and extensive, and natural weathering clearly brings out a strong three-fold division, into a basal silt-mud recessive unit, like that of the underlying beds, a coarse grained, sand-dominated, thick bedded median unit, 50 m thick, forming an upstanding ridge or crest, and an uppermost recessive unit with a variety of thin bedded carbonate, minor conglomerate, sandstone, and mudstone. The basal recessive unit has an *Attenuatella* faunule (Eta zone) of Late Asselian age (Unit d in Fig. 4), and the sandstone-dominated unit (Unit e in Fig. 4) contains the *Yakovlevia transversa* Zone (Ey zone). The upper recessive unit (Unit f in Fig. 4) has brachiopods of the uppermost Ey zone, followed by the *Ogilviecoelia inflata* Zone (Eog zone, formerly Ea zone) and thick beds with the *Jakutoproductus verchoyanicus* Zone (Ej zone), deemed Sakmarian to Early Artinskian (Aktastinian) age.

Tahkandit Formation

The Tahkandit Formation was proposed by Mertie (1930) with the type section located on the northeast bank of the Yukon River near the mouth of the Nation River in eastern Alaska (Brabb and Grant, 1971). It continues into the Yukon Territory (Bamber and Waterhouse, 1971), where it is largely confined to the northern Ogilvie Mountains and rests directly on the Jungle Creek Formation. In the northern Richardson Mountains, coeval beds were termed "Unnamed Sandstone Unit" (Bamber and Waterhouse, 1971). The Tahkandit Formation consists of reddish brown skeletal limestone and calcareous chert-pebble conglomerate in the lower part and spicular glauconitic chert with siltstone and limestone in the upper part. Faunally, it is characterized by the "F" and "G" brachiopod faunas (Waterhouse *in* Bamber and Waterhouse, 1971; see Table 2), yet to be described, throughout the unit except in the Tatonduk River section 116C-2, where the base of the formation contains brachiopods characteristic of the *Jakutoproductus verchoyanicus* Zone of the underlying Jungle Creek Formation (see Fig. 3). Bamber and Waterhouse (1971) assigned the formation to Late Artinskian (Baigendzinian) to Kazanian (Wordian), based on data from brachiopods and foraminifers.

BRACHIOPOD ZONES AND CORRELATION

Permian chronology

It has long been recognized that the Permian marine faunas show strong provincialism (Stehli, 1971; Waterhouse and Bonham-Carter, 1975; Archbold, 1983a; Shi and Waterhouse, 1990b), and various regional biostratigraphic schemes have been developed (see discussion in Waterhouse, 1976; Kozur, 1981). At present, there is no universally accepted Permian chronological standard. The scheme proposed by Harland et al. (1982), recently revised by Harland et al. (1990, p. 48), is here followed, with slight modification, as a reference of worldwide Permian chronology (see Table 3). The North American scale is also shown in Table 3, giving alternative stage names.

Brachiopod zones of the upper Jungle Creek Formation

Waterhouse (*in* Bamber and Waterhouse, 1971) proposed two faunas (D and E faunas) and six zones to distinguish different biostratigraphic units of the Jungle Creek Formation (Table 4). Sarytcheva and Waterhouse (1972) and Waterhouse and Waddington (1982) added two more biozones, *Kochiproductus–Attenuatella* Zone (Eka) and *Orthotichia* Zone (Eo) in ascending order, between the Dos zone and Eta zone in the lower part of the Jungle Creek Formation (Table 4) and transferred the Ck zone at the top of the Ettrain Formation to the Dk zone. The *Tornquistia* Zone (Et zone) was downgraded to subzone by Waterhouse (1977c), within the basal *Jakutoproductus verchoyanicus* Zone (Ej zone). No material from this subzone was available for the present study; the zone is thin and was known only from a few localities chiefly in the

Peel and Tatonduk rivers (Waterhouse *in* Bamber and Waterhouse, 1971).

The brachiopod zones have been tabulated, discussed and analyzed more fully in a number of papers by Waterhouse (1975a, b, 1976, 1977a–c, 1978a). They are assemblage zones, and to some extent range and acme zones, with several component communities. Analyzed in a worldwide setting against comparable zones elsewhere, they were thought to indicate biotic response to worldwide climatic regimes and changes, through evolutionary development and synchronic worldwide migration, so that, overall, they were chronozones, temporally significant.

Table 3

Permian chronological scale

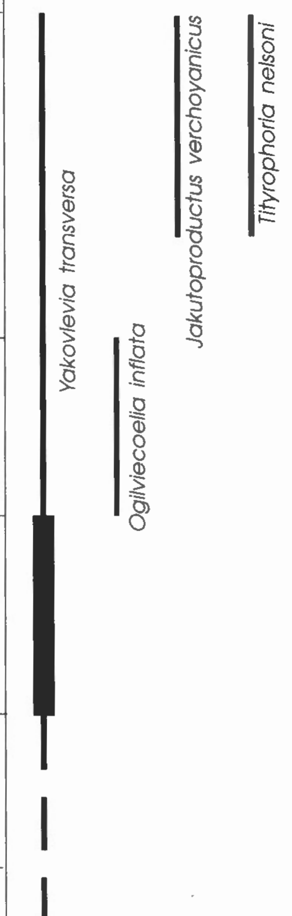
PERIOD	EPOCH	STAGE: International standard		STAGE: North American usage	BIOZONES: Fusulinid	BIOZONES: Ammonoid
PERMIAN	Late	CHANGXINGIAN (=DORASHIMIAN)		OCHOAN	*Palaeofusulina*	*Paratirolites* *Phisonites*
		LONGTANIAN			*Codonofusiella*	*Araxoceras*
		CAPITANIAN		GUADALUPIAN	*Yabeina*	*Cyclolobus*
		WORDIAN				
		UFIMIAN		LEONARDIAN		
	Early	KUNGURIAN			*Neoschwagerina*	*Waagenoceras* *Kufengoceras*
		ARTINSKIAN	BAIGENDZINIAN		*Parafusulina*	*Neocrimites*
			AKTASTINIAN			
		SAKMARIAN	STERLITAMAKIAN	WOLFCAMPIAN	*Pseudofusulina*	*Uraloceras*
			TASTUBIAN			
		ASSELIAN	KRUMAIAN		*Pseudoschwagerina*	*Juresanrites*
			USKALIKAN			
			SURENAN			

Detailed systematic study and stratigraphic analysis (Table 5; Figs. 7–9; Appendix Figs. 1–7) undertaken in the present study strongly support the differentiation of the *Yakovlevia*, "*Attenuatella*", and *Jakutoproductus* zones in the upper Jungle Creek Formation. The three brachiopod zones are renamed herein *Yakovlevia transversa* Zone (Ey zone), *Ogilviecoelia inflata* Zone (Eog zone), and *Jakutoproductus verchoyanicus* Zone (Ej zone). Each zone is symbolized with one or two lowercase letters for the sake of simplicity, following Waterhouse (*in* Bamber and Waterhouse, 1971). The three zones are discussed in

Table 4

Brachiopod zones of the Jungle Creek Formation and range of key species

FORMATION		Bamber and Waterhouse, 1971	Waterhouse and Waddington, 1982	Adopted in this work	Range of key species
TAHKANDIT		F and G Faunas	F and G Faunas	F and G Faunas	
JUNGLE CREEK FORMATION	Upper	*Jakutoproductus* Zone (Ej)	*Jakutoproductus* Zone (Ej)	*Jakutoproductus verchoyanicus* Zone (Ej)	
		Tornquistia Zone (Et)	*Tornquistia* Zone (Et)	*Tornquistia* Subzone (Et)	
		Attenuatella Zone (Ea)	*Attenuatella* Zone (Ea)	*Ogilviecoelia inflata* Zone (Eog)	
		Yakovlevia Zone (Ey)	*Yakovlevia* Zone (Ey)	*Yakovlevia transversa* Zone (Ey)	
		Tomiopsis - Attenuatella Zone (Eta)	*Tomiopsis - Attenuatella* Zone (Eta)	*Tomiopsis - Attenuatella* Zone (Eta)	
	Lower	*Orthotichia - Septospirifer* Zone (Dos)	*Orthotichia* Zone (Eo)	*Orthotichia* Zone (Eo)	
			Kochiproductus - Attenuatella Zone (Eka)	*Kochiproductus - Attenuatella* Zone (Eka)	
			Orthotichia - Septospirifer Zone (Dos)	*Orthotichia - Septospirifer* Zone (Dos)	



detail below in terms of faunal characteristics, regional distribution (see Table 6), and age. Correlations of the brachiopod zones with major Lower Permian marine sequences of North America and the Arctic region are presented in the next section.

Yakovlevia transversa *Assemblage Zone (Ey zone)*

Faunal characteristics

This biozone occurs above the *Tomiopsis-Attenuatella* Zone (Eta) and is distinguished overall by the predominant occurrence of *Yakovlevia transversa* (Cooper) and the absence of *Ogilviecoelia inflata* n. gen. et sp. The fauna of the Ey zone is diverse (Fig. 7), comprising 57 of the 67 brachiopod species described here (Table 5). It is dominated by productids and to a lesser extent by spiriferids (Fig. 7). Of the total 57 brachiopod species present in this zone, 20 are restricted to it, at least eight were also found in the underlying Eta zone, according to data in Waterhouse (*in* Bamber and Waterhouse, 1971), and 28 range into overlying zones. In terms of abundance, short range, and wide distribution, the diagnostic elements of this zone may include the following species: *Arctitreta peelensis* n. sp., *Komiella omolonensis* (Likharev), *Fimbrinia transversa* n. sp., *Tubersulculus maximus* Waterhouse, *Kutorginella yukonensis* Sarytcheva and Waterhouse, *Rugivestis arctica* n. sp., *Calliprotonia inexpectus* (Cooper), *Reticulatia uralica* (Chernyshev), *Antiquatonia cooperi* Shi, *Linoproductus dorotheevi* Frederiks, *Protoanidanthus umbonatus* n. sp., *Yakovlevia transversa* (Cooper), *Rhynchopora magna* Cooper, *Spiriferella pseudodraschei* Einor, *Yukonospirifer yukonensis* n. gen. et sp., *Domokhotia junglensis* n. sp., and *Spirelytha fredericksi* Archbold and Thomas, and bivalve *Acanthopecten licharewi* (Frederiks). Of these characteristic constituents, the nominal species *Yakovlevia transversa* is most widespread and abundant, as well as very diagnostic in morphology, and thus may be easily recognized in field. In the overlying *Ogilviecoelia inflata* and *Jakutoproductus verchoyanicus* zones, this species is less abundant, occurring sporadically. It is also possibly present in the underlying *Tomiopsis-Attenuatella* Zone (Table 5). The elements commonly associated with it are also different from those found in these zones.

The base of the Ey zone is defined by the disappearance of members of *Attenuatella* and the first appearance of such species as *Arctitreta peelensis, Rugivestis arctica, Protoanidanthus umbonatus, Spirelytha fredericksi,* and the co-occurrence of abundant *Fimbrinia transversa, Kutorginella yukonensis, Yakovlevia transversa,* and *Rhynchopora magna*. The upper boundary approximately corresponds to the lower limit of the overlying *Ogilviecoelia inflata* Zone.

Regional distribution

Tatonduk River area. In the Tatonduk River section 116C-2 (Figs. 5, 8), this zone extends from about 170 to 240 m above the base of the Jungle Creek Formation, and is documented at a number of localities (GSC locs. 56923, 56935, 56942, 56956, 57273, 57049, 57059, 57154). The fauna is small, represented by *Orthotetes canadensis* n. sp., *Calliprotonia inexpectus, Reticulatia uralica, Yakovlevia transversa, Alispiriferella ordinaria* (Einor), *Neospirifer* sp., and a bivalve *Acanthopecten licharewi.* The same fauna, with some different constituents, is also recognized about 2 km east in section 116C-1 (Fig. 5; Appendix Fig. 1). Here, the *Yakovlevia transversa* Zone is dominated by *Komiella omolonensis,* together with *Arctitreta peelensis, Kochiproductus porrectus, Chaoiella* sp., *Yakovlevia transversa, Tumarinia yukonica* n. sp., and *Larispirifer ettrainensis* n. sp.

Ettrain and Jungle creeks area. No collections from GSC localities containing elements of the Ey zone in section 116F-9 were available for this study, but this zone is well represented by large collections at JBW localities 109, 110, and 113 near section 116F-9 (Fig. 4). The Ey zone here is characterized by *Orthotetes canadensis* n. sp., *Komiella omolonensis, Tubersulculus maximus, Calliprotonia inexpectus, Kutorginella yukonensis, Rugivestis arctica* n. sp., *Waagenoconcha permocarbonica* Ustritskiy, *Kochiproductus porrectus, Reticulatia uralica, Linoproductus dorotheevi, Yakovlevia transversa, Camerisma (Callaiapsida) pentameroides* (Chernyshev), *Rhynchopora magna, Domokhotia junglensis, Spiriferella pseudodraschei, Spirelytha fredericksi, Yukonospirifer yukonensis* n. gen. et sp., and a bivalve *Exochorhynchus similis* Lyutkevich and Lobanova. Essentially the same faunule is also well developed 12 km south in section 116F-16 (Appendix Fig. 3) and nearby JBW localities (56, 58, 63, 88, 89, 506, 508) (see Fig. 4), *Protoanidanthus umbonatus* being particularly abundant at JBW locs. 88 and 89.

Peel River area. The Ey zone is recognized from approximately 24 to 210 m above the base of the Jungle Creek Formation in section 116H-1A (Fig. 9), where it has been documented at several localities (GSC locs. 53703-53705, 53710-53714) and many species, including *Arctitreta peelensis, Komiella*

Table 5

Distribution of brachiopod species in the brachiopod zones of the upper Jungle Creek Formation

Species	Jungle Creek Formation				Tahkandit Formation
	Tomiopsis–Attenuatella Zone	*Yakovlevia transversa* Zone	*Ogilviecoelia inflata* Zone	*Jakutoproductus verchoyanicus* Zone	F and G Faunas
Orbiculoidea sp.		+			
Arctitreta peelensis n. sp.		+			
Orthotetes canadensis n. sp.		+	+		
Orthotichia morganiana (Derby)		+		+	
Komiella omolonensis (Likharev)		+			
Dyoros (*Dyoros*) *pseudotrapezoidalis* (Miloradovich)		+	+	+	
Rugaria? sp.		+			
Fimbrinia transversa n. sp.		+	+	+	
Krotovia pustulata (Keyserling)		+		+	
Tubersulculus maximus Waterhouse		+	+	+	
Jakutoproductus verchoyanicus (Frederiks)				+	
Kozlowskia sp.		+	+	+	
Liosotella compacta n. sp.		+	+	+	
Anemonaria auriculata n. sp.		+	+	+	
Uraloproductus sp. B			+		
Uraloproductus sp. A				+	
Rugivestis arctica n. sp.		+		+	
Costispinifera paucispinosa n. sp.		+			
Kutorginella yukonensis Sarytcheva and Waterhouse	+	+	+	+	
Thamnosia spinosa n. sp.		+			
Calliprotonia inexpectus (Cooper)		+	+	+	
Waagenoconcha permocarbonica Ustritskiy		+	+	+	
Waagenoconcha parvispinosa Cooper		+			
Kochiproductus saranaeanus (Frederiks)		+			
Kochiproductus porrectus (Kutorga)		+	+	+	
Reticulatia uralica (Chernyshev)		+	+	+	
Chaoiella sp.		+		+	
Antiquatonia cooperi Shi		+			
Sowerbina bullocki Nelson and Johnson		+		+	+
Tityrophoria nelsoni Waterhouse				+	
Terrakea? sp.		+			
Protoanidanthus umbonatus n. sp.		+		+	
Anidanthus cf. *A. boikowi* Abramov and Grigor'yeva			+		

Table 5 (cont'd.)

Species	Jungle Creek Formation				Tahkandit Formation
	Tomiopsis–Attenuatella Zone	*Yakovlevia transversa* Zone	*Ogilviecoelia inflata* Zone	*Jakutoproductus verchoyanicus* Zone	F and G Faunas
Linoproductidae indet.		+			
Linoproductus dorotheevi Frederiks		+		+	
Schrenkiella sp.	+	+	+	+	
Globiella costellata n. sp.		+	+	+	
Cancrinella cancriniformis (Chernyshev)		+	+		
Cancrinella singletoni Gobbett		+		+	
Yakovlevia transversa (Cooper)		+	+	+	
Rhynoleichus dorsoconvexa n. sp.		+	+		
Septacamera triangulata n. sp.				+	
Rhynchopora magna Cooper	+	+	+	+	
Camerisma (*Callaiapsida*) *pentameroides* (Chernyshev)		+	+	+	
Stenoscisma mutablis (Chernyshev)		+	+	+	
Composita bamberi n. sp.		+			
Composita sp.		+			
Hustedia cf. *remota* (Chernyshev)		+		+	
Ogilviecoelia inflata n. gen. n. sp.			+		
Yukonospirifer yukonensis n. gen. et sp.		+			
Tumarinia yukonica n. sp.		+		+	
Yukonella plana n. gen. n. sp.				+	
Spiriferella saranae (Verneuil)	+	+	+	+	+
Spiriferella pseudodraschei Einor		+	+		+
Spiriferella sp.			+		
Alispiriferella ordinaria (Kutorga)	+	+	+		
Timaniella convexa n. sp.				+	
Neospirifer sp.		+	+		
Lepidospirifer? sp.		+			
Purdonella nikitini (Chernyshev)		+	+		
Domokhotia junglensis n. sp.		+			
Larispirifer ettrainensis n. sp.		+	+	+	
Spiriferidae gen. and sp. indet.		+			
Tomiopsis ovulum Waterhouse	+	+		+	
Spirelytha sp.		+			
Spirelytha fredericksi Archbold and Thomas		+			
Brachythryris sp.		+		+	
Brachythyrdidae indet.		+			
Tiramnia canadica n. sp.		+	+	+	
Spiriferellina? sp.		+			
Dielasma brevicostatum Cooper		+			
Dielasma rectimarginatum Cooper			+		

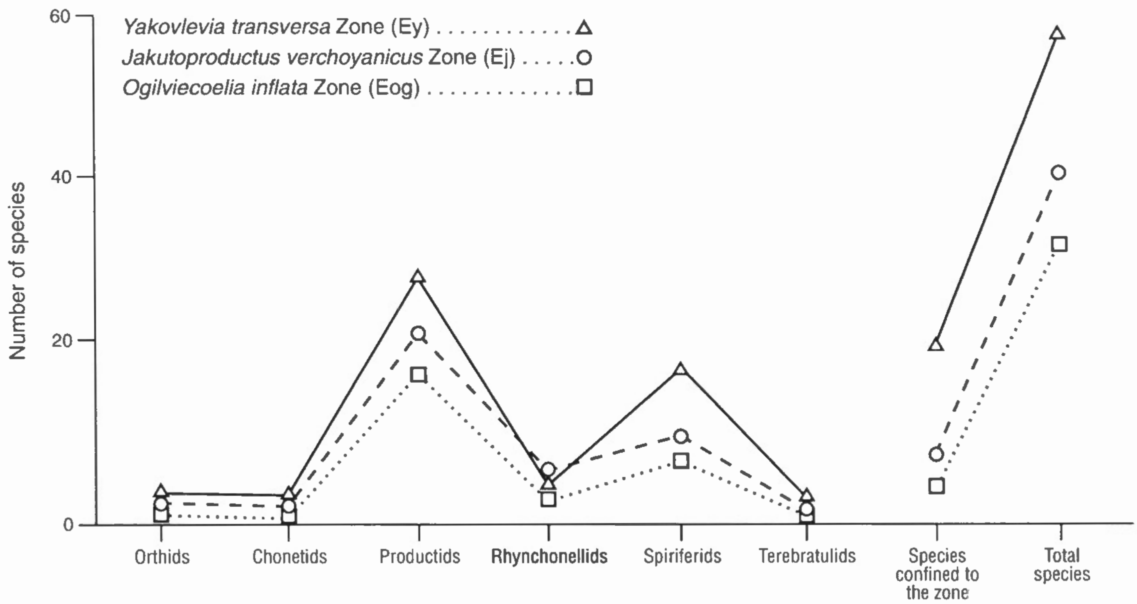


***Figure 7.** Number of taxa within the brachiopod biozones.*

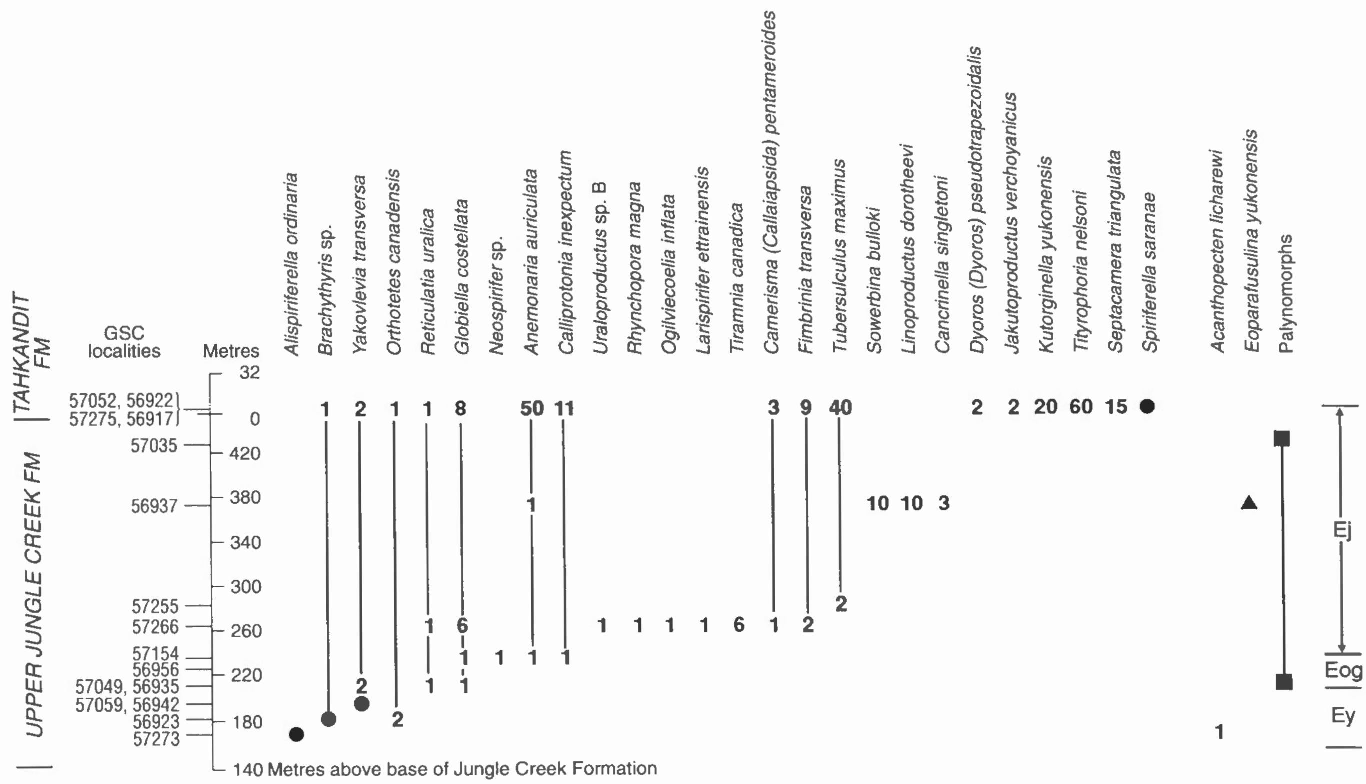


***Figure 8.** Range of brachiopod species in section 116C-2, Tatonduk River. Number of specimens given; black dots represent the occurrences of brachiopod species recorded by Bamber and Waterhouse (1971); and triangle indicates the fusulinid occurrence of Ross (1967a).*

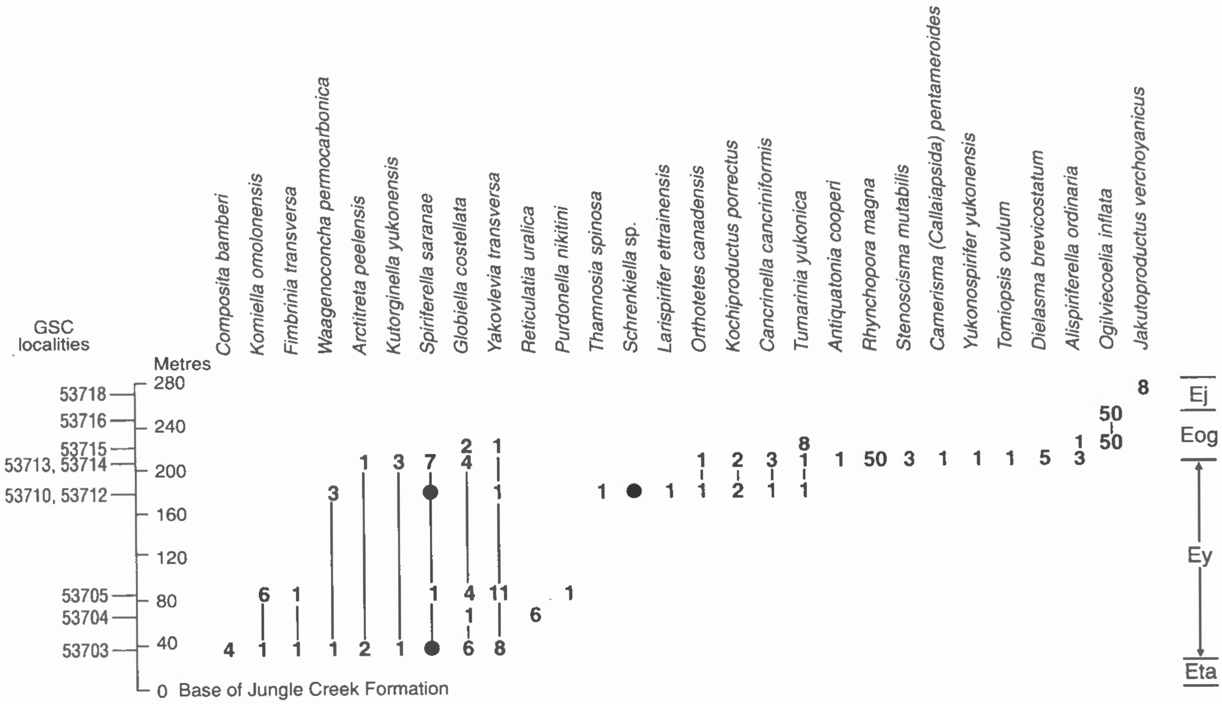


Figure 9. *Range of brachiopod species in section 116H-1A, Peel River. Number of specimens given; black dots represent the occurrences of brachiopod species recorded by Bamber and Waterhouse (1971).*

Table 6

Distribution of brachiopod zones of the upper Jungle Creek Formation in northern Yukon Territory

FORMATION	ZONE	AGE	Tatonduk River Sections 116C-1, 116C-2	Ettrain and Jungle Creeks 116-F9, 116F-16, JBW 39, JBW 44	Nahoni Range 116G-5	Peel River 116H-1A, 116H-1B, 116H-17	Northern Richardson Mtns 116P-10
JUNGLE CREEK FORMATION	Ej	AKTASTINIAN	*Jakutoproductus verchoyanicus* Zone	*Jakutoproductus verchoyanicus* Zone	*Jakutoproductus verchoyanicus* Zone	*Jakutoproductus verchoyanicus* Zone	
	Eog	STERELITA-MAKIAN	*Ogilviecoelia inflata* Zone	*Ogilviecoelia inflata* Zone		*Ogilviecoelia inflata* Zone	
	Ey	TASTUBIAN	*Yakovlevia transversa* Zone	*Yakovlevia transversa* Zone		*Yakovlevia transversa* Zone	*Yakovlevia transversa* Zone
	Eta	KRUMAIAN	*Tomiopsis-Attenuatella* Zone	*Tomiopsis-Attenuatella* Zone		*Tomiopsis-Attenuatella* Zone	

omolonensis, Fimbrinia transversa, Waagenoconcha permocarbonica, Reticulatia uralica, Kutorginella yukonensis, Globiella costellata n. sp., *Yakovlevia transversa, Composita bamberi* n. sp., *Spiriferella saranae, Dielasma brevicostatum* Cooper, with minor *Thamnosia spinosa* n. sp., *Camerisma* (*Callaiapsida*) *pentameroides*, and *Purdonella nikitini* (Chernyshev). In section 116H-1B (Appendix Fig. 6), the Ey zone is present at GSC locs. 53720 to 53723, with *Waagenoconcha permocarbonica, Kutorginella yukonensis, Yakovlevia transversa, Globiella costellata*, and minor occurrences of other species. *Yakovlevia transversa,* associated with *Rhynoleichus dorsoconvexa* n. sp., is also present at GSC loc. 53812 near the base of the Jungle Creek Formation in section 116H-17 (Appendix Fig. 5).

Northern Richardson Mountains. In section 116P-10, the northern Richardson Mountains, the Ey zone is known from the "Unnamed Carbonate Unit" of Bamber (*in* Bamber and Waterhouse, 1971) and characterized by a small fauna dominated by *Yakovlevia transversa, Komiella omolonensis,* and *Sowerbina bullocki* Nelson and Johnson, together with *Kochiproductus porrectus, Calliprotonia inexpectus,* and *Orthotetes canadensis* (Appendix Fig. 7).

Age

The brachiopods of the Ey zone appear to indicate a general Sakmarian age, most likely Early Sakmarian (Tastubian). Bamber and Waterhouse (1971) initially assigned a Late Asselian(?) to Early Sakmarian age to this zone according to brachiopod data. Waterhouse (1976, 1977b, 1987b) and Waterhouse and Waddington (1982) refined the age to Tastubian, followed by Bamber et al. (1989, Fig. 3). This assignment is also preferred here and is supported by the discovery of an ammonoid species from the same zone.

Many species characteristic of this zone are also common in the Sakmarian Stage of the Urals, as summarized by Miloradovich (1949), Stepanov (1951), and Kalashnikov (1986), notably *Reticulatia uralica, Tubersulculus maximus* (probably conspecific with *Productus pseudoaculeatus* Krotov of Chernyshev, 1902), *Kochiproductus porrectus, K. saranaeanus, Linoproductus dorotheevi-Linoproductus cora* (not d'Orbigny) of Chernyshev and also comparable with *L. rhiphaeus* Stepanov], *Cancrinella cancriniformis,* and *Purdonella nikitini.* Of these species, *Linoproductus rhiphaeus* was cited as being confined to the Tastubian in the Urals (Kalashnikov, 1986, p. 90), and *Reticulatia uralica* and *Tubersulculus maximus* first appeared in the Tastubian in the Urals (Stepanov, 1951, p. 104). *Yakovlevia transversa* is very close to *Y. mammatiformis* (Frederiks), a species that Kalashnikov (1986) figured as one of the leading forms of the Sakmarian Stage in the Urals. It is characteristic of the Sezim Suite of the Pechora Basin, northern Urals (Ifanova, 1972; Kalashnikov *in* Meyen, 1983), which has been well dated Late Asselian to Sakmarian using ammonoid data (Andrianov, 1985).

Two taxa of the Ey zone closely resemble species from the southern hemisphere and support a general Sakmarian age for the Ey zone. *Globiella costellata* n. sp. is a common species for the Ey zone and the overlying *Ogilviecoelia inflata* Zone in northern Yukon. It is somewhat similar to *Globiella umariensis* (Reed) from the Umaria Beds of peninsular India, of either Tastubian age or Sterlitamakian age (Waterhouse, 1976, 1987b). Specimens allied to this Indian species have been reported from (?)Tastubian in Afghanistan by Termier et al. (1974), and an allied species identified as *Globiella gracilis* Jin 1977 from the top of the Jilong Formation in southern Tibet (Jin, 1979). *Biconvexiella convexa* (Armstrong) has also been reported in the Jilong faunule, reminiscent of *Ogilviecoelia inflata* n. gen. et sp. A second southern hemisphere species, *Spirelytha fredericksi* Archbold and Thomas, is confined to the Ey zone in northern Yukon. It was first described from the Late Sakmarian (Sterlitamakian) fauna of the Callytharra Formation in Western Australia (Archbold and Thomas, 1984a).

An ammonoid species, *Tabantalites bifurcatus* Ruzhencev, is reported in this study from GSC loc. 57053 in Jungle Creek section 116F-16 (Appendix Fig. 3). In the southern Urals, *T. bifurcatus* is known only from Upper Asselian and Lower Sakmarian (Tastubian) strata (Ruzhencev, 1952). The Ey zone is overlain by the Eog zone and the minor *Tornquistia* level (Et subzone). The Et faunule is either Early Sakmarian (Tastubian) in age according to the associated ammonoid data or Late Sakmarian (Sterlitamakian) according to brachiopod data (Waterhouse and Waddington, 1982).

Judging from both brachiopod and ammonoid data summarized above, as well as stratigraphic position, it seems most likely that the Ey zone is of Early Sakmarian (Tastubian) age. This age assignment would be consistent with the Late Asselian age of the underlying *Tomiopsis-Attenuatella* Zone (Eta zone) proposed by Waterhouse (1971a) and Waterhouse and Waddington (1982).

Ogilviecoelia inflata *Assemblage Zone (Eog zone)*

Faunal characteristics

The *Ogilviecoelia inflata* Zone is less diverse than the other two zones (Ey and Ej) discussed here (Fig. 7). Twenty-nine of the 67 described brachiopod species have been found in this zone, of which 25 are shared with both underlying and overlying zones and four are confined to it (see Table 5). The nominate species, *Ogilviecoelia inflata* n. gen. et sp., is possibly restricted to this zone. It is commonly associated with *Kutorginella yukonensis, Globiella costellata, Yakovlevia transversa, Rhynoleichus dorsoconvexa, Dielasma rectimarginatum,* and *Spiriferella* sp.; the last two forms are confined to the Eog zone.

Though sharing fairly common *Yakovlevia transversa* and several other species with the Ey zone (Table 5), the Eog zone is clearly distinguished from the Ey zone by the possession of a small ambocoeliid species *Ogilviecoelia inflata,* which occurs locally in great abundance, such as at GSC loc. 53999 (section 116F-9, Appendix Fig. 2) and at GSC loc. 53715 (section 116H-1A, Fig. 9). Many Ey zone diagnostic species are not found in the Eog zone, such as *Arctitreta peelensis, Rugivestis arctica, Komiella omolonensis, Antiquatonia cooperi,* and *Spirelytha fredericksi.* Other constituents of the Ey zone, such as *Tubersulculus maximus, Calliprotonia inexpectus, Kutorginella yukonensis, Kochiproductus porrectus, Rhynchopora magna,* and *Spiriferella pseudodraschei,* persist in the Eog zone but are less abundant and restricted in occurrence.

Regional distribution

Tatonduk River. Ogilviecoelia inflata is present at GSC loc. 57266 in section 116C-2 (Fig. 8) and GSC loc. 53952 in section 116C-1 (Appendix Fig. 1), associated with *Fimbrinia transversa, Tiramnia canadica* n. sp., and *Yakovlevia transversa.*

Ettrain and Jungle creeks area. Abundant specimens of *Ogilviecoelia inflata,* together with *Tubersulculus maximus, Anemonaria auriculata* n. sp., *Calliprotonia inexpectus, Yakovlevia transversa,* and *Dielasma rectimarginatum,* have been found at GSC loc. 53999 in section 116F-9 (Appendix Fig. 2). The equivalent horizon occurs sporadically in section 116F-16 (Appendix Fig. 3) to the south and nearby JBW localities (Fig. 4). Bamber and Waterhouse (1971) included GSC loc. 57153 from section 116F-16 in the "Ea" zone (now Eog zone), which occurs near the top of the Jungle Creek Formation at this section. JBW loc. 57 containing *Ogilviecoelia inflata, Kozlowskia* sp., *Liosotella paucispinosa* n. sp., *Spiriferella* sp., and *Larispirifer ettrainensis* n. sp. is also assigned to the Eog zone.

Peel River area. The Eog zone is best developed in the Peel River section 116H-1A (Figs. 6, 9), at GSC locs. 53715 and 53716 from about 210 to 250 m above the base of the Jungle Creek Formation. The two localities are dominated by very small but abundant *Ogilviecoelia inflata,* associated with minor *Globiella costellata, Yakovlevia transversa,* and *Alispiriferella ordinaria.*

Age

The age of the Eog zone is most likely Sakmarian, according to brachiopod data, and judging by its stratigraphic position, as proposed by Waterhouse and Waddington (1982), perhaps Late Sakmarian (Sterlitamakian).

About 83 percent of the brachiopod species from this zone persist from the Ey zone and indicate only a general Sakmarian age, as for the Ey zone discussed above. *Ogilviecoelia inflata* resembles in overall appearance both *Attenuatella*? *omolonensis* Zavodovskiy and *A.*? *taimyrica* Chernyak. The former was originally described from the Paren Horizon of the Kolyma–Omolon Massif, northeastern Siberia, of probable Asselian age (Waterhouse, 1976). *Attenuatella*? *taimyrica* is known from the Birrang Horizon of central Taimyr, north Siberia, of Artinskian age. *Dielasma rectimarginatum* Cooper is confined to the Eog zone in northern Yukon Territory and is elsewhere known only from the Coyote Butte Formation in central Oregon, of probably Late Sakmarian (or Artinskian) to (?)Early Kungurian age (Wardlaw et al., 1982). (The age of the Coyote Butte fauna will be discussed in more detail below.) Two other unidentified species are confined to the Eog zone: *Uraloproductus* sp. B and *Spiriferella* sp., the former represented by a single specimen from GSC loc. 57266 in the Tatonduk River section 116C-2 (Fig. 8); the latter known from three ventral valves in a single locality JBW loc. 57. *Uraloproductus* sp. B resembles both *U. bilobatus* Abramov and Grigor'yeva from the Upper Carboniferous lower Kigiltas Suite in the Verchoyan Mountains, northeastern Siberia, and *U. stuckenbergianus* (Krotov), a species known chiefly from the Sakmarian in the Urals (Miloradovich, 1949; Ustritskiy, 1971). *Spiriferella* sp., with alate cardinal extremities and a deep, angular sulcus, is close to *Spiriferella digna* Barchatova from the Pel Horizon in the northern Timan Range, of Late Sakmarian (Sterlitamakian) age (Barchatova, 1964).

The Eog zone underlies the Et faunule in the Tatonduk and Peel River sections (Figs. 5, 6) and the Ej zone (*Jakutoproductus verchoyanicus* Zone) in the Ettrain and Jungle Creek sections (see Fig. 3). The Et faunule was assigned a Late Sakmarian (Sterlitamakian) age by Waterhouse and Waddington (1982) based on brachiopod evidence, but this zone may be as old as Early Sakmarian (Tastubian) as indicated by the associated ammonoid fauna (Nassichuk, 1971). The Ej zone, discussed below, is believed to be of Early Artinskian (Aktastinian) age. Thus, the age of the Eog zone cannot be younger than Aktastinian and may be as old as Tastubian.

A minor biostratigraphic interval characterized by the brachiopod *Tornquistia* and ammonoids was recognized as Zone Et by Bamber and Waterhouse (1971, p. 160), and relegated to subzonal status by Waterhouse (1977c). This faunule is best developed in two sections along the Peel River, in concretions found in dark shales, in section 116H-1D (Fig. 6) just above the Ey faunules, and in section 116H-1C (Fig. 6). *Tornquistia* is also found in thinner deposits with *Jakutoproductus* at GSC loc. 53718 in section 116H-1A, approximately 268 m above the base of the Jungle Creek Formation, but the specimens are from different blocks that were assigned the same collection number, and may not have been from exactly the same stratigraphic level. *Tornquistia* has also been collected from the type section of the Jungle Creek Formation in the Tatonduk River section 116C-2, about 265 m above the base of the formation, in a silty, less shaly rock. We did not examine specimens from this minor level, and more material is required. Ammonoids are predominant in terms of biomass and diversity in the Peel River outcrops [Nassichuk (1971) recorded nine species of about Tastubian age]. Overall, if the interval has, in brachiopod terms, any measure of validity, it may serve as a biostratigraphic marker either immediately above the Eog *Ogilviecoelia inflata* Zone or within the basal Ej *Jakutoproductus verchoyanicus* Zone.

Jakutoproductus verchoyanicus *Assemblage Zone (Ej zone)*

Faunal characteristics

The Ej zone occurs at the top of the Jungle Creek Formation and persists into the lowermost unit of the overlying Tahkandit Formation in the Tatonduk River section 116C-2 (see Fig. 8). Thirty-nine of the 67 described species have been recognized within this zone. Seven species are restricted to it, 32 range from the Ey zone, two from the Eog zone, and about five, perhaps more, persist into the overlying F fauna in the Tahkandit Formation (see Table 5). The Ej zone is clearly distinguished from underlying zones by the first occurrences of the strongly wrinkled overtoniinid *Jakutoproductus verchoyanicus* and the faintly costate horridoniinid *Tityrophoria nelsoni* Waterhouse. Other elements confined to this zone are a small, reticulate specimen of *Uraloproductus* sp. A [similar to *U. stuckenbergianus* (Krotov)], coarsely costellate *Anidanthus* cf. *A. boikowi* Abramov and Grigor'yeva, a large triangle-shaped, moderately costate rhychonellid *Septacamera triangulata* n. sp., a simply costate licharewiinid with a distinct delthyrial plate, *Yukonella plana* n. gen. et sp., and a very transverse and strongly convex *Timaniella convexa* n. sp. Species *Sowerbina bullocki, Spiriferella saranae,* and *Tiramnia canadica* n. sp. persist from the underlying zones but are more common in the Ej zone. Species characteristic of the underlying Eog zone, such as *Ogilviecoelia inflata* and *Dielasma rectimarginatum,* were not found.

Regional distribution

Tatonduk River area. The Ej zone is present at the Tatonduk River section 116C-2 (Fig. 8), from approximately 287 m above the base of the Jungle Creek Formation to the lowermost 10 m of the overlying Tahkandit Formation. Here, the Ej zone is identified by *Jakutoproductus verchoyanicus,* associated with abundant *Tubersulculus maximus, Anemonaria auriculata, Calliprotonia inexpectus, Kutorginella yukonensis, Tityrophoria nelsoni, Septacamera triangulata, Sowerbina bullocki,* and *Linoproductus dorotheevi,* as well as a fusulinid species *Eoparafusulina yukonensis* (Skinner and Wilde) (see Fig. 8). The same level was also reported by Waterhouse (*in* Bamber and Waterhouse, 1971, p. 161) from GSC locs. 53946 to 53951 at approximately 34 m above GSC loc. 53952 of the Eog zone in the eastern Tatonduk River section 116C-1 (Appendix Fig. 1), where *Jakutoproductus* sp. was found together with abundant *Orthotichia morganiana, Anemonaria auriculata,* and especially *Tiramnia canadica* n. sp.

Ettrain and Jungle creeks area. Jakutoproductus verchoyanicus has not been recognized in the present study in the Ettrain–Jungle Creeks area (sections 116F-9, 116F-16), but was previously reported by Bamber and Waterhouse (1971) at GSC locs. 54000 and 54001 in section 116F-9 (Appendix Fig. 2) and at the top of section 116F-16 (Appendix Fig 3). JBW loc. 56 (Fig. 4) also appears to belong to the Ej zone according to both stratigraphic position and palaeontological evidence. It occurs at about 30 m above JBW loc. 57 of the Eog zone and contains *Tityrophoria nelsoni* and *Septacamera triangulata,* both found elsewhere only in the Ej zone in Tatonduk River area. JBW loc. 512 from the same area (Fig. 4) contains *Anemonaria auriculata* and *Yakovlevia transversa* but has so few specimens that its precise correlation with either Eog or Ej zone must await further collecting.

Nahoni Range East, northern Ogilvie Mountains. A small, probably immature, specimen of *Jakutoproductus verchoyanicus* was found at GSC loc. 53774 in section 116G-5 (Appendix Fig. 4), associated with a licharewiinid species *Yukonella plana* n. gen. et sp. that is extremely abundant and restricted locally. This small fauna probably represents a distinctive assemblage living in a very shallow nearshore environment.

Peel River. A small Ej zone assemblage was recognized in section 116H-17 (Appendix Fig. 5), where *Jakutoproductus verchoyanicus* was found at GSC loc. 53818 near the top of the Jungle Creek Formation (Bamber and Waterhouse, 1971). This species occurs with *Anidanthus* cf. *A. boikowi, Linoproductus dorotheevi, Spiriferella pseudodraschei,* and *Tomiopsis ovulum.* About 5 km to the east of section 116H-17, the Ej zone is well developed in section 116H-1A at GSC loc. 53718 (Fig. 9). Here, the zone is dominated exclusively by the nominate species.

Age

The Ej zone is likely to be Early Artinskian (Aktastinian) according to brachiopod data. Bamber and Waterhouse (1971) initially assigned this zone to the Sterlitamakian–Aktastinian, and later Waterhouse and Waddington (1982) refined it to the Aktastinian.

Jakutoproductus verchoyanicus is well known and widely distributed in the Russian Arctic. It is restricted to the Osennin Horizon (lower part of the Echii Suite or equivalents) in the Verchoyan Mountains, northeastern Siberia, assigned to the Artinskian by Abramov and Grigor'yeva (1988), or more precisely Aktastinian according to Andrianov (1974, Table 2) based on ammonoid evidence. Usually associated with *J. verchoyanicus* and also restricted to the same horizon in the Verchoyan Mountains is *Anidanthus boikowi,* a species that may well prove to be conspecific with specimens from the Yukon Ej zone. The Yukon material is here identified as *Anidanthus* cf. *A. boikowi* because of insufficient dorsal material, but the ventral details are strikingly similar to those of the Verchoyan species.

A brachiopod fauna with *Jakutoproductus* sp. and other characteristic elements of the Yukon Ej zone (Waterhouse *in* Thorsteinsson, 1974, p. 56) was also discovered from an unnamed unit on Bjorne Peninsula, southwestern Ellesmere Island. This unit also yielded ammonoids, described by Nassichuk et al. (1965), of Aktastinian age.

An Aktastinian age for the Ej zone seems to conflict with the age derived from a small fusulinid assemblage described by Ross (1967a) from GSC loc. 56937 (in section 116C- 2, see Fig. 8) in the middle part of the Ej zone. This assemblage consists of *Eoparafusulina yukonensis* (Skinner and Wilde) and *Schwagerina* sp. The former was said to resemble species from the middle McCloud Limestone of northern California, of middle Wolfcampian (Tastubian) age (Ross, 1967a; Mamet and Ross *in* Bamber and Waterhouse, 1971). But the genus *Eoparafusulina* Coogan ranges in west Texas from upper Neal Ranch Formation to Skinner Ranch Formation (Ross, 1967b *in* Cooper and Grant, 1977), of Late Asselian to Aktastinian age. In the Ural Mountains and Russian Platform, *Eoparafusulina* is most abundant in the Aktastinian, and very rare in the Sakmarian, according to data in Gorsky et al. (*in* Kotljar and Stepanov, 1984, p. 41–50). We therefore prefer an Aktastinian age for the Ej faunules.

Correlation of the brachiopod zones

North America

Canadian Arctic Archipelago

A small Permian brachiopod fauna that is possibly correlated to the Yukon Ej zone is known from an unnamed unit on top of the Asselian to Lower Artinskian Belcher Channel Formation on Bjorne Peninsula of southwestern Ellesmere Island (Table 7). This unit was originally mapped as Assistance Formation by Thorsteinsson (1974) but considered by Nassichuk (1975) and Nassichuk and Wilde (1977) (see also Beauchamp et al., 1989, Fig. 3) to be a new formation, as yet unnamed, on the basis of both lithological and faunal characteristics. The Assistance Formation at its type locality on Grinnell Peninsula of Devon Island has yielded a modest Permian brachiopod fauna, first described by Harker (*in* Harker and Thorsteinsson, 1960). This fauna contains several species commonly found in the Kungurian assemblages

Table 7

Correlation of the upper Jungle Creek Formation biozones with faunules from North America and the Arctic

FORMATION	BIOZONE	AGE	ELLESMERE ISLAND	VANCOUVER ISLAND	BRITISH COLUMBIA	CENTRAL OREGON	NOVAYA ZEMLYA	TAIMYR	VERCHOYAN MOUNTAINS	KOLMA-OMOLON	EAST ZABAIKAL	SPITSBERGEN
TAHKANDIT	F Fauna	BAIG-KUNG	*GREAT CAPE BEAR FORMATION*		*ROSS CREEK FORMATION*	↑	?	*Birrang Horizon*	*Pobedin Horizon*	*Djeltin Horizon*		
JUNGLE CREEK FORMATION	Ej	AKTASTINIAN	*Unnamed unit with* ***Jakutoproductus***		*TELFORD FORMATION*		? / *Unnamed unit*		*Osennin Horizon*	*Munugudjak Horizon*	*Hipkhoshin Suite*	*Cora Limestone*
							Jakutoproductus verchoyanicus Zone					
	Eog	STERLITAMAKIAN			*JOHNSTON FORMATION*	*COYOTE BUTTE FORMATION*						*Cancrinella Limestone*
	Ey	TASTUBIAN	*BELCHER CHANNEL FORMATION*	*"FORMATION B"*	*BELCOURT FORMATION*	↓	*Barents Series*	*Upper Turuzov Horizon*	*Afonin Horizon*	*Yasachnin and Irbichan Horizons*		*Upper Wordiekammen Limestone*
	Eta	ASSELIAN								*Paren Horizon*		

of the Arctic region, including *Arctitreta kempei* (Anderson), *Thuleproductus arcticus* (Whitfield), and "*Spirifer*" *striato-paradoxus* Toula. Examination of the Assistance fauna from GSC loc. 26406 on Devon Island revealed no species in common with the Yukon Ey, Eog, or Ej zones.

On the other hand, the small brachiopod fauna recovered from the lower part of the unnamed unit on Bjorne Peninsula (listed by Waterhouse *in* Thorsteinsson, 1974, p. 56) has several close affinities to those of the Yukon Ej zone, including *Jakutoproductus* sp. (very close to *J. verchoyanicus*), *Kutorginella* sp. (close to *K. yukonensis*), ?*Linoproductus simensis* (Chernyshev), *Yakovlevia* sp., *Stenoscisma mutabilis*, and *Camerisma* aff. *C. pentameroides*. The assemblage from Bjorne Peninsula as a whole may be compared to the Ej zone of northern Yukon Territory as suggested by Waterhouse (*in* Thorsteinsson, 1974). The ammonoids from the same assemblage, described by Nassichuk et al. (1965), were said to indicate a Late Sakmarian (Sterlitamakian) or Early Artinskian (Aktastinian) age, but the latter assignment was favoured by Nassichuk et al. (1965, p. 9, footnote) and was supported recently by the discovery of conodonts from the same unit (see Beauchamp et al., 1989). Andrianov (1985, Table 6) also correlated the Canadian Arctic ammonoid fauna with a similar fauna found from the lower Echii Suite in the Verchoyan Mountains, of Aktastinian age (Andrianov, 1974, Table 2).

Canadian Rocky Mountains

The Permian Ishbel Group of the Rocky Mountains in Alberta and British Columbia is made up of six formations, as proposed by McGugan and Rapson (1963). In ascending order they are: the Belcourt, Johnston Canyon, Telford, Ross Creek, Ranger Canyon, and Mowitch formations, ranging in age from Asselian to ?Wordian (MacRae and McGugan, 1977; Henderson, 1989). The only sizeable brachiopod fauna is known from the Telford Formation in southeastern British Columbia, which was listed and in part described by McGugan (1963), Logan and McGugan

(1968), and MacRae and McGugan (1977). The fauna included the following identifiable species: *Kutorginella* cf. *D. neoinflatus* (Likharev), *Anidanthus eucharis* (Girty), *Yakovlevia* cf. *Y. greenlandica* Dunbar (probably *Y. transversa*), *Spiriferella saranae,* and *Alispiriferella* cf. *A. ordinaria, Purdonella* cf. *P. nikitini,* and *"Spirifer" osborni* Harker. As a whole, this assemblage appears to suggest a generalized, perhaps condensed or latitudinally differentiated, correlation with the Yukon Ey, Eog, and Ej zones. Correlation with the Ey zone is more likely because the two characteristic zonal species of the Yukon Eog and Ej zones, *Ogilviecoelia inflata* and *Jakutoproductus verchoyanicus,* are absent from the Telford Formation. Conodont data from the Telford Formation indicate a Sakmarian age for the unit, according to Henderson (1989).

Vancouver Island

The Yukon Ey zone appears to be well matched with the fauna from the Lower Permian "Formation B" in the Buttle Lake area of Vancouver Island. The fauna from this unit was listed and mostly illustrated by Yole (1963). Of some 15 brachiopod species found in this unit, nine are also found in the Yukon Ey zone, including *Calliprotonia inexpectus, Kochiproductus porrectus, Antiquatonia cooperi, Sowerbina bullocki, Yakovlevia transversa, Neospirifer* sp., *Rhynchopora magna, Spiriferella saranae,* and *Camerisma* (*Callaiapsida*) *pentameroides.* No specific age other than Early Permian was proposed by Yole for this fauna, but it was assessed as Early Sakmarian (Tastubian) because of similarities to the Yukon Ey zone fauna by Waterhouse (1976, p. 87), with support from fusulinid data (Monger and Ross, 1971) for a late Wolfcampian (Lenox Hill Formation)–Leonardian age. This is confirmed in the present study.

Central Oregon

There seems to exist a great similarity between the Yukon Ey and Ej faunules and brachiopods from the Coyote Butte Formation in central Oregon, northwestern United States, described by Cooper (1957). Although Cooper considered the Oregon fauna most likely correlable with that of the Road Canyon Formation (of Roadian or Kungurian age) of west Texas, as opposed to the Sakmarian to Early Artinskian age Yukon faunas, there was no single species found in common between the Roadian and Coyote Butte faunas. On the other hand, Waterhouse (*in* Bamber and Waterhouse, 1971) pointed out a close similarity between several Coyote Butte and Jungle Creek species. This may be affirmed. Ten species from the Oregon fauna have also been found in the Yukon zones. Four of the species are known from all three zones (Ey, Eog, and Ej): *Calliprotonia inexpectum, Yakovlevia transversa, Rhynchopora magna, Spiriferella pseudodraschei*; one species from both the Ey and Eog zones: *Kochiproductus porrectus*; two species from both the Ey and Ej zones: *Krotovia pustulata, Linoproductus dorotheevi;* two species from the Ey zone: *Waagenoconcha parvispinosa, Antiquatonia cooperi*; and one species from the Eog zone: *Dielasma brevicostatum* (see Table 5).

The large Oregon fauna includes a total of 60 brachiopod species (including unidentifiable forms) described from more than 50 isolated outcrops of the Coyote Butte limestone. The Coyote Butte limestone is now assigned to the Grindstone terrane of east-central Oregon (Blome and Nestell, 1991), a sedimentary mélange of Paleozoic slide-and-slump blocks that became detached from a carbonate shelf fringing a volcanic edifice, intermixed with Permian–Triassic slope and basinal deposits. Blome and Nestell (1991) recommended that the Coyote Butte Formation be reduced to informal status, because it cannot be mapped or traced beyond limited areas, and it is now chaotically intermixed with younger sediments. Late Wolfcampian (Sakmarian)–early Leonardian (Artinskian) fusulinaceans are found widely (Skinner and Wilde, 1966; Bostwick and Nestell, 1967; Nestell, 1983), and Early Permian conodonts are also known (Blome and Nestell, 1991, p. 1289). The brachiopods described by Cooper (1957) come from stratigraphically higher parts of the Coyote Butte limestone (Wardlaw et al., 1982) and have been interpreted as no older than Kungurian, to perhaps as young as Wordian. This correlation requires reconsideration for two main reasons. Firstly, the discussion of Cooper (1957) clearly needs reassessment. He based the age on three major correlations. One of the correlations, the mid-Permian of the Cache Creek faunules of British Columbia, has little value. It was based on a mere preliminary list of brachiopods, never substantiated by full systematic studies, published as long ago as 1935 by Crockford and Warren. The collections have been examined (by JBW) and show little resemblance to Coyote Butte faunules. Secondly, Cooper made extensive comparisons with Early Permian brachiopod faunas of the Urals. Cooper (1957, p. 19) indicated the presence of these species favoured an Artinskian age: *Kochiproductus porrectus, Krotovia pustulata, Stenoscisma mutabilis, Cleiothyridina gerardi, Squamularia rostrata,* and *Spiriferella draschei.* However, *C. gerardi* is the type species of a Late Permian Himalayan genus *Himathyris* Waterhouse (1985) and may be set aside. The rest are Early

Permian, Sakmarian or older, and certainly do not favour an Artinskian age. Indeed, several other Russian species found in the Asselian-Sakmarian Schwagerina Limestone of the Urals were also mentioned by Cooper in his systematic descriptions, including *Chonetes timanicus, Avonia tuberculatus*, and species of "*Alexenia*", "*Muirwoodia*" (= *Yakovlevia*), *Linoproductus, Echinoconchus*, ?*Proboscidella*, and *Rostranteris*, all of which indicate strongly a general Sakmarian age, yet were omitted from Russian correlations by Cooper (1957, p. 19). Overall, the entire array of genera and species allied to Russian-Urals species overwhelmingly points to a roughly Sakmarian age. Such a correlation is further endorsed by occurrences in various Siberian faunules, which were not mentioned by Cooper (1957).

The prime reason for assigning a younger, post-Sakmarian age to the Coyote Butte brachiopods was assessed by Cooper as due to "*Muirwoodia*" (= *Yakovlevia*). "Chiefly on the basis of the presence of *Muirwoodia* the Oregon Permian seems to ally itself with Word No. 1" (Cooper, 1957, p. 18). This was after all the first record of "*Muirwoodia*" or *Yakovlevia* in North America, and Cooper therefore naturally compared the presence of "*Muirwoodia*" with the first entry of "*Muirwoodia*" into the Glass Mountains sequence of west Texas. Overall, the composition of the Coyote Butte brachiopods is Arctic (Canadian-Siberian), with secondary strong ties to the Urals. Any resemblance to the Glass Mountains faunules is very much weaker. It therefore appears likely that the presence of *Yakovlevia* in the Coyote Butte Formation reflects Arctic age parameters, not Glass Mountain parameters. The many Sakmarian species preclude assigning a younger age.

There is a second major reason for caution over the supposedly Roadian age for the Coyote Butte brachiopods from the Canadian succession. The specific and generic ties for Canada point to Sakmarian-Early Artinskian. These are reinforced by the position of the Yukon faunules below the Tahkandit Formation, which contains Artinskian fusulinids and Late Artinskian-Kungurian brachiopods in the lower part, followed by early Wordian brachiopod faunules in the upper part. In the northern Richardson Mountains, Tahkandit brachiopods are accompanied by a Baigendzinian ammonoid *Neouddenites caurus* Nassichuk et al. (1965). Stratigraphy and faunal sequence reinforce the Sakmarian-Early Artinskian age.

A few conodonts were reported from the Coyote Butte limestone in Wardlaw et al. (1982). These include *Neostreptognathudus* sp. B. of Wardlaw and Collinson, 1978, originally found in the basal Roadian of the Great Basin, and two other formally named species that range into Aktastinian-Kungurian faunules elsewhere. Various fusulinaceans were also recorded by Wardlaw et al. (1982). *Parafusulina* (*Skinnerella*) *superba* was found sparsely in the upper unit but was more abundant in the underlying unit. The presence of this species was thought to indicate a correlation between the fusulinacean-bearing Coyote Butte limestones and McLoud Limestone H, but the evidence indicates it could easily be older, equivalent to McLoud zone G and lower Bone Spring if not older (Decie Ranch of the Wolfcampian), as argued by Wilde (1971). These fossils were not found with the brachiopods, so the possibility of either leakage of small fossils and/or reworking of fossils, and miscorrelation between similar lithotypes, cannot yet be discounted. Basically, the fusulinaceans and brachiopods consistently point to a late Wolfcampian-early Leonardian (Sakmarian-Aktastinian) age. One unnamed conodont species, from similar lithology and different locality, suggests a late Leonardian (Baigendzinian)-Roadian (Kungurian) age. Wardlaw et al. (1982) offered no evidence of a Roadian age for the brachiopods, and the evidence for a greater age, discussed by Bamber and Waterhouse (1971) and Waterhouse (1976), was not rebutted. Wardlaw et al. (1982) stated that the Coyote Butte limestone remained stratigraphically "right-side-up", so that the mélange was not chaotic, but further study by Blome and Nestell (1991) showed that the blocks had rotated, and that some were overturned.

Clearly studying the Coyote Butte Formation and its faunules is a challenge. The clear age and stratigraphic relevance of the Yukon Ey-Ej sequences have helped to resolve some of the problems, and indicate some degree of faunal mixing, or sedimentary reworking, in the upper unit of the Coyote Butte Formation.

Russia

Western slopes of the Ural Mountains

Correlation of the Lower Permian brachiopod succession of northern Yukon Territory with the Russian standard sequence is greatly facilitated by the close affinity between the faunas of this age in the two regions. However, the very rich Early Permian brachiopod faunas of the Urals have not been revised for many years, apart from Kalashnikov (1986) who recently refigured some of the more characteristic species. We do not know clearly the succession of brachiopod assemblages at substage or zonal level. These rich faunas were described as from the "Upper

Carboniferous'' in many early studies, notably Stuckenberg (1875, 1898), Krotov (1888), Chernyshev (1902), Gerasimov (1929), and were summarized by Miloradovich (1949), Stepanov (1951), and Likharev (1966). Most of the taxonomic names used by Chernyshev (1902) are in need of modern revision.

There is a second difficulty in correlating the Lower Permian Russian standard section with other successions of the Arctic region based on brachiopods, and that is the real age of the ''Schwagerina Horizon'' applied by Chernyshev (1902) to the Lower Permian exposures in northern Timan and the Urals. The so-called ''Schwagerina Horizon'' is, as subsequent studies have shown, not equivalent to the original concept of the Schwagerina Horizon of Nikitin, which was proposed for the limestone outcropping in the Samara Bend of the Russian Platform (Barchatova, 1964). Dunbar (1940), Rauser-Chernousova (1960), and Barchatova (1964) pointed out that the brachiopod faunas described by Chernyshev (1902) from his ''Schwagerina Horizon'' actually came from horizons overlying the true Schwagerina Horizon and therefore were all younger (mostly Sakmarian) than the typical Schwagerina Horizon, which is now generally regarded as Asselian in age (Stepanov, 1954, 1973).

Because a detailed zonal succession of the brachiopod faunas in the Urals is not available, the only practical correlation between northern Yukon and the Urals based on brachiopod evidence is a provisional one, only at stage level. More accurate information should be obtained from associated fusulinid and ammonoid data, because these have been described in more recent times, with better, but not completely adequate stratigraphic control. Even these fossils are not yet able to offer a completely satisfactory standard. Of all the correlation tools, ammonoids are the most readily used and have been recorded in substantial monographs by Ruzhencev (1952, 1956). The lower Tastubian is dominated by Asselian survivors, joined by *Juresanites karakhorum* Ruzhencev as the sole, strong discriminant. The upper Tastubian is better defined, with many new genera, including *Synartinskia*, *Medlicottia*, *Metalegoceras, Uraloceras*, and *Propopanoceras*. But the Sterlitamakian is much the same, with no new genera. Basically, in terms of Ural occurrences, ammonoids offer a basal Sakmarian division, easily confused with Asselian, and an upper division of upper Tastubian plus Sterlitamakian. The Aktastinian is a little better defined, with only five species persisting from the Sterlitamakian, and as few as two new genera, *Aktubinskia* and *Neoshumardites*, joined by the long-lived *Agathiceras*. Brachiopod species and individuals are much more abundant, so may be more useful for subdivision and correlation. Fusulinaceans have been used as the prime basis for subdivision. However, in Russia, there is nomenclatural confusion (Waterhouse, 1976) because the rules of zoological nomenclature have not been followed, and successive zones show considerable overlap from persistent species. Many of the critical genera persist into much younger beds (e.g., *Pseudofusulina*). From what we have seen in the field, both Asselian and Sakmarian deposits of the southern Urals are a complex heterogeneous array of carbonates and basinal deposits, with high potential for some degree of reworking — especially of fusulinids — and indicate depth and facies interrelationships. All this should be reassessed in modern terms for eustatic changes, local erosion, and reworking. For such reasons, correlation with the southern Urals must remain extremely tentative.

The Asselian brachiopod assemblage in the Urals is of transitional character from the Late Carboniferous to Early Permian. According to Kalashnikov (1988), the Asselian fauna contains *Orthotichia* Hall and Clarke, *Derbyia* Waagen, *Chonetinella* Ramsbottom, *Krotovia* Frederiks, *Avonia* Thomas, *Kozlowskia* Frederiks, *Linoproductus* Chao, *Juresania* Frederiks, *Brachythyrina* Frederiks, *Brachythyris* M'Coy, *Stenoscisma* Conrad, and *Choristites* Fisher de Waldheim, genera which were all widely distributed in the Late Carboniferous. The Asselian Stage also shares genera of typical Permian aspect: *Rugivestis* Muir-Wood and Cooper, *Urushtenia* Likharev, *Rostranteris* Gemmellaro, *Elivina* Frederiks, *Purdonella* Reed; and genera transitional to those of the Sakmarian Stage: *Calliprotonia* Muir-Wood and Cooper, *Kochiproductus* Dunbar, *Hustedia* Hall and Clarke, and *Septacamera* Stepanov. Kalashnikov (1980) listed about 50 Asselian species from the western slope of the Urals, of which less than 20 percent are also present or closely allied in the Yukon Ey zone. These species are: *Orthotichia morganiana*, *Krotovia pustulata*, *Calliprotonia sterlitamakensis* (compared to the Yukon *C. inexpectum*), *Rugivestis kutorgae* (Chernyshev) (compared to the Yukon *R. arctica*), *Cancrinella cancriniformis*, *Kochiproductus porrectus*, *Stenoscisma mutabilis*, and *Camerisma* (*Callaiapsida*) *pentameroides*. Apparently, species characteristic of the Yukon Ey zone, such as *Tubersulculus maximus*, *Kutorginella yukonensis*, *Linoproductus dorotheevi*, *Yakovlevia transversa*, *Alispiriferella ordinaria*, and *Spiriferella pseudodraschei*, are not present in the Asselian Stage of the Urals.

More evidence favours correlation of the Yukon Ey and Eog zones with the brachiopod assemblages from the Sakmarian Stage of the Urals. According to

Kalashnikov (1988), the Sakmarian brachiopod faunas are characterized by *Lissochonetes* Dunbar and Condra, *Dyoros* Stehli, *Chaoiella* Frederiks, *Cancrinella* Frederiks, *Schrenkiella* Barchatova, *Ovatia* Muir-Wood and Cooper, *Marginifera* Waagen, *Thuleoproductus* Sarytcheva and Waterhouse (probably *Thamnosia* Cooper and Grant), and *Rhynchopora* King. Stepanov (1951, p. 104) listed those species that apparently first appeared in the Sakmarian Stage (names of some genera are altered from those on the original list according to present taxonomy): *Reticulatia uralica*, *Chaoiella grüenewaldti* Krotov (compared to the Yukon *Chaoiella* sp.), *Linoproductus dorotheevi*, *Tubersulculus maximus* (= *Productus pseudoaculeatus* Krotov of Chernyshev), *Waagenoconcha irginae** Stuckenberg, "*Spinomarginifera*" *tuberculatiformis** Frederiks, *Marginifera kolwae** Stepanov, "*Spirifer*" *marcoui** (not Waagen) of Chernyshev, *Brachythyris supracarbonica** Chernyshev, and *Purdonella nikitini*. Some of these species are also prominent elements of the Yukon Ey and Eog zones, but species with an asterisk are not present. *Yakovlevia mammata* (Chernyshev), a close ally of *Yakovlevia transversa*, was also assigned to the Sakmarian Stage by Miloradovich (1949). This species is probably not known in pre-Sakmarian rocks; it was not listed in the Asselian by Kalashnikov (1980) nor in the Upper Carboniferous according to Miloradovich (1949). In addition to the species mentioned above, some forms from the Sakmarian Stage in the Urals are also present or closely resemble representatives from the Yukon Ey and Eog faunas (see Table 8).

The key species of the Yukon Ej zone, *Jakutoproductus verchoyanicus*, is not present in the Urals. Nevertheless, a general Early Artinskian (Aktastinian) age is indicated by both brachiopod and fusulinid data. The Aktastinian brachiopod assemblage of the south Urals, as summarized by Miloradovich (1949) and Stepanov (1951), is characterized by the first appearances of many species, of which the following are also present or have close representatives in the Yukon Ej zone: *Derbyia regularis* (not Waagen) Chernyshev (comparable with the Yukon *Orthotetes canadensis*), *Dyoros* (*Dyoros*) *pseudotrapezoidalis*, *Uraloproductus stuckenbergianus* (comparable with the Yukon *U.* sp. A), *Sowerbina timanica* (Stuckenberg) (comparable with the Yukon *S. bullocki*, a species that is most common in the Ej zone in northern Yukon). In addition, some species first appearing in the Sakmarian Stage become abundant in the Aktastinian in the Urals, notably *Spiriferella saranae* (Stepanov, 1951). The same seems also true in northern Yukon Territory. *Spiriferella saranae* is comparatively more common in the Ej zone than in the underlying Ey zone in which *S. pseudodraschei* is dominant.

The correlation of the Ej zone with fauna from the lower Artinskian substage appears to be supported by fusulinid evidence. *Eoparafusulina yukonensis* (Skinner and Wilde) from the Ej zone was not specifically compared to any species from the Urals by Ross (1967a), but *Eoparafusulina* is known to be most common in the Aktastinian Substage in the Urals. According to Gorsky et al. (*in* Kotlyar and Stepanov, 1984, p. 41–52), only one questionable species of *Eoparafusulina* Coogan is present in the Lower Sakmarian (Tastubian), in contrast to 11 species found in the Aktastinian and nine in the overlying Upper Artinskian (Baigendzinian).

In the Upper Artinskian (Baigendzinian) of the southern Urals, many brachiopod species persist from underlying stages, and are joined by some new elements, as summarized by Miloradovich (1949). The equivalent northern Yukon fauna is probably represented by the *Antiquatonia* Zone (Fa zone) and *Sowerbina* Zone (Fs zone) of the basal Tahkandit Formation (Bamber and Waterhouse, 1971; Waterhouse, 1976), with support from ammonoids. According to the list provided by Miloradovich (1949), of the 153 brachiopod species from the Baigendzinian Substage, only six are present in the Yukon Ey, Eog, and Ej zones.

Novaya Zemlya

Important systematic studies of Permian brachiopods from this island have been done by Holtedahl (1924), Miloradovich (1935, 1936a), and Likharev (1937). Likharev and Einor (1939) described 138 brachiopod species (including unidentified forms and subspecies) from a number of localities on both the north and south islands and concluded that most were either Late Carboniferous or Early Permian. The majority were collected from the Barents Series on the western coast of the north island, between Sedov Bay and Russian Harbour. This fauna, also partly described by Miloradovich (1935), consists of 63 species, of which five are also found in the Yukon Ey zone: *Orthotichia morganiana*, *Kochiproductus saranaeanus*, *Reticulatia uralica*, *Spiriferella pseudodraschei*, and *S. saranae*. In addition, a few more species may be compared with representatives from the Yukon Ey zone, including *Calliprotonia sterlitamakensis*, *Schrenkiella schrenki*, and *Rhynchopora nikitini*. On the other hand, the Barents Series also contains *Thuleproductus arcticus* and *Anemonaria pseudohorrida*, which normally occur in younger Permian (Kungurian) deposits in the Arctic region. The Barents Series may therefore have a longer age range than the Yukon Ey zone; or the fauna listed for the Barents Series may have been mixed from two or more assemblages of different ages.

Table 8

Comparison between Sakmarian Ural fauna and Yukon Ey and Eog zone fauna

Species from the Sakmarian Urals (from Miloradovich, 1949; Stepanov, 1951; Likharev, 1966; Kalashnikov, 1980, 1986, 1988)	Similarities to the Ey and Eog zones in the Yukon Stage
Orthotichia morganiana	Present
Krotovia pustulata	Present
Calliprotonia sterlitamakensis	Close to *C. inexpectum*
Kochiproductus porrectus	Present
K. saranaeanus	Present
Cancrinella cancriniformis	Present
Rhynchopora nikitini (Chernyshev)	Close to *R. magna*
Stenoscisma mutabilis	Present
Camerisma (Callaiapsida) pentameroides	Present
Spiriferella saranae	Present
Purdonella nikitini	Present
Tiramnia uralica (Chernyshev)	Close to *T. canadica*

A number of species were also described by Likharev and Einor (1939) from the eastern coast of the north island, between Cape Stary Navolok and Cape Shevtechenko, including *Jakutoproductus verchoyanicus*, a typical element of the Yukon Ej zone. *Anidanthus aagardi* (not Toula) from the same assemblage resembles *A.* cf. *A. boikowi*, also characteristic of the Ej zone in Yukon Territory.

Taimyr

The Permian brachiopods of Taimyr Peninsula were described by Einor (1939, 1946) and Ustritskiy and Chernyak (1963). The fauna from the upper Turuzov Horizon, assigned an Asselian to Sakmarian age by Ustritskiy and Chernyak (1963), appears to be at least in part correlative with the Yukon Ey zone. Species common to both areas are *Dyoros* (*Dyoros*) *pseudotrapezoidalis*, *Fimbrinia transversa,* and *Waagenoconcha permocarbonica*. Although it also occurs in the upper part of the upper Turuzov Horizon, *Jakutoproductus verchoyanicus* is most common in, and typical of, the overlying lower part of the Birrang Horizon in Taimyr, which is clearly correlated with the Yukon Ej zone. The Birrang Horizon is divisible into two subhorizons in terms of faunal characteristics (Ustritskiy, 1971). The lower subhorizon is distinguished by the possession of *Jakutoproductus verchoyanicus*, and the upper subhorizon by *Cancrinella koninckiana* (Keyserling), *Rhynchopora arctica* Likharev and Einor, and *Dielasma elliptica* Nechaev, and by numerous bivalves. Ustritskiy (1971) assigned a Sakmarian to Kungurian age to the Birrang Horizon. But a more accurate dating, an Early Artinskian (Aktastinian) age, is proposed for the lower subhorizon according to the present correlation scheme (Table 8). The upper subhorizon is probably of Late Artinskian (Baigendzinian) to Kungurian age.

Verchoyan Mountains

Permian marine rocks and faunas are widely distributed in the Verchoyan Mountains in northeastern Siberia. Brachiopods are the most abundant and well studied group in the Verchoyan region and have been used for delineating biozones and regional correlations. Permian brachiopods have been described by a number of palaeontologists, including Kashirtsev (1959), Solomina (1970), Abramov (1974), Abramov and Grigor'yeva (1983, 1988), and Ganelin (1991). Ganelin (*in* Kotlyar and Stepanov, 1984) recognized 17 successive brachiopod zones for all the Permian deposits of northeastern Siberia (Verchoyan Mountains and the Kolyma-Omolon Massif) and only recently (1991) described many of the nominal species. The faunal characteristics, reference sections, and regional distribution and correlation of his zones have yet to be documented. At present, it is difficult to correlate the Yukon brachiopod succession with Ganelin's zonal scheme.

Ganelin's biostratigraphic zonation was also not followed by Abramov and Grigor'yeva (1988) in their monographic study of Permian brachiopods and the biostratigraphy of the Verchoyan Mountains. These authors recognized six horizons for the Permian deposits of the Verchoyan region, each characterized by a distinctive assemblage of brachiopods and other fossils. In their scheme, the Lower Permian is composed of two horizons: Afonin and Osennin, in ascending order. The Afonin Horizon incorporates the upper Kigiltas Suite or equivalent beds as referred to by earlier workers (e.g., Kashirtsev, 1959; Solomina, 1970); and the Osennin Horizon includes the lower part of the Echii Suite or equivalent. Faunas of both horizons seem to be closely related to the Ey, Eog, and Ej faunas in northern Yukon Territory.

The Afonin Horizon appears to be in part correlative with the Yukon Ey zone. Abramov and Grigor'yeva (1988) described nine brachiopod species from the Afonin Horizon, of which one species, *Anidanthus*? *sarytchevae* Zavodovskiy, is very close to *Protoanidanthus umbonatus* characteristic of the Yukon Ey zone. The fauna from the upper Kigiltas Suite (equivalent to the Afonin Horizon) of western Verchoyan figured by Kashirtsev (1959) has more species in common with the Yukon Ey zone, including *Fimbrinia transversa* (identified by Kashirtsev as *F. cristatotuberculata* Kozlowski), *Kochiproductus porrectus*, "*Marginifera*" *peregrina* (not Frederiks) (in part conspecific with the Yukon *Rugivestis arctica)*, and *Cancrinella cancriniformis*.

The Afonin Horizon also contains a small assemblage of ammonoids in the Khorokyt Complex of Andrianov (1985), which was said to be correlative with the fauna from the Asselian–Sakmarian stages of the Urals, and with the fauna from the Holmwood Shale of Western Australia, of Tastubian age (Glenister and Furnish, 1961; Waterhouse, 1976; Archbold, 1982b).

The brachiopod fauna of the Osennin Horizon immediately above the Afonin Horizon contains 47 taxa (Abramov and Grigor'yeva, 1988), of which the most characteristic are *Jakutoproductus verchoyanicus* and *Anidanthus boikowi*. Both species also occur in the Yukon Ej zone. The latter is identified in this report as *Anidanthus* cf. *A. boikowi* because of poor preservation of its dorsal valve, but the ventral details are strikingly similar to the shell from Verchoyan. In addition, several species from the Osennin Horizon compare closely with forms characteristic of the Yukon Ej zone, including *Spiriferella* sp. (close to the Yukon *S. saranae*) and *Timaniella*? sp. (close to the Yukon *T. convexa* n. sp.). Although an Artinskian age was assigned to the Osennin Horizon by Abramov and Grigor'yeva (1988), a more specific dating, Early Artinskian (Aktastinian), appears to be likely, judged by ammonoids found in the same horizon (Andrianov, 1974).

The Osennin Horizon is overlain by the Pobedin Horizon of probable Late Artinskian (Baigendzinian) to Kungurian age (Andrianov, 1985; Abramov and Grigor'yeva, 1988). Abramov and Grigor'yeva (1988) described 18 brachiopod species from the Pobedin Horizon, none of which are present in the Yukon E faunas.

Kolyma–Omolon Massif

The Permian brachiopod faunas of this large area are essentially the same as those in Verchoyan Mountains discussed above, and are closely related to those from northern Yukon Territory and Arctic Canada. Detailed monographic studies of the Permian brachiopods from the Kolyma–Omolon Massif were provided by Likharev (1934a, b), Kashirtsev (1959), and Zavodovskiy and Stepanov (1970). Zavodovskiy and Stepanov (1970) divided the Lower Permian into six horizons. These are Burgali, Paren, Irbichan, Yasachnin, Munugudjak, and Djeltin in ascending order. The first was assigned to the Asselian, the next three to the Sakmarian, and the upper two to the Artinskian and Kungurian respectively. The Carboniferous/Permian boundary is now different, redrawn at the base of the Munugudjak Horizon by Chernyak (1975) and Ganelin (1977; *in* Kotlyar and Stepanov, 1984). However, the fauna from the Paren Horizon, which contains *Attenuatella*? *omolonensis* Zavodovskiy may be correlated with the Yukon Eta zone of Asselian age, as suggested by Waterhouse (1976, p. 57). The overlying Irbichan Horizon seems correlative with the Yukon Ey zone and, to a lesser extent, with the Eog zone. The fauna from the Irbichan Horizon, as described by Zavodovskiy and Stepanov (1970), contains several species that are also present, or have close allies, in the Yukon Ey and Eog zones. These are: *Overtonia gijigensis* Zavodovskiy (close to the Yukon *Fimbrinia transversa*), *Cancrinella cancriniformis*, *Anidanthus aagardi* (not Toula) (close to the Yukon *Protoanidanthus umbonatus*), *Yakovlevia mammatiformis* (close to the Yukon *Y. transversa*), *Kitakamithyris stepanovi* (Zavodovskiy) (comparable with the Yukon *K.* sp.). There also exist some links between the Yasachnin Horizon and the Yukon Ey and Eog zones. Although there are no shared species, the following two forms from the Yasachnin Horizon may be compared with species from the Yukon Ey and Eog zones: *Orthotetes regularis* (not Waagen), close to Yukon *O. canadensis*, and *Fimbrinia kolymaensis* Zavodovskiy, close to

Yukon *F. transversa*. The Munugudjak Horizon contains a large brachiopod fauna, in which the most distinctive species are *Jakutoproductus verchoyanicus* and *Anidanthus boikowi*. The presence of these species strongly suggests a correlation with the Osennin Horizon in the Verchoyan Mountains, the lower Birrang Horizon of Taimyr, and the Ej zone in Yukon Territory (Table 8).

East Zabaikal

Kotlyar and Popeko (1967) described a small brachiopod fauna from the Hipkhoshin Suite in east Zabaikal, southern Siberia, which is likely to be Early Artinskian (Aktastinian). Five species are known from the Hipkhoshin Suite. Two of them, *Jakutoproductus verchoyanicus* and *Anidanthus boikowi*, clearly indicate a correlation with the Yukon Ej zone and the Osennin Horizon in the Verchoyan Mountains. The Shazagaitui Suite, immediately underlying the Hipkhoshin Suite in eastern Zabaikal, contains a large brachiopod fauna, including abundant *Orulgania* Solomina and Chernyak. *Orulgania* is generally considered to be restricted to the Upper Carboniferous in the Russian Arctic (Grigor'yeva, 1977).

Spitsbergen

Permian brachiopod faunas were described by a number of palaeontologists, notably Toula (1874, 1875), Wiman (1914), Frebold (1937), Stepanov (1937b), Gobbett (1964), and Czarniecki (1969). Nakrem (1991) has provided a modern overview. From Bunsowland (inner Isfjorden), central Vestspitsbergen, Gobbett (1964), following Forbes et al. (1958), recognized four informal stratigraphic units to represent the Upper Carboniferous and Permian deposits. This stratigraphic framework was later revised by Cutbill and Challinor (1965). The upper division of the Wordiekammen Limestone was assigned to the Asselian by Cutbill and Challinor (1965) because of the presence of *Pseudoschwagerina* Dunbar and Skinner, but may be as young as Sakmarian as suggested by brachiopod data (Waterhouse, 1976, p. 85). Gobbett (1964, p. 21) recorded 19 brachiopod species and unidentified forms from the upper division, of which *Reticulatia uralica*, *Linoproductus dorotheevi*, and *Cancrinella singletoni* also occur in common with the Yukon Ey zone. The overlying Upper Gypsiferous Series, or the Gipshuken Formation, contains a small brachiopod fauna that is very similar to the assemblage from upper Wordiekammen Limestone, with *Linoproductus dorotheevi* and *Cancrinella singletoni*. Nakrem (1991) reported the Artinskian conodont *Neostreptognathodus* from the Gipshuken Formation. There is a substantial hiatus between the Upper Gypsiferous Series and overlying Spirifer Limestone (Voringen Member of Kapp Starostin Formation), which has "Artinskian" conodonts (Nakrem, 1991). Gobbett (1964) recorded 24 brachiopod species from the whole Kapp Starostin Formation and assigned to it a "Svalbardian" (Kungurian) age. Examination of the faunal lists and Gobbett's illustrations of the faunas indicates nothing in common at species level with the Jungle Creek faunas. Nakamura et al. (1987) concluded that the age of the Kapp Starostin Formation might range from Kungurian to Dorashamian. Upper Starostin conodonts were evaluated as Kungurian–Ufimian by Nakrem (1991).

Gobbett (1964) also identified a small brachiopod assemblage from the Cora Limestone in Bjørnoya, southern Svalbard. The Cora Limestone overlies, with a distinct unconformity, the Fusulina Limestone containing *Pseudoschwagerina* of Asselian age. A general Artinskian age was suggested by Cutbill and Challinor (1965) for the Cora Limestone. "*Horridonia*" *geniculata* Gobbett from this unit is very close to *Tityrophoria nelsoni* confined to the Ej zone in northern Yukon Territory, indicating a possible correlation.

Early Permian brachiopods were also recorded from Hornsund, southwestern Vestspitsbergen. Czarniecki (1969) described a large fauna from the Treskelodden Beds on the northeastern coast of Hornsund and concluded that the Treskelodden Beds were probably correlative with the middle or lower division of the Wordiekammen Limestone in Billefiorden, rather than with the upper division of the Wordiekammen Limestone as suggested by Gobbett (1964). However, Czarniecki's correlation scheme is not supported by comparison of the brachiopod faunas from both the Treskelodden Beds and the the Wordiekammen Limestone. We agree with Gobbett's view that the Treskelodden Beds are correlative with the upper division of the Wordiekammen Limestone. Czarniecki (1969) recorded 29 brachiopod species from the Treskelodden Beds, of which 16 are found in the upper division of the Wordiekammen Limestone, and only two in the lower division of the same limestone. A possible correlation of the Treskelodden Beds with the Yukon Ey zone is indicated by such brachiopod species in common as *Linoproductus dorotheevi* and *Cancrinella singletoni*.

Birkenmajer and Logan (1969) described 13 brachiopod species and unidentified forms from the Cancrinella Limestone on the west slope of

Kopernikusfjellet, Vestspitsbergen, immediately overlying the Treskelodden Beds. No species are found in common with the Yukon zones under discussion, but this unit may be correlated with the Ey or Eog zone in northern Yukon Territory by its stratigraphic relationship to other Permian units discussed above and by comparison with other Spitsbergen faunas. Birkenmajer and Logan (1969) indicated that the Cancrinella Limestone may be correlated either with the Cora Limestone in Bjørnoya (which is considered to be correlative with the Yukon Ej zone) or the upper division of Wordiekammen Limestone of central Vestspitsbergen, which is correlated here with Yukon Ey zone.

PALEOCOMMUNITIES

This chapter investigates the pattern of distribution and mutual occurrence of major faunal elements in the upper Jungle Creek Formation as a means of recognizing possible fossil communities. Selected fossil data from the three brachiopod zones (Ey, Eog, and Ej) discussed earlier were quantitatively analyzed together rather than separately. This is because communities are believed to be recurrent both in space and time; and this recurrence, if present, should be revealed by analyzing a single data matrix compiled from the three brachiopod zones. We also point out that for any strictly limited time-controlled paleocommunity analysis, beds should be studied and collected layer by layer, to reduce post-mortem mixing, and reduce the time span, but this was beyond our resources, and in most cases, beyond the scope of feasible data acquisition.

Methods

Data collection

A data matrix consisting of 27 localities (columns) and 47 species (rows) was prepared for this analysis. Only those localities containing more than two species were included, except for GSC loc. 53718 which had two species. It was included because it contains the best preserved suite of specimens of *Jakutoproductus verchoyanicus* and represents a distinct biostratigraphic level. The 47 species were selected out of the total 75 described forms on the basis that they are represented by five or more specimens and/or occur in two or more localities. Selection of the raw data can reduce some of the unpredicted "noise" of the raw data, which would make the results difficult to interpret (Gauch, 1982, p. 7, 11).

At each locality, abundance counts (number of specimens) of each selected species were taken for the quantitative analysis. We believe most of the benthic forms counted were essentially in place or had experienced only minor transport, not enough to alter significantly the life associations. This is always a difficult matter to establish but is supported by 1) a high proportion of conjoined valves, 2) similar numbers of disarticulated valves, and 3) the well preserved delicate ornament on fossils from most of the localities considered. As discussed below, some localities show some evidence of minor post-mortem transportation; others, however, show evidence of a near life assemblage. There may also have been cryptic thrusting and repetition, which although difficult to determine in the limited exposures of the Peel and Tatonduk river valleys, was judged to be highly likely in the Peel area (cf. Nassichuk, 1971). Only the Ettrain–Jungle Creek headwaters offer outcrops that extend far along strike, rather than in section.

The 47 species considered in the analysis consist of one bivalve and 46 brachiopods. Other rarer groups of fossils excluded from the quantitative analysis are bryozoans, solitary corals, foraminifers, bivalves, gastropods, echinoderms, and ammonoids. In most cases these forms have been identified to generic level and are listed in Table 9.

The present study follows Spicer and Hill (1979), Beus (1984), and Springer and Bambach (1985) and, as in most studies of modern community analysis follows Gauch (1982) in the use of abundance data rather than presence–absence data for discriminating fossil communities. Johnson (1990) also used relative abundance data in recognizing Devonian benthic communities. Of course, relative abundance relationships among component taxa of a life community may have been altered because of preservation and sampling error; consequently, one fossil community may be dominated by one extremely "abundant" species, and the role of other elements is overshadowed. This disadvantage in using abundance data can be partly overcome by transforming the raw data set before the analysis is processed, as discussed below. Ideally, we should proceed to biomass calculations, as done for the Nepal Permian by Waterhouse (1978), but this is deferred until a full Permian column can be evaluated.

Principal components analysis

Paleocommunities were constructed from the pooled data matrix using principal components analysis (PCA) based on a centred covariance matrix. PCA is an

Table 9

Faunal components of benthic paleocommunities (excluding brachiopods), showing presence (x) and absence (–)

Fossil groups	*Rhynchopora magna* Paleocommunity	*Fimbrinia–Tubersulculus –Kutorginella* Paleocommunity	*Ogilviecoelia inflata* Paleocommunity	*Tityrophoria nelsoni–Septacamera triangulata* Paleocommunity
Bivalves				
Deltopecten sp.	–	x	–	–
Acanthopecten licharewi	–	x	–	–
Etheripecten spp.	–	x	–	–
Streblochondria sp.	–	x	–	–
Exochorhynchus similis	–	x	–	–
Gastropods				
Straparolus sp.	–	x	–	–
Omphalotrochus sp.	–	x	–	–
Bryozoans				
Fenestella sp.	x	x	–	–
Polypora sp.	–	x	–	–
Echinoderm fragments	–	x	–	–
Solitary corals	–	x	–	–
Foraminifers	–	x	–	x
Ammonoids	–	x	–	–
Burrowers	–	x	–	–
Zoophycos	–	x		

ordination technique first applied to ecological data by Goodall (1954) and has since been widely recognized in ecology as a useful tool to simplify the raw data and detect major patterns of species distribution controlled by environmental attributes. Like many other ordination techniques (Gauch, 1982; Ludwig and Reynolds, 1988; Shi, 1993), PCA reduces the dimensionality of the raw data, allowing major trends (or patterns) in the data to be observed more easily than by studying the raw data alone. As indicated above, species abundance may vary considerably in the raw data, with some species numerically dominating a particular locality. Such variation in abundance can be moderated by transforming the data logarithmically (using base 10 in this study). Comparing results from raw and logarithmically transferred data, Spicer and Hill (1979) concluded that logarithmic transformation produced a more interpretable result (also see Digby and Kempton, 1987, p. 13), because the skewness of the data is reduced and random variation (such as "noise" in the data derived from sampling) is diminished without distorting species relationships (Spicer and Hill, 1979).

It must be emphasized that although there may be flexibility over the choice of numerous multivariate methods, the ordination technique used in the present study appears to give an interpretable result, which is in good agreement with the depositional model previously established for the study area by Bamber (*in* Bamber and Waterhouse, 1971) (see below for further discussion).

The calculation of PCA for the present study was performed on an IBM compatible computer by MVSP (Multivariate Statistical Packabundance) written by Kovach (unpublished, 1986). The output of the calculation consisted of 12 eigenvalues and their percentage of total variance, principal component loadings of species on the 12 eigenvectors, and principal component scores of localities on the 12 eigenvectors. The first three eigenvectors account for about 46 per cent of the total variation of the data matrix. This indicates that the data could be summarized on the three axes.

Results

The resulting three dimensional plot of species derived from PCA (Fig. 10) and congruent locality plot (Fig. 11) reveal four major fossil groups, typified by their dominant elements: *Rhynchopora magna*, *Fimbrinia-Tubersulculus-Kutorginella*, *Ogilviecoelia inflata*, and *Tityrophoria nelsoni-Septacamera triangulata*. These groups are considered to represent possible paleocommunities.

Notes on the paleocommunities

A paleocommunity is defined as "a community that existed in geologic history and (is) represented only by fossils or other evidence of past organisms" (Kauffman and Scott, 1976, p. 18). Like a modern community, a paleocommunity may be recurrent both in space and time; but the latter differs from a living community "by the absence of certain of its members and by the absence of active energy flow" (Kauffman and Scott, 1976, p. 19).

The four paleocommunities may be analyzed in terms of faunal composition and probable environment and bottom substrate.

Rhynchopora magna *Paleocommunity*

This fossil community has the lowest species diversity of the four paleocommunities recognized here (Fig. 10) and is almost restricted to GSC loc. 53714 in the Peel River area (Fig. 11), in predominantly skeletal-micritic and dolomitic limestone. The paleocommunity is characterized by abundant small, globose *Rhynchopora magna*, together with minor elements (Fig. 10) including *Arctitreta peelensis*, *Kochiproductus porrectus*, *Cancrinella cancriniformis*, *Globiella costellata*, *Stenoscisma mutabilis*, and *Tumarinia yukonica*, all epifaunal suspension feeders. The associated productid brachiopods were probably adapted to living on, or slightly within, the substrate by using ventral spines to support them above the sea floor. *Rhynchopora magna* is characterized by strong ribs, a deep sulcus, and a high fold. These features probably helped the brachiopod separate the water sucked in from that which was expelled. This form was attached by a pedicle, probably to seaweed or other firm objects within the substrate.

The fauna of this paleocommunity is well preserved, probably representing a near-life assemblage, as indicated by the nearly normal size-frequency distribution (Fig. 38) of *Rhynchopora magna* specimens. All *Rhynchopora magna* specimens from GSC loc. 53714 are conjoined shells, as is *Tumarinia yukonica* from the same locality. The low species diversity, the abundance of small, strongly ribbed *Rhynchopora magna*, together with micritic to micritic-skeletal and dolomitic facies, seem to indicate a very shallow, restricted, and probably slightly hypersaline marine environment. The energy must have been low, but limited turbulence would have been necessary for supplying food to the suspension feeders. The substrate may have consisted of muddy lime containing many particles large enough to anchor the small, globose *Rhynchopora magna* and/or seaweed for attachment. The presence of seaweed would also indicate a shallow-water environment, possibly nearshore.

Fimbrinia-Tubersulculus-Kutorginella *Paleocommunity*

This fossil community is the most abundant and diverse of the four paleocommunities (Figs. 10, 11). It is dominated by spiny productid species such as *Fimbrinia transversa*, *Tubersulculus maximus*, *Kutorginella yukonensis, Calliprotonia inexpectus, Yakovlevia transversa*, and infaunal *Exochorhynchus similis* (Table 9). It also includes locally abundant *Spiriferella pseudodraschei* and wide-hinged *Yukonella plana*. Minor burrows and *Zoophycos* feeding traces have been reported at some localities, especially in Nahoni Range East, at section 116G-5 (Bamber, 1972).

Most species in this paleocommunity were sessile epifaunal forms, probably living on a sandy substrate and supported by body spines or pedicles. *Waagenoconcha permocarbonica* is common in this paleocommunity. This species was probably adapted to a muddy to sandy substrate by virtue of its numerous, fine, closely spaced spines, which would have acted as a sieve between gaping valves (Grant, 1966). The fewer and coarser ventral spines in other productid species such as *Kutorginella yukonensis*, *Fimbrinia transversa*, *Tubersulculus maximus*, and *Calliprotonia inexpectus* were for stabiliziers. *Camerisma* (*Callaiapsida*) *pentameroides* is common in some localities where it is usually associated with fine, calcareous siltstone. The life habit of this species has been studied by Ivanova (1949), Ager (1967), and Grant (1971). Grant depicted it lying on the ventral valve, with the deepest part of the ventral valve lowermost, buried to the level of the edge of the dorsal fold. Species of *Camerisma* (*Callaiapsida*) were believed to have inhabited muddy

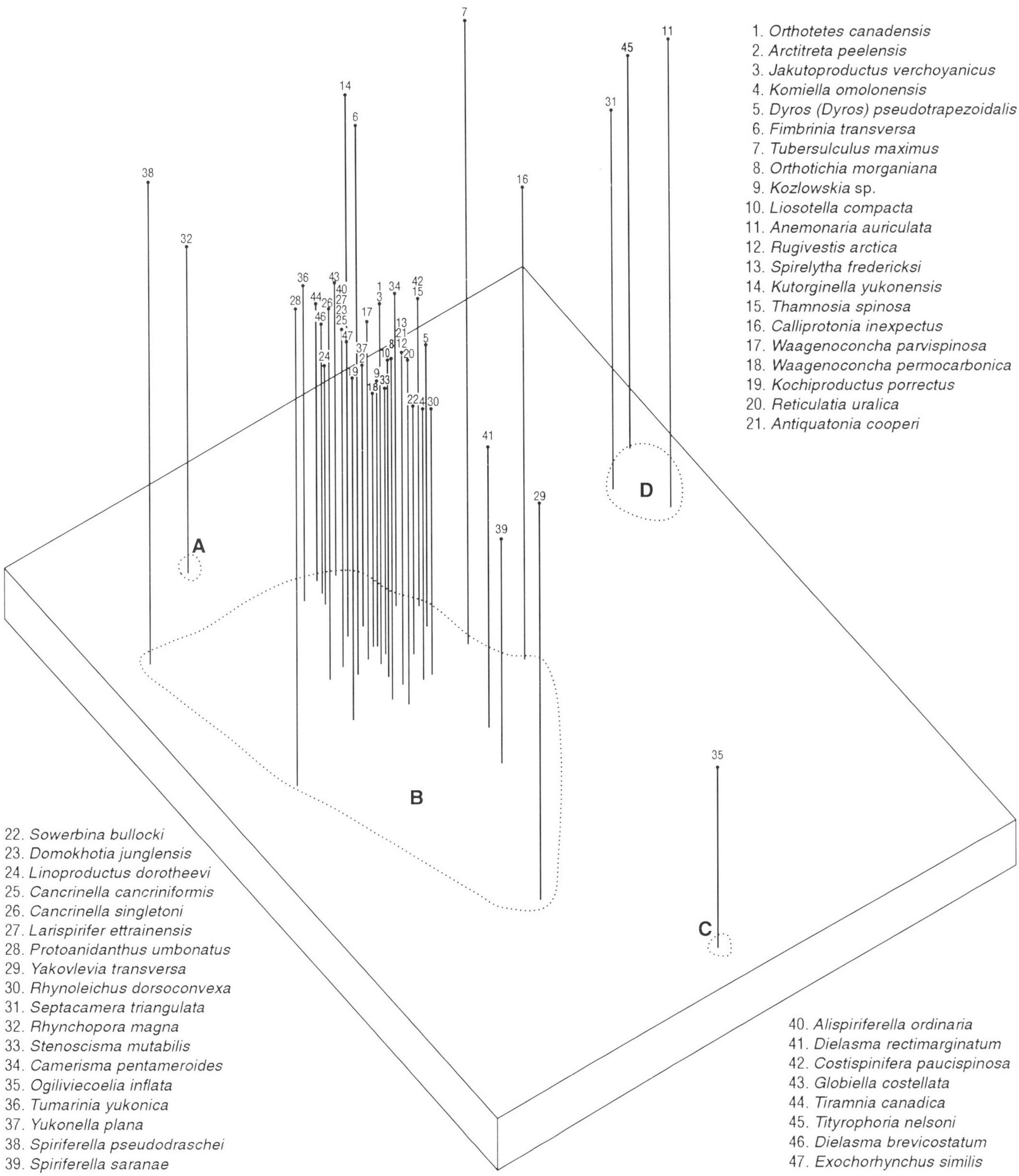


Figure 10. *Three-dimensional plot showing distribution of brachiopod species ordinated by the first three principal axes. The length of rods is proportional to the principal component loadings on axis 1. Numbers refer to the species code. Letters indicate paleocommunities:* ***A, Rhynchopora magna*** *Paleocommunity;* ***B, Fimbrinia–Tubersulculus–Kutorginella*** *Paleocommunity;* ***C, Ogilviecoelia inflata*** *Paleocommunity;* ***D, Tityrophoria nelsoni–Septacamera triangulata*** *Paleocommunity.*

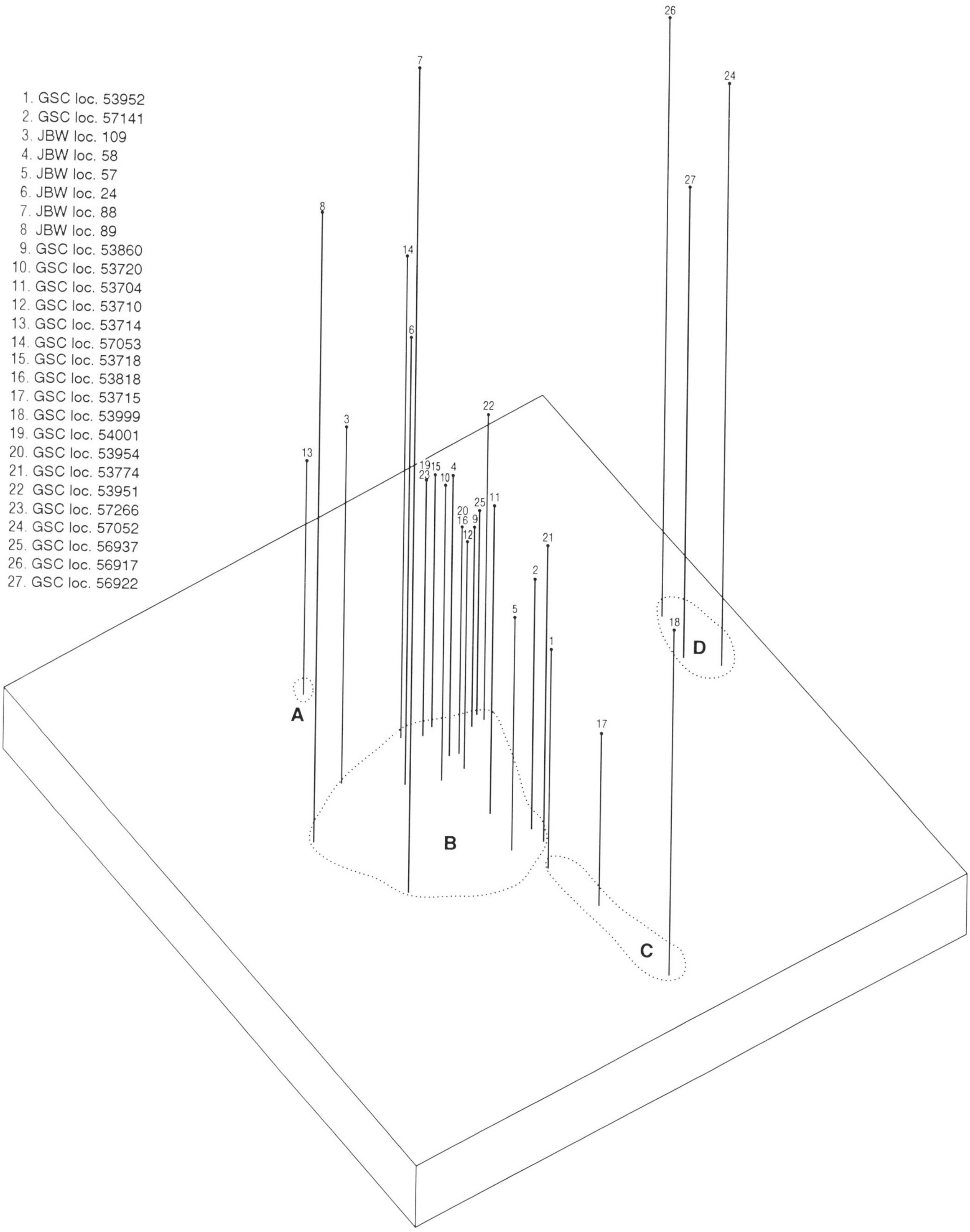


Figure 11. *Three-dimensional plot of localities arranged by the first three principal axes. The length of rods is proportional to the component scores of the localities on the first axis. Numbers refer to the locality code. Abbreviations as for Figure 10.*

sea bottoms. *Spiriferella pseudodraschei* was probably attached to the sandy substrate by a pedicle. *Yukonella plana* is unique to GSC loc. 53774, where it is found in fine to medium grained sandstone. The brachiopod has a strongly thickened umbo, a wide hinge, and a large delthyrial plate delimiting a small delthyrial opening near the hinge margin. It was probably stabilized on the sandy sea bottom primarily by its wide hinge with support from the small pedicle, with the posterior side (ventral umbo) lowermost. The same is also probably true with *Tumarinia yukonica*, but this species has a larger delthyrial opening, indicating the significance of the pedicle in supporting the shell.

Bivalves are also common in this paleocommunity (Table 9). They are mainly epifaunal types (e.g., *Acanthopecten licharewi* and *Etheripecten* spp.) that lived either attached by byssal threads to other shells and sand, or swimming (Waterhouse, 1982b). Infaunal bivalves are represented by *Exochorhynchus similis* and some burrows.

The dominant feeding habits of the paleocommunity were suspension feeding and passive predation. Lower levels of suspension feeding were probably represented by small chonetids (e.g., *Komiella omolonensis*), and small productids (e.g., *Fimbrinia transversa*), and the higher levels by solitary corals, bryozoans, and large productid and spiriferid brachiopods. Infaunal deposit feeders were less common, and are represented by *Exochorhynchus similis* and traces of *Zoophycos*. Burrowing structures are restricted, reported only from GSC loc. 53774 in Nahoni Range East (section 116G-5) and in the Peel River area (section 116H-1B) (Bamber, 1972).

The shell preservation in this paleocommunity is comparatively poor compared to that of other Jungle Creek paleocommunities. Brachiopod valves are normally disarticulated and broken to varying degrees (Fig. 12), indicating some post-mortem transport. Yet, the ratio of separated brachiopod ventral and dorsal valves at certain localities is usually high, and distinct sorting is lacking, implying that only minor action and short-distance transportation were involved.

The *Fimbrinia–Tubersulculus–Kutorginella* Paleocommunity occurs in predominantly fine sandstone and siltstone facies in the northern Ogilvie and northern Richardson mountains, but it is also recognized in skeletal limestone and calcareous mudstone at a few localities, especially in the Peel River sections.

The high diversity, the abundance of suspension feeders, the presence of minor deposit feeders and burrowers, the generally poor preservation, together with common occurrence in sandstone and siltstone, suggest a normal marine, shallow-water, well circulated clastic shelf environment that was probably within the normal wave base zone and subject to moderate wave action. The depositional environment, however, may have been different. The relatively firm bottom and the turbulence favoured epifaunal suspension feeders and some infaunal deposit feeders. Subdivision of the paleocommunity may be possible by taking the type of substrate into account in the statistical analysis. The fauna from GSC loc. 53774, Nahoni Range East, northern Ogilvie Mountains, could be used as an example for this subdivision. The locality is characterized by fine to medium grained sandstone, and is dominated primarily by *Yukonella plana*, together with some *Waagenoconcha permocarbonica*; with no *Fimbrinia transversa, Tubersulculus maximus*, or *Kutorginella yukonensis*. However, this assemblage is statistically linked to the *Fimbrinia– Tubersulculus–Kutorginella* Paleocommunity through the presence of *Waagenoconcha permocarbonica* and other minor shared elements. It may represent a subcommunity adapted to a coarser substrate in a shallower environment.

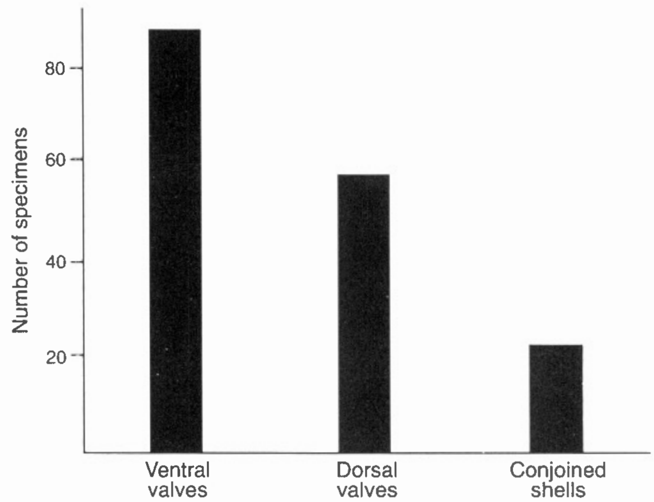


Figure 12. Ventral-dorsal-conjoined frequency distribution of brachiopod species in JBW loc. 88, showing moderately high percentage of disarticulated valves.

Ogilviecoelia inflata *Paleocommunity*

This paleocommunity is recognized at three localities (GSC 53715, 53952, 53999; Fig. 11) and also possibly at JBW loc. 57 and GSC loc. 57266. The last two localities contain a small number of *Ogilviecoelia inflata* and were shown statistically to be closer to the *Fimbrinia–Tubersulculus–Kutorginella* Paleocommunity. Further sampling from the two localities may produce more abundant *Ogilviecoelia inflata,* and if so, they could be grouped with the *Ogilviecoelia inflata* Paleocommunity. The *Ogilviecoelia inflata* Paleocommunity has a moderate species diversity and is usually found in calcareous mudstone and siltstone. The paleocommunity is dominated by the very small, nearly smooth *Ogilviecoelia inflata*, together with other minor elements, notably *Tubersulculus maximus, Globiella costellata*, and *Dielasma rectimarginatum* (Fig. 10). Bryozoans and bivalves are rare.

All species in this paleocommunity were sessile epifaunal suspension feeders, living on a muddy to silty, relatively firm bottom. *Ogilviecoelia inflata*, probably like *Attenuatella* Stehli, lived propped up in sediments without a distinct pedicle (Waterhouse, 1973). This species often forms thin shell beds, with the shells crowded together in place, indicating that conditions were quiet and no significant post-mortem transportation was involved.

The fauna of the *Ogilviecoelia inflata* Paleocommunity probably inhabited an outer shelf, quiet-water environment. The bottom must have consisted of relatively soft lime mud and conditions of minor turbidity.

Tityrophoria nelsoni–Septacamera triangulata *Paleocommunity*

This paleocommunity is recognized at three localities (Fig. 11) and appears restricted to the Tatonduk River area (section 116C-2), associated with limestone and calcareous mudstone and siltstone. It has moderate species diversity and is characterized by a small productid *Anemonaria auriculata* with few strut spines, a large nearly smooth horridonid species *Tityrophoria nelsoni*, which also possesses scattered coarse spines, and a large triangular-shaped rhynchonellid species *Septacamera triangulata*. Also conspicuous in the paleocommunity are *Kutorginella yukonensis, Calliprotonia inexpectus*, and *Yakovlevia transversa*. Bivalves and bryozoans are rare or absent, and foraminifers are restricted.

Most of the productid species of the paleocommunity are preserved with long body spines, and the ratio of ventral to dorsal valves is high, indicating quiet conditions and absence of significant post-mortem transportation. The *Tityrophoria nelsoni–Septacamera triangulata* Paleocommunity appears to represent a relatively deep-water muddy shelf community. The few, large strut spines in *Anemonaria auriculata, Tityrophoria nelsoni*, and *Yakovlevia transversa* may have served to anchor the animals above the muddy bottom. The triangular, ribbed *Septacamera triangulata* was probably attached to other firm objects, such as pebbles or buried shells, within the soft substrate by its pedicle, with the beak lowermost (Grant, 1971).

Discussion

The four paleocommunities described above appear to record positions in an onshore to offshore sequence across a shallow marine shelf (Fig. 13). Anderson (1971) proposed two sedimentary models to explain the distribution patterns of epeiric sea communities. The Yukon data seem comparable with his Model 1. This model applies to very low slope, stable or transgressive seas. Five sedimentary environments, each characterized by a distinct benthic community, were recognized. These are, from onshore to offshore: tidal flat, restricted subtidal, open shelf above wave base, open shelf near wave base, and open shelf below wave base. In this model, the *Rhynchopora magna* Paleocommunity would be in the shallow, subtidal restricted position, the *Fimbrinia–Tubersulculus–Kutorginella* Paleocommunity would fit into the open shelf above wave base zone, the *Ogilviecoelia inflata* Paleocommunity in the open shelf at or near wave base, and the *Tityrophoria nelsoni–Septacamera triangulata* Paleocommunity in the low energy position farther offshore in the shelf below wave base zone (see Fig. 13).

This model also appears to confirm the Early Permian Asselian to Sakmarian depositional model of northern Yukon Territory proposed by Bamber (*in* Bamber and Waterhouse, 1971) (see Fig. 14). The *Rhynchopora magna* Paleocommunity is restricted to the Peel River area, where shallow-marine carbonates, dolomitic in places, and fine grained terrigenous clastics were accumulated during the Asselian and Sakmarian. In the northern Richardson and northern Ogilvie mountains, Early Permian deposition was characterized by coarse terrigenous sediments and skeletal carbonates containing abundant organic material. This indicates open marine, moderately high energy conditions in these areas. To the south of Ettrain and Jungle creeks, there was deeper water deposition, as indicated by the presence of fine grained limestone and mudstone.

Profile	Subtidal	Sea level	Open marine shelf	Wave base
ENERGY	Low, restricted	High, above wave base	Moderately high, near wave base	Low, below wave base
PRINCIPAL SEDIMENT TYPE	Dolomitic mudstone, dolomitic limestone, calcareous siltstone	Sandstone, siltstone with abundant skeletal material	Calcareous siltstone and mudstone	Mudstone, siltstone and shale
COMMUNITY	*Rynchopora magna* Paleocommunity	*Fimbrinia-Tubersulculus -Kutorginella* Paleocommunity	*Ogilviecoelia inflata* Paleocommunity	*Tityrophoria nelsoni-Septacamera triangulata* Paleocommunity
BRACHIOPOD ZONE	Ey	Ey and Ej	Eog	Mainly Ej

Figure 13. *Inferred depositional environment of the upper Jungle Creek Formation and position of paleocommunities.*

SYSTEMATIC PALEONTOLOGY

Introduction

Classification

Unless otherwise discussed, the present classification of brachiopods above the generic level follows that of Muir-Wood and Cooper (1960), Cooper and Grant (1974, 1975, 1976a, b), Waterhouse (1968a, 1987a; *in* Waterhouse and Briggs, 1986), and Ivanova (1972). New subclasses proposed by Afanas'yeva and Dagys (1989) and Lazarev (1987) are not adopted here because they are not consistent with phylogenetic relationships. For instance, Afanas'yeva and Dagys classed the Rhynchonellida Kuhn with the Orthida Schuchert and Cooper and the Pentamerida Schuchert and Cooper under Subclass Orthata. But phylogenetic studies by Williams and Hurst (1977) and Carlson (1990) have suggested that the rhynchonellids might be more closely related to spiriferids as both are characterized by the reversal of mantle rudiment during larval growth.

Classification of bivalves follows Waterhouse (1982b); and the classification of an ammonoid species follows Nassichuk (1971).

Terminology

The terminology used for brachiopods largely follows Williams and Rowell (1965), but adopts some other concepts created by Brown (1952; *adminicula*), Waterhouse (1968a; *tabellae*), and Cooper and Grant (1974, p. 258–259; *dentifer* and *erismata*). We prefer the term *fold*, as commonly used, over *fastigium* of Cooper and Grant (1976a, p. 2173) in describing spiriferids. In addition, we have employed the term *geniculation angle*, in describing some productids, to denote an angle of bending of the trail away from its growth plane (Fig. 29B). This term may be applied to both ventral and dorsal valves. The smaller the angle, the more strongly (narrowly) geniculated the trails (or valves). The terminology used for molluscs largely follows that of Cox et al. (1969).

Synonymy and diagnosis

The generally accepted synonymies of genera and the diagnoses of well known genera have been omitted. References are made to diagnoses available from the literature for some of the genera in this study. In these cases, the main interest is obviously on the Yukon species of well known genera. The opportunity to

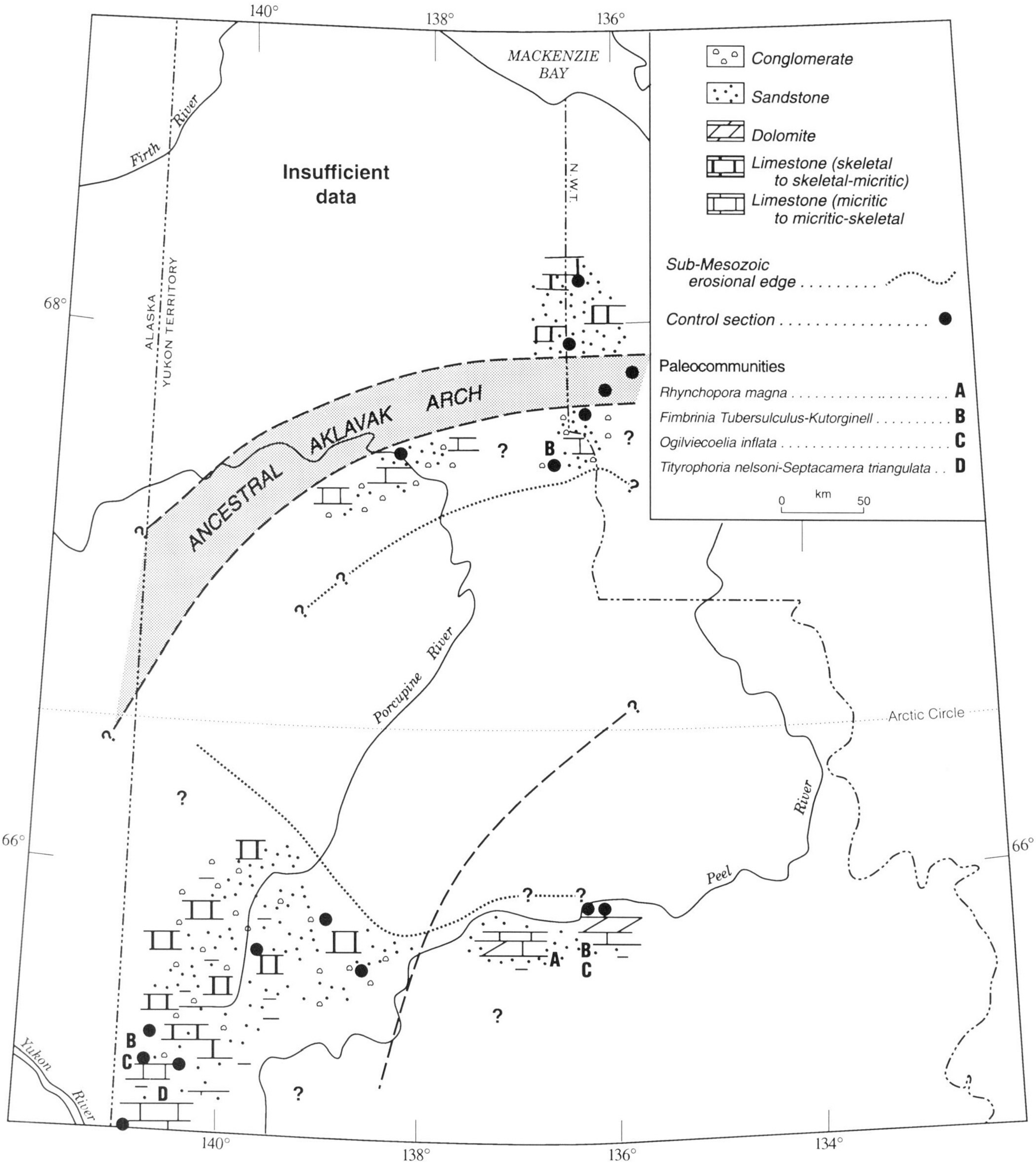


Figure 14. *Depositional facies of the Early Permian (Asselian to Sakmarian) Jungle Creek Formation (Bamber and Waterhouse, 1971). Plotting the paleocommunities on the map reveals good agreement between the inferred depositional environment (see Fig. 13) based on paleocommunities and differentiation of the depositional facies.*

provide first-time English translations of several significant Russian genera was taken.

Material and occurrences

All specimens from the study area examined in the present work are listed under *Material*, the basis for the present species descriptions. Number of specimens in the material tables refer to exterior specimens, unless otherwise specified as follows: *im*–internal mould; *em*–external mould. Previously reported material considered conspecific with Yukon species, from the Yukon or outside the Yukon, is listed under *Occurrences*. Some species, unidentifiable because of incomplete and poor preservation and/or lack of sufficient material, are discussed under *Remarks*.

Preservation

Much of the material examined is moderately well preserved; nearly half of the specimens occur as natural internal or external moulds with the shell leached out by weathering, and the rest occur as calcareous shells; very few are silicified. Specimens occur in a variety of rocks ranging from limestone through calcareous siltstone, sandstone, and minor conglomerate. The natural moulds are commonly associated with sandstone and siltstone, like those from JBW locs. 88, 89, and 109. Limestone, mudstone, and calcareous siltstone have usually yielded external moulds, like those from GSC locs. 53712, 53714, and 56922.

Measurements and quantitative approaches

Dimensions are given for a small number of relatively complete, well preserved specimens, and the following abbreviations:

VEN - ventral valve
DOR - dorsal valve
CON - conjoined shell
DIM - dorsal internal mould.

Using quantitative analysis to examine the variations of species from a single or various localities and phyletic relationships between allied species or genera, as demonstrated by Temple (1987) and Shi and Waterhouse (1990a), was not applicable in this study, because most species are represented by few, inadequately preserved specimens. However, attempts have been made to plot some measurements in graphs where it is possible to compare specimens or species.

Repository

All figured specimens and most measured specimens are registered by the prefix GSC and deposited in the type collections of the Geological Survey of Canada, Ottawa. References are also made to specimens with prefixes shown below. The institution in which these specimens are housed are as follows:

CNIGR - Catalogue of Monographic Palaeontology Collection, St. Petersburg (Chernyshev Museum), Russia.

CNPM - Geological Museum of the Central Scientific Naturalists Museum in Kiev, Ukraine.

CPC - Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Geology and Geophysics, Canberra.

PIN - Palaeontology Institute, Russian Academy of Science, Moscow, Russia.

QM - Queensland Museum, Brisbane, Australia.

SME - Sedgwick Museum, Cambridge, London, England.

UA - University of Alberta, Edmonton, Alberta, Canada.

UQF - University of Queensland Geology Museum Fossil Collection, Brisbane, Australia.

USNM - U.S. National Museum of Natural History, Washington, D.C., United States.

SYSTEMATIC DESCRIPTIONS

Phylum BRACHIOPODA

Class INARTICULATA Huxley, 1869

Order ACROTRETIDA Kuhn, 1949

Suborder ACROTRETIDINA Kuhn, 1949

Superfamily DISCINACEA Gray, 1949

Family DISCINIDAE Gray, 1949

Subfamily ORBICULOIDEINAE Schuchert and LeVene, 1929

Genus *Orbiculoidea* d'Orbigny, 1847

Type species. (SD by ICZN, 1965). *Orbicula forbesi* Davidson, 1848.

Orbiculoidea sp.

Plate 1, figure 1

Remarks. One dorsal exterior from GSC loc. 53714. It is small, about 8 mm in diameter and 3 mm in height; circular and asymmetrical in outline; apex slightly posteriorly placed with gentle anterior slope and steeper posterior slope. Concentric growth lines obscure.

Occurrence. Ey zone, Tastubian.

Class ARTICULATA Huxley, 1869

Order RHIPIDOMELLIDA Cooper and Grant, 1976

Superfamily ENTELETACEA Waagen, 1884

Family SCHIZOPHORIIDAE Schuchert and LeVene, 1929

Genus *Orthotichia* Hall and Clarke, 1892

Type species. (OD) *Orthis*? *morganiana* Derby (1874).

Diagnosis. Large schizophoriinid shell distinguished by possessing relatively long, thin adminicula in ventral interior, and bitruncate vascular media in dorsal interior.

Discussion. The distinguishing criteria of high, thin adminicula and long ventral median septum between *Orthotichia* and *Schizophoria* King, 1850, were not recognized by Dunbar and Condra (1932) and Lazarev (1969). Lazarev (1969, 1976b) stressed that a distinction of greater taxonomic significance lay in the vascular system of the dorsal interior between the two genera: *Orthotichia* is characterized by bitruncate vascular media, whereas *Schizophoria* has quadri-truncate vascular media.

Orthotichia morganiana (Derby, 1874)

Plate 1, figures 2–18

1874 *Orthis*? *morganiana* Derby, p. 29, Pl. 3, figs. 1–9, 11, 34; Pl. 4, figs. 6, 14, 15.
1902 *Orthotichia morgani* (Derby); Chernyshev, p. 594, Pl. 26, figs. 8–10; Pl. 48, figs. 1–3.
1914 *Orthotichia morganiana* (Derby); Kozlowski, p. 62, Pl. 3, figs. 11, 12.
1925 *Orthotichia morganiana* (Derby); Reed, p. 76, Pl. 3, fig. 7.
1927b *Orthotichia morganiana* (Derby); Chao, p. 99, Pl. 1, fig. 2; Pl. 2, figs. 2a–c, 3a–d.
1934 *Orthotichia morganiana* (Derby); Grabau, p. 9, Pl. 1, fig. 4.
1954 *Orthotichia morganiana* (Derby); Dresser, p. 24, Pl. 1, figs. 8–11, 13.
1969 *Orthotichia morganiana* (Derby); Lazarev, p. 211, Pl. 10, figs. 6–12; Figure 3a–f.
1971 *Orthotichia* sp. Waterhouse *in* Bamber and Waterhouse, Pl. 13, fig. 1.
1976 *Orthotichia morganiana* (Derby); Li and Gu, p. 230, Pl. 151, fig. 3.
1985 *Orthotichia morganiana* (Derby); Dong and Li *in* Ding et al., p. 101, Pl. 32, figs. 1–3.

Lectotype (here selected). A specimen with valves conjoined figured by Derby (1874) in Plate 4, figure 6 from the Upper Carboniferous Itaituba Formation at Bomjardim, Brazil, kept at Cornell University, Ithaca, New York.

Diagnosis. Moderately large, subrounded shell with low anterior sulcus and fine uninterrupted costellae; hinge line 0.6 to 0.8 of shell width; ventral median septum extending slightly beyond adminicula; socket plates long, anteriorly surrounding muscle field.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53857		1	1
GSC loc. 53946	5	2	
JBW loc. 24	2	3	
JBW loc. 89	2(im)		
JBW loc. 590	2, 1(im)	3, 1(em)	1

Description. External. Shell medium to large, subrounded to subtriangular outline; anterior commissure uniplicate; widest at, or just in front of, midlength.

Ventral valve resupinate: posterior half moderately to strongly inflated with low, massive, moderately incurved umbo; anterior part flatly convex to broadly concave, bearing shallow, broad median depression at maturity; umbonal slopes straight to gently concave in outline, gently convex in section; umbonal angle approximately 20°; interarea small, triangular; delthyrium proportionally large, open, with delthyrial angle close to 25°; hinge line 0.6 to 0.8 of shell width; cardinal extremities broadly rounded at about 110°. Costellae distinct, not interrupted by pits or tubercles, four costellae in 1 mm at 10 mm from umbo, increasing anteriorly by intercalation; concentric growth ornament poorly developed, occasionally visible on umbonal region.

Dorsal valve slightly more strongly and evenly convex than ventral valve, no prominent median fold; umbonal region swollen with high straight or gently concave slopes, umbo apparently incurved with umbonal angle of about 100°. Dorsal ornament similar to that on ventral valve.

Internal. Teeth strong at frontal edges of delthyrium, supported by large, prominent dental plates, which in turn are supported by long, thin adminicula (Pl. 1, fig. 5); adminicula diverging forward by about 15°, at least twice as long as dental plates, with anterior ends curving slightly inward, delimiting muscle field; median septum well formed, extending almost to midlength, 3 mm beyond anterior end of adminicula in mature specimens, rising to sharp elevated point at anterior extremity; muscle field elongate-oval in shape; adductor imprints obscure, medianly located each side of median septum (Pl. 1, fig. 5); diductor scars relatively large, marked by faint radial ridges and grooves.

Cardinal process consists of three separate nodes (Pl. 1, fig. 11), each finely pitted; dental sockets small, roofed apically by interarea; brachiophores large, projecting forward prominently (Pl. 1, fig. 17), supported by thick, high, long brachiophore bases which reach valve floor and extend anteriorly as low ridges around muscle field; dorsal muscle field well impressed, large, about 25 mm long and wide, occupying posterior half to two thirds of valve floor, elongate-oval in shape (Pl. 1, figs. 16, 17); anterior adductors medianly divided by low median ridge (myophragm); obliquely behind these scars and separated from them by low but prominent ridges are a pair of small, normally elongate, slightly depressed posterior adductor scars, each may be further divided by rather faint ridge in some specimens (Pl. 1, figs. 16, 17); bitruncate media located in front of muscle field (Pl. 1, fig. 12), distinct, each sometimes marked by fine radial grooves and ridges; vascular myaria broad, surrounding muscle field, weakly pitted or grooved (Pl. 1, fig. 12).

Dimensions (in mm).

Specimen	Valve	Length	Width	Height
GSC 96849	CON	38	28	27
GSC 96856	VIM	+25	32	—

Comparisons. The Yukon material appears conspecific with *Orthotichia morganiana* (Derby). Though this species is variable in its proportions, the slightly uniplicate anterior commissure, very broad, gentle sulcus, subrounded to slightly elongate outline, fine, usually uninterrupted costellae, and the absence of a prominent fold are relatively consistent characteristics that distinguish it from other representatives of *Orthotichia*.

Orthotichia javanapheti Yanagida (1964, p. 17, Pl. 2, figs. 2–4) from the Lower Kungurian Rat Buri Limestone of central Thailand may be related in overall ornamentation and appearance, but differs greatly in having a very narrow hinge line that results in a narrower umbo, and in having more divergent adminicula and a very long ventral median septum that extends well into the anterior third of the valve length. Specimens with frequently pitted costellae also from the Kungurian Rat Buri Limestone were assigned to *O. waterhousei* Grant (1976, p. 35, Pl. 2, figs. 16–21, 29–30, 22–28). In addition to its distinctively pitted costellae, *O. waterhousei* may be further distinguished by its very divergent adminicula and shorter socket plates.

Orthotichia chekiangensis Chao (1927b, p. 102, 103, Pl. 2, fig. 1) from the Sakmarian Liangshan Formation in south and southwest China, also recorded by Chang (1987, p. 755, Pl. 1, figs. 1-3), is comparable in overall appearance, but distinguished by its greater ventral convexity coupled with lateral compression, a prominent median fold at the dorsal anterior, and coarser costellae with a tendency toward "the development of faint and indefinite costation" (Chao, 1927b, p. 109).

Occurrence. Waterhouse (*in* Bamber and Waterhouse, 1971) figured a ventral valve from GSC loc. 53857 in the northern Richardson Mountains. Outside the Yukon Territory, *Orthotichia morganiana* has been found from the Upper Carboniferous Itaituba Formation (Mendes, 1961) in Brazil; the Asselian Copacabana Formation in Peru and Bolivia; the Sakmarian to Artinskian lower Qixia Formation in south China and the probably Upper Artinskian Zhesi Formation in northeast China; the Upper Carboniferous to Lower Permian beds in Pamirs and Chitral of west Karakorum; and the Gshelian (Late Carboniferous) to Sakmarian stages in the Urals and the Russian Platform. This indicates a widespread, long-ranging species, which we have not been able to subdivide from available data.

Order STROPHOMENIDA Öpik, 1934

Suborder ORTHOTETIDINA Waagen, 1884

Superfamily DERBYIACEA Stehli, 1954

Family STREPTORHYNCHIDAE Stehli, 1954

Genus *Arctitreta* Whitfield, 1908

Type species. (OD) *Arctitreta pearyi* Whitfield (1908).

Diagnosis. Triangular to ovate streptorhynchid with low dental plates, which may posteriorly reach valve floor through umbonal thickening; no ventral median septum. Dorsal interior with bilobate cardinal process and short recurved crural plates.

Discussion. Stehli and Grant (1971) and Manankov (1979b) have rejected the proposal of *Grumantia* Ustritskiy (*in* Ustritskiy and Chernyak, 1963, p. 70). Waterhouse (1982a), however, tentatively used *Grumantia* and noted that it could be a junior synonym of *Arctitreta*. Clarke (1990) used *Grumantia*. Examination of hypotypes of *Streptorhynchus kempei* Anderson (Wiman, 1914), and the type species of *Grumantia*, from the Assistance Formation on Devon Island (GSC loc. 26406) (see Harker and Thorsteinsson, 1960) shows variably developed low dental ridges, which posteriorly reach the valve floor of the heavily thickened umbonal cavity. It is difficult to objectively justify separation of the two taxa.

Taimyropsis Ustritskiy (*in* Ustritskiy and Cherynak, 1963, p. 69) is distinguished by possessing parallel dental plates that reach the valve floor.

Arctitreta peelensis n. sp.

Plate 1, figures 19–24; Figure 15

Etymology. Named from Peel River, Yukon Territory.

Holotype. GSC 96860 from GSC loc. 53713, section 116H-1A, Peel River, Plate 1, figure 23.

Diagnosis. Medium-sized, elongate-triangular shell with small, but distinctively impressed, ventral muscle field; 15 costellae in 5 mm over dorsal umbo, little differentiated.

Material. One ventral internal mould and one dorsal valve from GSC loc. 53703; one conjoined shell from GSC loc. 53713; one ventral internal mould and two dorsal valves from GSC loc. 56942.

Description. External. Shell of average size for genus, elongate-triangular in outline, widest at anterior third of shell length.

Ventral valve gently convex in umbonal region, anteriorly flatly convex or flattened; umbo prominent, suberect and slightly distorted; umbonal slopes slightly swollen with posterior margins diverging forward approximately at 117°; hinge line narrow with cardinal extremities bluntly rounded at 145° (Pl. 1, fig. 23); anterior and lateral margins broadly rounded; interarea apsacline, flat, triangular in shape, 25 mm wide and 12 mm high in holotype; delthyrium narrow with

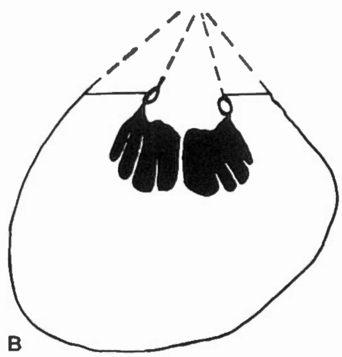


Figure 15. Arctitreta peelensis n. sp. ***A***, transverse serial sections of ventral valve (x1). ***B***, ventral muscle field (GSC 96863, x1). The measurements refer to distance from ventral umbo.

delthyrial angle of 25°, posterior two thirds covered by distinct pseudodeltidium made up of convex growth laminae (Pl. 1, fig. 23); perideltidium obscure; no sulcus. Ventral ornament poorly preserved.

Dorsal valve conspicuously more convex than opposite valve (Pl. 1, fig. 19), subrounded in outline. Fine costellae numerous (Pl. 1, fig. 19), 15 costellae in 5 mm near umbo, anteriorly increasing by intercalation, little differentiated, separated by slightly narrower interspaces, crossed by very fine growth increments; five to six broad, concentric lamellae over anterior portion.

Shell pseudopunctate; pseudopunctae typical of the *Arctitreta–Streptorhynchus* type (Manakov, 1979a), appearing as pits on the inner sides of valves, preserved on internal moulds as small tubercles arranged in regular radial rows along interspaces separating costellae, seven costellae in 1 mm anteriorly (Pl. 1, fig. 24).

Internal. Teeth sturdy, supported by low dental ridges below delthyrium (Fig. 15); dental ridges may reach valve floor posteriorly, but are obscured by posterior shell thickening; muscle field small, well impressed, extending over posterior third of shell length, elongate-oval in shape, outlined by slightly raised ridges, of which the median ridge is usually the strongest (Pl. 1, figs. 20–22).

Dimensions (in mm).

Specimens	Valve	Length	Width	Height	Muscle Field	
					Length	Width
GSC 96860	CON	35	32	20	—	—
GSC 96861	VEN	30	28	+10	—	—
GSC 96862	VIM	36	40	—	15	12
GSC 96863	VIM	+40	42	—	12	11

Comparisons. The Yukon species differs from *Arctitreta pearyi* Whitfield (1908, p. 57, Pl. 2, figs. 1–4) from the Kungurian beds of Ellesmere Island in being smaller and having finer costellae.

Three other species from the Permian of the Arctic have been reported (Manakov, 1979b): *A. triangularis* (Wiman, 1914, p. 55, Pl. 10, figs. 1–19, 28, 29), *A. kempei* (Anderson) of Wiman (1914, p. 58, Pl. 10, figs. 22–27; Pl. 11, figs. 1–10; Pl. 12, figs. 1–8; Pl. 13, figs. 11–13), and *A. macrocardinalis* (Toula, 1875, p. 253, Pl. 8, fig. 5; Wiman, 1914, p. 56, Pl. 9, figs. 1–23; Pl. 10, figs. 20, 21), all originally described from the Kungurian lower Kapp Starostin Formation in Spitsbergen. The first two also occur in correlative beds of the Assistance Formation of the Canadian Arctic Archipelago (Harker and Thorsteinsson, 1960). *A. kempei* and *A. macrocardinalis* are less elongate in outline than the present species and have a much larger muscle field occupying two thirds or more of the ventral valve floor. *Arctitreta triangularis* differs in having a narrower interarea, smaller size, and a larger muscle field, though it is close in outline.

Arctitreta percostata Waterhouse (1982c, p. 341, Pl. 1, figs. 1–7; Fig. 4a) from the Upper Asselian or possibly Lower Sakmarian pebbly mudstone of the Phuket Group in south Thailand approaches the Yukon species in shape and size, but differs in having a feeble sulcus on both valves and well differentiated costellae. *Arctitreta bapensis* Waterhouse and Rao [1989, p. 26, Fig. 3(1–4)] from the Asselian Bap Formation of Peninsula, India is also similar in size but distinguished by its broader umbo and coarser costellae, which number 10–12 in 5 mm.

Occurrence. Ey zone, Tastubian.

Superfamily ORTHOTETACEA Waagen, 1884

Family ORTHOTETIDAE Waagen, 1884

Subfamily ORTHOTETINAE Waagen, 1884

Genus *Orthotetes* Fischer de Waldheim, 1829

Type species. (SD by Girty, 1908, p. 86) *Orthotetes radiata* Fischer de Waldheim, 1850.

Diagnosis. Moderate to large biconvex to resupinate shells, finely costellate; dental plates well developed, apically convergent and meeting through secondary shell thickening at posterior edge of median septum, defining a small, very posteriorly placed secondary spondylium. Cardinal process with two low, separate lobes, quadrilobate in posterior view; crural plates low and short, recurved toward hinge margin, forming cup-like sockets; dentifers usually weakly developed.

Discussion. The above diagnosis is translated and reworded from that of Manakov (1979b), who draw attention to the secondary nature of the spondylium in *Orthotetes*.

Comparisons of internal structures between *Orthotetes*, *Derbyia* Waagen (1884), type species *D. regularis* Waagen, *Tethoretes* Manakov (1979b), type species *Derbyia grandis* (not Waagen) Sokolskaya, and *Permorthotetes* Thomas (1958) with type species *P. callytharraensis* Thomas, are shown in Figure 16.

Derbyia and *Tethoretes* have distinct erismata and hence are readily distinguished from *Orthotetes*.

Relationships between *Orthotetes* and *Permorthotetes* remain to be clarified. The latter was proposed by Thomas (1958) for a Permian group of Western Australian species said to possess a secondary spondylium and recurved crural plates, distinct from what was believed to be the primary spondylium of *Orthotetes*. Archbold (1990) used *Permorthotetes*. Cooper and Grant (1974) considered that a "minute" primary spondylium was present in the very early stages of *Orthotetes*, and stressed that "The so-called spondylium in *Permorthotetes* appears to be a secondary structure and the genus is a valid separation from *Orthotetes*, . . ." (Cooper and Grant, 1974, p. 258). Re-examination of *Orthotetes radiata* by Manakov (1973, 1979b), however, failed to reveal the minute primary spondylium in *Orthotetes*, and instead Manakov emphasized that the spondylium in *Orthotetes* was also of secondary origin (Fig. 16A). This confirms the observation by Sokolskaya (1954), who stated that the spondylium in *Orthotetes* could be obliterated by growth of shell callus. Thus, if Manakov's indication of a secondary spondylium in *Orthotetes* is accepted, *Permorthotetes* appears to be a subjective junior synonym of *Orthotetes*, in agreement with Manakov (1979b).

Orthotetes canadensis n. sp.

Plate 2, figures 1-10; Plate 3, figures 1-9, 11

Etymology. After Canada.

Holotype. GSC 96877 from JBW loc. 109, Ettrain Creek, northern Ogilvie Mountains, Plate 2, figure 9.

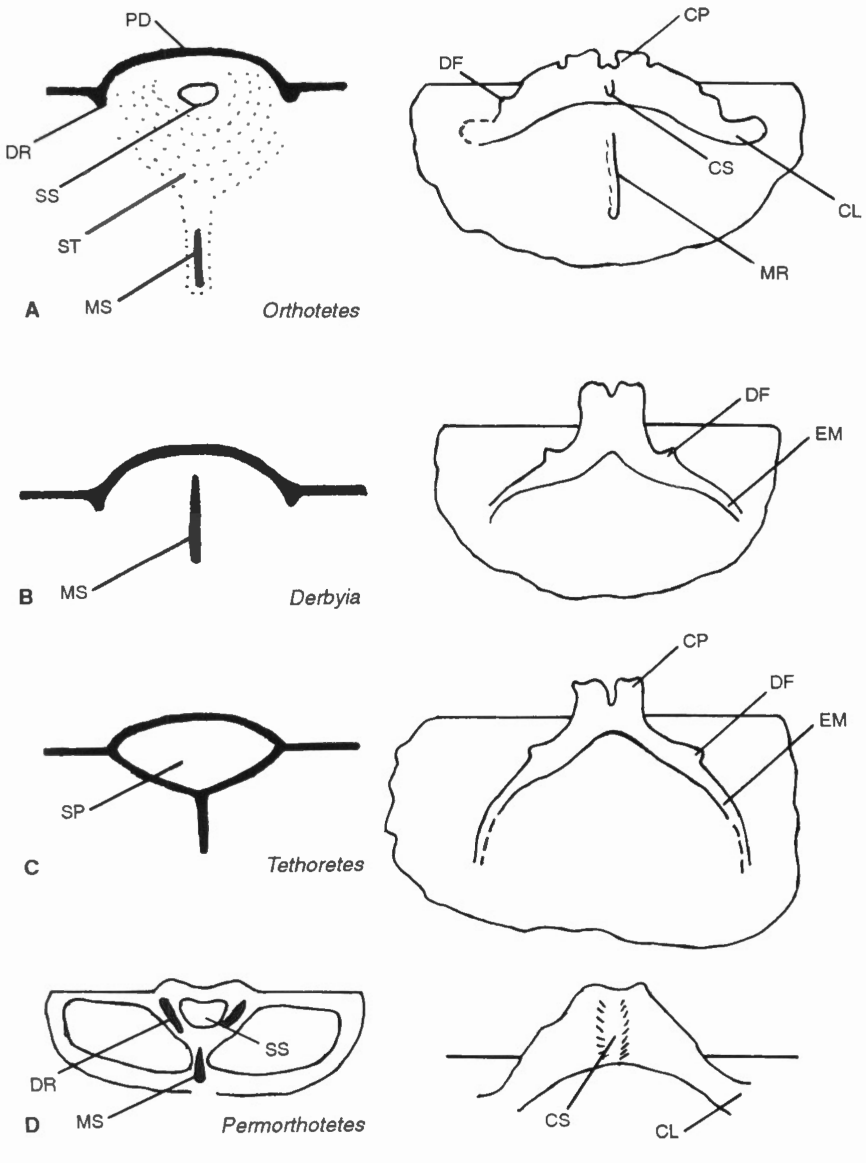


Figure 16. *Comparison of internal structures between* ***Orthotetes, Derbyia, Tethoretes,*** *and* ***Permorthotetes.*** *(A and B after Manakov, 1979b; C drawn from data provided by Manakov, 1979b, p. 50, Fig. 20, and Sokolskaya, 1968, Figs. 9, 10; D after Thomas, 1958). CP, crural plate; CS, carina; DF, dentifer; DR, dental ridge; EM, erismata; MR, median ridge; MS, median septum; PD, pseudodeltidium; SP, spondylium; SS, secondary spondylium; ST, secondary thickening. (All approx. x1).*

Diagnosis. Large, subrounded shell with flatly convex ventral valve and strongly inflated dorsal valve; maximum width placed slightly in front of hinge line; seven to eight costellae in 5 mm at midlength of both valves; no sulcus or fold at maturity.

Material.

Locality	Ventral	Dorsal
GSC loc. 53710		1(im)
GSC loc. 53714		1(im)
GSC loc. 53859		1
GSC loc. 53947	1(em)	1
GSC loc. 56922		1(im)
GSC loc. 56942		2
JBW loc. 24		1(em)
JBW loc. 58		1
JBW loc. 88	2(im)	5(im), 3(em)
JBW loc. 109	1(em)	4, 2(im)
JBW loc. 113		1(em)
JBW loc. 537		1(em)
JBW loc. 545	1(em)	
JBW loc. 546		1

Description. External. Shell of large size at maturity; subrounded to slightly transverse in outline, slightly wider than long (Pl. 2, fig. 9); maximum width just in front of hinge line.

Ventral valve flatly convex; umbo small and low (Pl. 3, fig. 5), moderately swollen, slightly distorted, suberect, well demarcated from rest of valve; interarea broad and low (Pl. 3, fig. 7); umbonal angle 160°; delthyrium narrow, delthyrial angle at 16° measured from apex, entirely covered by strongly convex, pseudodeltidium with median groove; perideltidial plates obscure; hinge line normally 0.75 of shell width; cardinal extremities bluntly rounded at 110° to 130°; no sulcus at maturity, immature specimens have gentle anterior deflection at margin. Costellae uniform in most specimens, slightly to moderately differentiated in others (Pl. 3, fig. 5), increasing by frequent intercalation, generally 7 to 8 costellae in 5 mm over midlength of both valves, seven to eight in 5 mm near anterior margin, narrowly rounded on crests, separated by narrow interspaces. Micro-ornament of rather fine growth increments (Pl. 3, fig. 11), four to five in 1 mm, crossing straight over costellae; about five concentric rugae low and broad, 4 to 5 mm apart (Pl. 3, fig. 5).

Dorsal valve much more inflated than ventral valve (Pl. 2, fig. 8), approximately equally arched in both longitudinal and transverse directions; umbonal region flattened; no distinct sulcus or fold except for very gentle median depression observed from one small, probably immature, specimen GSC 96868 (Pl. 3, fig. 4) (possibly formed by crushing); anterior commissure rectimarginate in large specimens. Dorsal ornament similar to that on ventral valve but rugae indistinct.

Internal. Spondylium observed only from internal moulds (Pl. 3, figs. 2, 3), very small, about 2 mm in diameter, located just below apex of delthyrium, supported by prominent median septum 1 mm across, which extends over posterior quarter of valve length (Pl. 3, figs. 2, 3); muscle field obscure.

Dorsal interior with low, broad cardinalia (Pl. 2, figs. 1-3); cardinal process bifid with two completely separate lobes, each divided by fine median groove on dorsal face, so that cardinal process is quadrilobate in dorsal view (Pl. 3, figs. 6, 8), sometimes bearing carina (cardinal crest); crural plates low and short, anterior ends recurved toward hinge margin to form cup-like sockets overhanging muscle field in small, probably immature, specimens (Pl. 2, fig. 2); dentifers low, ill-defined in most specimens, extending from base of cardinal process forward along crural plates for two thirds of the latter (Pl. 3, fig. 6); muscle field very weakly impressed without raised muscle ridges in small specimens (Pl. 2, fig. 1), but distinctively depressed in mature specimens with prominent surrounding ridges and low median ridge (Pl. 2, fig. 3).

Dimensions (in mm).

Specimens	Valve	Length	Width	Height	Hinge width
GSC 96864	DIM	52	60	?12	?40
GSC 96867	DIM	37	50	6	42
GSC 96868	DIM	30	50	—	44
GSC 96872	DIM	50	68	13	55
GSC 96875	DOR	75	80	26	60
GSC 96876	DIM	55	72	18	60
GSC 96877	DIM	60	76	21	64
GSC 96881	DIM	+50	80	—	+65

Comparisons. *Orthotetes* aff. *O. regularis* (Waagen) Ustritskiy (1960, p. 99, Pl. 1, fig. 13; Pl. 2, figs. 1-5) from the Baigendzinian to Kungurian Talatin Suite of Pai Hoi Range, north Urals, appears to be related to the new species in many respects, but it was said to have a prominently sulcate dorsal valve. No prominent sulcus or fold is found in the dorsal valve of mature specimens of the Yukon species although the anterior commissure may be very gently deflected in some immature specimens. The Yukon valves are also more inflated. Type specimens of *Derbyia regularis* Waagen (1884, Pl. 53, figs. 1, 2, 4) from the Kungurian Wargal

Formation of the Salt Range in Pakistan is less convex than the Yukon material and has distinct erismata.

Orthotetes jugorica Ustritskiy (1960, p. 100, Pl. 2, figs. 6–8), from the Kungurian Vorkut Suite of the Pai Hoi Range, differs from the Yukon material in having a concave ventral valve, a slightly convex, sulcate dorsal valve, a very narrow visceral cavity, and a wide hinge margin representing the shell width.

Ustritskiy and Chernyak (1963, p. 70, Pl. 2, figs. 5–7) figured three specimens as *Orthotetes* ex. gr. *O. regularis* (Waagen). The one illustrated in Figure 5 from the Upper Carboniferous Makarov Horizon of central Taimyr is large, over 80 mm in width, and has six coarser costellae in 5 mm. The other two specimens from the Asselian to Sakmarian upper Turuzov Horizon of central Taimyr appear to be closer to some small shells of the Yukon species, but differ in possessing a distinct dorsal sulcus.

Occurrence. Ey and Eog zones, Sakmarian.

Order PRODUCTIDA Sarytcheva and Sokolskaya, 1959

Suborder CHONETIDINA Muir-Wood, 1955

Superfamily CHONETACEA Bronn, 1862

Family RUGOSOCHONETIDAE Muir-Wood, 1962

Subfamily SVALBARDIINAE Archbold, 1982

Genus *Komiella* Barchatova, 1970

Type species. (OD) *Chonetes omolonensis* Likharev (1934b).

Diagnosis. Small to medium-sized shells with transverse to rectangular outline; hinge line equal to, or slightly narrower than, maximum width, seldom drawn into sharp cardinal extremities; anterior commissure varying from rectimarginate to very gently dorsally deflected, sulcus and fold absent or ill defined; shell surface smooth, pseudocapillate when worn; pseudodeltidium prominent, chilidium absent or poorly defined. Ventral interior with prominent median septum extending well beyond midlength. Dorsal interior with excavated quadrilobate cardinal process; breviseptum reaching midlength or beyond it; lateral septa prominent; brachial ridges poorly developed or absent.

Discussion. This is the first diagnosis provided for the genus; it is based on the description and illustration of the type species given by Likharev (1934b), reinforced by observations from present Yukon material.

Komiella was created by Barchatova (1970, p. 62) in a footnote with reference to *Chonetes omolonensis* Likharev (1934b), a species that has long been interpreted as belonging to *Lissochonetes* Dunbar and Condra, 1932 (Sokolskaya, 1968; Zavodovskiy and Stepanov, 1970; Afanas'yeva, 1977, 1988). The genus was recognized by Sarytcheva (1974) and Archbold (1981a, 1982a).

Waterhouse (*in* Waterhouse and Briggs, 1986) discussed *Leurosina* Cooper and Grant (1975), *Lissochonetes* Dunbar and Condra (1932), and *Tivertonia* Archbold (1983a), and noted that they were all very similar. Shi and Waterhouse (1990a) statistically examined the phenetic relationship and differences among the three genera, as well as *Komiella*, and concluded that *Komiella omolonensis* (Likharev) and *Tivertonia yarrolensis* (Maxwell), type species of *Tivertonia*, were indistinguishable from *Leurosina marginata* Cooper and Grant, type species of *Leurosina*, in terms of the 16 characters examined. But the 16 characters may not have been statistically significant and other characters of generic significance may need to be evaluated. For instance, Dr. N.W. Archbold (pers. comm., 1989) pointed out that the nature of brachial ridges may prove to be significant. *Leurosina marginata* is characterized by possessing distinct brachial ridges with raised anterior recurved portions. *Tivertonia yarrolensis* seems to have variably developed brachial ridges; they are weakly impressed without prominent anterior recurved portions in the holotype UQF 43037, inspected at the Department of Geology, University of Queensland; and weakly to strongly developed with or without anterior recurved ridges (Archbold, 1983a, 1986; Waterhouse et al., 1983). What appears to be the main feature in distinguishing *Komiella omolonensis* from both *Leurosina marginata* and *Tivertonia yarrolensis* is the lack of, or very weak development of, brachial ridges. These ridges are not present in the reasonably well preserved dorsal interior originally figured by Likharev (1934b); nor are they known from specimens ascribed to *Lissochonetes omolonensis* by Afanas'yeva (1977) although these specimens may not be truly conspecific (see discussion below), nor are the ridges known from present material, which shows a dorsal median septum, lateral septa, and socket ridges. A dorsal internal mould figured as *Lissochonetes omolonensis* (Likharev) by Sokolskaya (1968) shows very weakly impressed brachial ridges without anterior recurved portions. There may be other subtle differences between *Komiella* and *Tivertonia*, which may be of little generic significance. For instance, Dr. N.W. Archbold (pers. comm., 1990) has pointed out that *Tivertonia yarrolensis* has an entirely rectimarginate anterior commissure, to be distinguished from the distinctively dorsally deflected anterior commissure of *Leurosina*. The anterior commissure of *Komiella omolonensis* from Yukon seems to vary from rectimarginate to very gently dorsally deflected.

Komiella is provisionally accepted here, but the nature of its brachial ridges needs to be investigated.

Leurosina, *Tivertonia*, and *Komiella* are clearly distinguished from *Lissochonetes* by having a hinge line usually narrower than maximum width, obtuse cardinal extremities, absence of distinct sulcus, and presence of a long, prominent dorsal median septum and lateral septa (Shi and Waterhouse, 1990a). Archbold (1981b) discussed the relationship and distinction between *Komiella* and *Svalbardia* Barchatova (1970).

Komiella omolonensis (Likharev, 1934b)

Plate 3, figures 12-23; Figure 17

1934b *Chonetes omolonensis* Likharev, p. 11, Pl. 9, figs. 1-3, 5-7.
1934b *Chonetes* aff. *C. omolonensis* Likharev, Pl. 9, fig. 4.
1946 *Chonetes omolonensis* Likharev; Einor, p. 15, Pl. 10, figs. 4-7.
1959 *Chonetes omolonensis* Likharev; Kashirtsev, p. 32, Pl. 21, figs. 1-6.
1968 *Lissochonetes omolonensis* (Likharev); Sokolskaya, p. 73, Pl. 4, figs. 25-30, Textfig. 18.
1970 *Lissochonetes omolonensis* (Likharev); Zavodovskiy and Stepanov, p. 75, Pl. 61, figs. 8-12, 19.

Diagnosis. Small, subrectangular shell with narrow hinge line and rectimarginate to gently dorsally deflected anterior commissure; ventral median septum thick and extending well into anterior third of shell

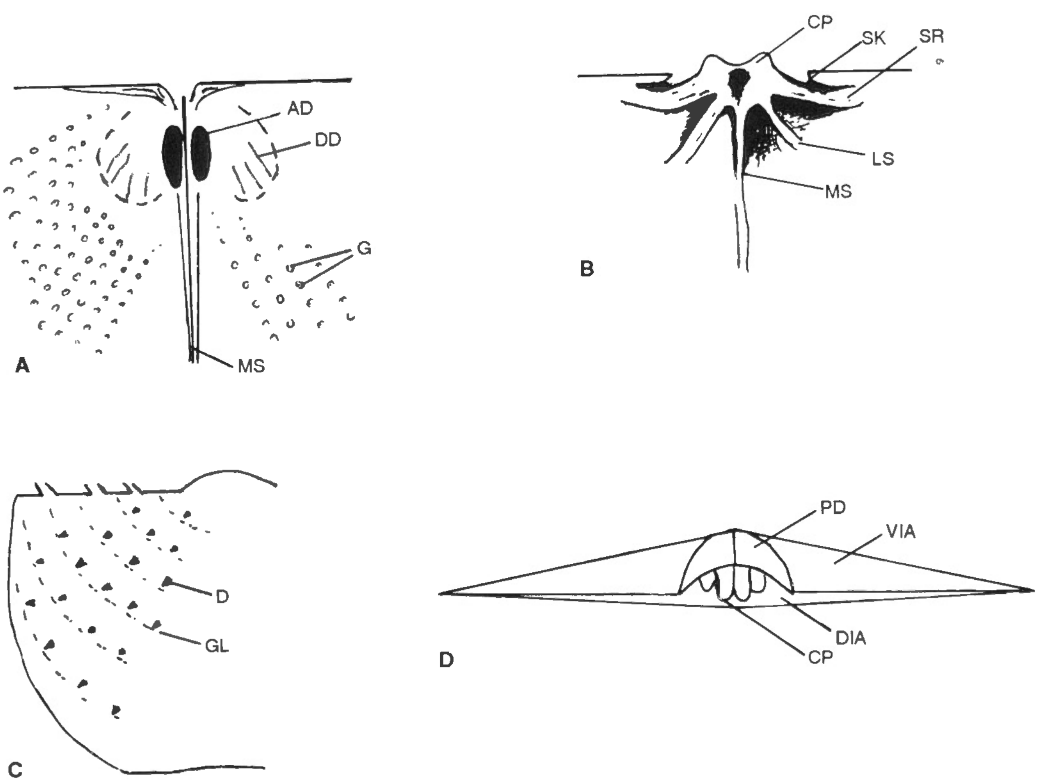


***Figure 17. Komiella omolonensis** (Likharev). A, ventral interior (GSC 96888); B, dorsal interior (GSC 96885); C, ventral surface (GSC 96890); D, posterior aspects of a conjoined specimen (GSC 96887). (All approx. x5). AD, adductor; CP, cardinal process; D, dimples; DD, diductor; DIA, dorsal interarea; G, granules (pseudopunctae); GL, growth lamellae; LS, lateral septum; MS, median septum; PD, pseudodeltidium; SK, socket; SR, socket ridge; VIA, ventral interarea.*

length; brachial ridges absent or very weakly developed.

Holotype. CNIGR Museum 4/10901 from the Lower Permian of the Kolyma-Omolon Massif, northeastern Siberia, figured by Likharev (1934b) in Plate 9, figure 3.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53703		1(im)	
GSC loc. 53705	1(im)		4
GSC loc. 53856	6	5	
GSC loc. 53955			16
JBW loc. 113			15

Description. External. Shell small, rectangular in outline, widest at, or in front of, hinge line; cardinal extremities bluntly rounded on average at 100°.

Ventral valve strongly convex, most inflated at midlength; umbo small, low; interarea low, about 1 mm in height; delthyrium covered by strongly convex pseudodeltidium (Pl. 3, fig. 15), semicircular in section; no sulcus except for very broad dorsal deflection along anterior commissure in some specimens (Pl. 3, figs. 13, 21, 22), others having rectimarginate anterior commissure. Surface smooth, no body spines, but pseudocapillate when worn (Pl. 3, fig. 16), correspond to radial arrangement of pseudopunctae; numerous dimples present, particularly on better preserved specimens from JBW loc. 113 (Fig. 17C), due to emergence of pseudopunctae (taleolae); growth lines numerous on all specimens, six to seven in 1 mm, better defined on specimens from JBW loc. 113, where broad growth lamellae are also developed (Fig. 17C), and may overlap near anterior margin; three to four hinge spines present on each side of umbo, projecting outward at about 40° angle to hinge margin (Pl. 3, fig. 23).

Dorsal valve deeply concave; chilidium either absent or extremely low. Dorsal ornament similar to that on ventral valve.

Internal. Visceral cavity narrow; shell thin, pseudopunctate, endopunctae expressed on inner surface of shell by numerous small granules arranged in radial rows on anterior and lateral portions, less frequent over umbonal floor (Fig. 17A; Pl. 3, figs. 17, 23).

Ventral interior with small blade-shaped teeth located at anterolateral edges of delthyrium (Pl. 3, fig. 17); median septum strong, about 1 to 2 mm in diameter, extending well into anterior third of shell length, tapering anteriorly; muscle field weakly impressed, adductor scars sited beside posterior part of median septum, narrow and elongate, slightly raised, smooth (Fig. 17A); diductors large, flabellate, smooth, or with few faint radial markings.

Dental sockets narrow, shallow, well defined by hinge and strong prosocket ridges (Fig. 17B) subparallel to hinge line and recurving toward it at anterior ends; cardinal process excavated, quadrilobate in posterior view with two high central lobes (Fig. 17D); breviseptum beginning from alveolus, thin, extending beyond midlength; lateral septa prominent, short, diverging from median septum at 20° to 30°; brachial ridges not observed.

Dimensions (in mm).

Specimen	Valve	Width	Length	Height	Hinge width	Cardinal angle
GSC 96883	VEN	18	12	5	18	85°
GSC 96884	VEN	15	10	3.5	15	?110°
GSC 96885	VEN	13	8.5	4.5	12	103°
GSC 96886	DIM	16	12	3.5	16	90°
GSC 96887	VEN	12	8.5	4.5	11	91°
GSC 96891	VIM	11	8	3	?10	—

Remarks and comparisons. Brachial ridges are not present in the only dorsal specimen from JBW loc. 113 available for the present study (Pl. 3, fig. 20), although impressions of a fine median septum and lateral septa are present. It is likely that the brachial ridges are either absent or very poorly defined. The dorsal interior of *K. omolonensis* originally figured by Likharev (1934b, Pl. 9, fig. 5) is better preserved than in this Yukon specimen, with details of septa and granules, but does not show brachial ridges. Afanas'yeva (1977, p. 22, Pl. 1, figs. 22–24, Textfigs. 15, 16) figured as *Lissochonetes omolonensis* (Likharev) three specimens from the Upper Carboniferous Magar Horizon of the Kolyma-Omolon Massif. These specimens are similar in size and shape to the type material of *K. omolonensis* and the Yukon hypotypes, and also lack observable brachial ridges, but differ in having a shorter ventral median septum.

Lissochonetes magnus Afanas'yeva (1977, p. 24, Pl. 2, figs. 7–9, Textfigs. 17, 18) from the Lower Permian of the Kolyma-Omolon Massif is generally close, and its brachial ridges are also unknown. It differs from *K. omolonensis* in being larger and semicircular in outline and having a narrower ventral median septum.

As indicated above, *Tivertonia yarrolensis* (Maxwell, 1964) appears to be related to *Komiella* in its overall shape and external morphology and internal structures. The Australian species is common in eastern Australian Sakmarian strata (Archbold, 1986), originally described from the Yarrol Formation, Yarrol Basin (Maxwell, 1964, p. 35, Pl. 6, figs. 9-14) and recently redescribed by Archbold (1983a, 1986) and Waterhouse et al. (1983). It is slightly larger than *K. omolonensis,* though sharing a similar outline, and usually has weakly to moderately developed brachial ridges and more numerous hinge spines (six to eight pairs). In addition, the Australian species appears to have an entirely rectimarginate anterior commissure and rare dimples on the surface.

Occurrence. Komiella omolonensis is present in the Ey and Ej zones in northern Yukon Territory. The species was originally described from Lower Permian strata outcropping along banks of the Omolon and Munugudjak rivers in the Kolyma-Omolon Massif, northeastern Siberia. The type specimens were refigured by Kashirtsev (1959), who also indicated an Early Permian age for the type locality, as did Afanas'yeva (1977). But Zavodovskiy and Stepanov (1970) cited the type material as coming from the Omolon Horizon of Ufimian age. This age assignment is much younger than that inferred from other occurrences of the species. *Komiella omolonensis* has also been found from the Lower Permian beds (no stratigraphic name provided) from the left bank of the Makarov River of west Taimyr (Einor, 1946), northern Russia, and from the Upper Carboniferous (Gshelian) to Lower Permian (Asselian) Kokpecten Complex of east Kazakhstan (Sokolskaya, 1968).

Genus *Dyoros* (*Dyoros*) Stehli, 1954

Type species. (OD) *Chonetes consanguineus* Girty, 1929.

Discussion. Cooper and Grant (1975) recognized three subgenera of *Dyoros* based on differences in shell outline and degree of the development of sulcus and fold. *Dyoros* (*Dyoros*) is distinguished from *Dyoros* (*Lissosia*) Cooper and Grant in having a distinct sulcus; and from *Dyoros* (*Tetragonetes*) Cooper and Grant in possessing a wider hinge line and alate ears.

Dyoros (*Dyoros*) *pseudotrapezoidalis*
(Miloradovich, 1949)

Plate 3, figure 10; Plate 4, figures 1-6; Figure 18

1902 *Chonetes trapezoidalis* (Waagen); Chernyshev, p. 595, Pl. 27, figs. 6-8.
1934 *Chonetes trapezoidalis* (Waagen); Stepanov, p. 11, Pl. 1, fig. 3.
1949 *Chonetella pseudotrapezoidalis* Miloradovich, p. 63.
1964 *Chonetina pseudotrapezoidalis* (Miloradovich); Mironova, p. 93, Pl. 1, figs. 1-3.
1972 *Dyoros*? *pseudotrapezoidalis* (Miloradovich); Ifanova, p. 100, Pl. 3, figs. 3-7.

Holotype. The ventral valve figured by Stepanov (1934) in Plate 1, figure 3 from the Sakmarian Bryozoa Limestone in Kolva River, north Urals, kept at the CNIGR Museum, Leningrad.

Diagnosis. Small with broad, deep sulcus; sulcal floor well rounded; ears alate.

Material.

Locality	Ventral	Dorsal
GSC loc. 56922	2	
GSC loc. 57141	2	
GSC loc. 57266	1	
JBW loc. 54		1 (juvenile)
JBW loc. 109	1	

Description. External. Shell small for genus, well preserved ventral valve measuring 17 mm wide, 8 mm long, and 3 mm high; transversely trapezoidal in outline with well extended hinge line and alate ears; widest along hinge margin.

Ventral valve moderately convex; umbo small and extended slightly beyond hinge line; umbonal slopes low and distinctively concave in outline; ears prominent, triangular in shape (Pl. 4, fig. 1), flatly

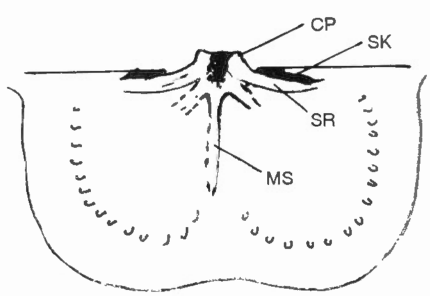


Figure 18. Dyoros (Dyoros) pseudotrapezoidalis *(Miloradovich), showing dorsal interior (drawn from a poorly preserved dorsal internal mould, approx. x6). Abbreviations as in Figure 17.*

convex, well demarcated from hump-shaped flanks; cardinal extremities moderately alate with angle between 40° and 60°; sulcus commencing at umbo with sulcal angle at 40° measured from umbo (Pl. 4, figs. 2, 4), widening and deepening forward, broadly V-shaped in section; flanks hump-shaped and broadly rounded on crests.

Dorsal valve moderately concave; visceral disc flattened, clearly separated from short, geniculate anterior portion; fold running from visceral disc to anterior margin, narrow and low.

Shell surface pseudocapillate when worn (Pl. 4, fig. 3); material too poorly preserved to show hinge spines.

Internal. Ventral interior with short median septum extending over posterior third of valve length (Pl. 4, fig. 6); muscle field obscure; shell pseudopunctate with floor covered by small granules, common over posterolateral parts, about two to three in 1 mm, arranged in irregular radial rows.

Dorsal interior poorly preserved in mature specimens, cardinal process low; prosocket ridges comparatively prominent, almost parallel to hinge line, enclosing elongate, deep sockets (Fig. 18); breviseptum low, extending a little beyond midlength, terminating in a small swelling; lateral septa short and thin, oblique to median septum at 20°; anterolateral and lateral margins of visceral region fringed by small, close-set granules.

Remarks and comparisons. The very small dorsal interior figured in Plate 3, figure 10 is considered to be an immature individual; it has a well developed fold but no median septum or brachial ridge. It is 7 mm wide and smaller than other material.

Miloradovich (1949) named *Chonetella pseudotrapezoidalis* for a specimen of *Chonetes trapezoidalis* (Waagen) described by Stepanov (1934) from the Sakmarian Bryozoa Limestone in Kolva River, north Urals. *Chonetes trapezoidalis* (Waagen, 1884, p. 623, Pl. 59, figs. 3, 4) from the Capitanian lower-middle Chhidru Formation of the Salt Range is distinguished by possessing a deeper, broader sulcus and a few broad, faint costae on flanks.

Dyoros was first correctly reported from Russia by Ifanova (1968), who described *Dyoros vorkutanus* Ifanova (1968, p. 321, Pl. 4, figs. 16–18) from the Lower Artinskian Gusin Suite of the Pechora Basin, northern Urals. The Pechora specimens are also small, like the Canadian form, but possess a very narrow, deep, trough-like sulcus. Internally, the dorsal median septum of *vorkutanus* is slightly shorter than that found in the Yukon material, and its fringe around the visceral region is more strongly defined, "like that of *Marginifera*" (Ifanova, 1968, p. 322).

Specimens figured as *Chonetina* cf. *C. timanica* (Chernyshev) by Harker (*in* Harker and Thorsteinsson, 1960, Pl. 17, fig. 7; Pl. 23, fig. 8) from the Lower Artinskian upper Belcher Channel Formation on Devon Island, Arctic Canada, appear to be very close in overall features, particularly in their wide hinge and pronounced sulcus, but may differ in being smaller and having a slightly narrower sulcus.

Occurrence. Dyoros (Dyoros) pseudotrapezoidalis is present in the Ey, Eog, and Ej zones in northern Yukon Territory. Elsewhere, this species is known from the Sakmarian Stage in the Urals and the Lower Artinskian (Aktastinian) Gusin Suite and the Upper Artinskian (Baigendzinian) to Kungurian Talatin Suite in the Pechora Basin, north Urals, according to Ifanova (1972) who figured specimens that are indistinguishable in the figures from the type.

Subfamily PLICOCHONETINAE Sokolskaya, 1960

Genus *Rugaria* Cooper and Grant, 1969

Type species. (OD) *Chonetes hessensis* King (1931).

Diagnosis. See Grant (1976, p. 71).

Discussion. Rugaria and allied genera have been discussed by Cooper and Grant (1975, p. 1295), Grant (1976, p. 71), and Waterhouse (1978, p. 60). Two south Asian genera are also related. *Waterhousiella* Archbold (1983a, p. 71) was proposed for *Waagenites speciosus* Waterhouse and Piyasin (1970) from the Lower Kungurian Rat Buri Limestone of Thailand; it is arguably distinguished from *Rugaria* by its conspicuous sulcus and fold, coarser and less fasciculate costae, and the presence of lateral septa in the dorsal interior. *Sulcirugaria* Waterhouse (1983a, p. 112) was diagnosed as having a distinct sulcus and fold and this distinguishes it from *Rugaria*.

Rugaria? sp.

Plate 4, figures 7, 8

Material. One ventral valve and one dorsal valve separated from the same shell from JBW loc. 109.

Description. External. Shell small, 15 mm wide, 6 mm long, and 5 mm high; transversely rectangular in outline; widest along hinge line; strongly concavo-convex, most inflated over posterior third of shell length; ears small; cardinal extremities laterally drawn out at 35°; anterolateral margins broadly rounded; sulcus and fold very weak, commencing from midlength; anterior commissure broadly and gently deflected in dorsal direction. Ventral interarea about 1 mm high; delthyrium small and open; two hinge spine bases observed at one side of umbo, projecting outward at about 30° to hinge. Costae start from umbo, 20 in total, with three simple median costae over feeble anterior sulcus and fold (Pl. 4, fig. 8), increasing anteriorly by bifurcation at varying distances from umbo, producing weakly fasciculate aspect, crossed by low growth increments.

Internal. Ventral interior poorly preserved; teeth large, triangular blade-shaped (Pl. 4, fig. 7); median ridge short and low; valve floor covered by granules, arranged in radial striations, approximately 3 to 4 per mm along striae.

Discussion. The species is very distinctive in its coarse, weakly fasciculate costae and gently dorsally deflected anterior commissure. No comparable species are known. It is distinguished from *Rugaria hessensis* (King) (Cooper and Grant, 1975, p. 1296, Pl. 496, figs. 18–25; Pl. 498, figs. 1–12; Pl. 499, figs. 70, 71) from the Artinskian Hess and Cathedral Mountain Formations of west Texas, U.S.A., by possessing a weak anterior ventral sulcus.

Afanas'yeva (1978) considered that *Rugaria* was confined to the paleotropical Tethyan region, but members of this genus have also been found in Nepal (Waterhouse, 1978), in strata reflecting warm temperate conditions (Waterhouse and Bonham-Carter, 1972, 1975). Present material suggests that this genus may also occur in the warm to cold temperate conditions of the northern Boreal Province.

Occurrence. Ey zone, Tastubian.

Suborder PRODUCTIDINA Waagen, 1883

Superfamily PRODUCTELLACEA Schuchert and LeVene, 1929

Family OVERTONIIDAE Muir-Wood and Cooper, 1960

Subfamily OVERTONIINAE Muir-Wood and Cooper, 1960

Genus *Fimbrinia* Cooper, 1972

Type species. (OD) *Overtonia plummeri* King, 1938.

Diagnosis. Small, suboval; hinge line generally narrower than maximum width; ventral ornament of broad concentric ridges, each bearing single row of stout, recumbent to suberect spines; dorsal valve strongly lamellose with small spines and dimples. Ventral adductors elongate, slightly raised; diductors weakly impressed. Cardinal process bilobate, resting on strongly thickened posterior platform; dorsal adductors posteriorly encircled by loop-shaped ridges; breviseptum short, not reaching midlength; brachial ridges run obliquely.

Discussion. The posterior platform of the dorsal valve in *Fimbrinia* is often complicated by the presence of a pair of curved ridges encircling the posterior parts of adductor scars (Pl. 4, fig. 20). The inner parts of the loop-shaped ridges, next to the breviseptum, converge medianly and look like buttress plates of buxtoniids; they either appear to join the base of the cardinal process to the posterior end of the breviseptum, encircling a V-shaped "antron" as seen in *F. transversa* n. sp. (Pl. 4, fig. 20); or they may be entirely independent from the breviseptum and are vertical and parallel with one another, as found in *F. plummeri* (Muir-Wood and Cooper, 1960, Pl. 46, figs. 8, 9). The inner parts were interpreted as the median extensions of cardinal ridges by Muir-Wood and Cooper (1960, p. 187). Cooper and Grant (1975, p. 964) described them as loop-shaped ridges surrounding the posterior edges of the adductors, independent of the cardinal ridges. The inner parts of the loop-shaped ridges appear to be highly variable in degree of convergence and in strength, even within a species; they are probably of little specific significance. The outer parts are also variable in development, indistinct in *F. plummeri*, but well defined in *F. ovata* Cooper and Grant (1975, Pl. 310, figs. 1–31) and *F. transversa* n. sp.

Fimbrinia transversa n. sp.

Plate 4, figures 9–20

1959 *Pustula cristatotuberculata* (Kozlowski); Kashirtsev, p. 38, Pl. 15, figs. 6, 7.
1960 *Pustula cristatotuberculata* (Kozlowski); Mironova, p. 35, Pl. 1, figs. 4, 5.
1963 *Overtonia cristatotuberculata* (Kozlowski); Ustritskiy and Chernyak, p. 77, Pl. 4, figs. 11, 12.
1970 *Fimbriaria cristatotuberculata* (Kozlowski);

Solomina, p. 79, Pl. 4, figs. 4, 5.
1970 *Fimbriaria cristatotuberculata* (Kozlowski); Zavodovskiy and Stepanov, Pl. 24, figs. 11, 17.

Etymology. Latin *transversus*, wide.

Holotype. GSC 97092 from GSC loc. 53720, section 116H-1B; Ey zone, Jungle Creek Formation, Plate 4, figures 11, 17.

Diagnosis. Comparatively large transverse *Fimbrinia* with large ears; ventral valve bearing moderately high concentric ridges and rounded to slightly elongate spine bases; dorsal valve strongly lamellose.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53703	1		
GSC loc. 53705	1		
GSC loc. 53720	3	5(em)	1
GSC loc. 53999	1		
GSC loc. 56917	4		
GSC loc. 56922	5		
GSC loc. 57053	6		
GSC loc. 57266	1		
JBW loc. 24		1(em)	
JBW loc. 58	1(em)		
JBW loc. 63	1(em)		
JBW loc. 88	13, 3(im)	5, 6(im)	2
JBW loc. 89	2(em), 1(im)		
JBW loc. 109	1(em)		

Description. External. Shell large for genus, up to 15 mm wide and 13 mm long; transverse in outline when well preserved (Pl. 4, figs. 11, 17); widest along hinge line.

Ventral valve strongly arched in profile (Pl. 4, fig. 16), most inflated at umbo, attenuated posteriorly, moderately to strongly convex in transverse direction with high, steep lateral slopes; umbo strongly incurved with beak extended beyond hinge line by about 2 to 3 mm (Pl. 4, fig. 12); umbonal slopes high and nearly vertical, straight or very gently convex in outline, diverging forward by 25°; ears large when well preserved as shown in holotype (Pl. 4, figs. 11, 17), transverse, well defined, clearly demarcated from rest of valve by deep concavity, flatly convex in section; cardinal extremities angularly rounded at 105°; no sulcus. Ventral ornament of distinct concentric ridges and spines (Pl. 4, figs. 14, 16, 18); concentric ridges moderately high with approximately symmetrical anterior and posterior slopes, crests angular or narrowly rounded, 6 to 10 crests from umbo to anterior margin, separated by flat-bottomed interspaces that gradually increase in width anteriorly, more closely spaced over umbo and umbonal slopes; each ridge bearing single row of recumbent to suberect spines; spines arising from conspicuous, round swollen bases on crests of concentric ridges or, more often, on posterior slopes of ridges; spine bases generally 1 to 2 mm in diameter, 1.5 to 2.5 mm apart, slightly smaller in umbonal region.

Dorsal valve moderately concave, not geniculate; ears flat, sharply demarcated; no fold. Dorsal valve strongly lamellose (Pl. 4, figs. 12, 17), lamellae flattened over posterior portion, becoming free standing anteriorly in some specimens, step-like in appearance, generally 1.5 to 2.5 mm apart, each bearing single row of fine recumbent to suberect spines along anterior edge of band; spines much thinner than ventral spines, less than 0.5 mm in diameter, arising from lamellae without prominent swollen bases, 2 to 3 mm apart. Growth increments distinct on well preserved exteriors of both valves, approximately 4 to 5 per mm.

Internal. Ventral muscle field slightly impressed, often obscure; adductor scars elongate in shape, slightly raised and divided by thin narrow myophragm (Pl. 4, fig. 18), poorly dendritic; diductor scars weakly impressed, marked by few fine radial ridges.

Cardinal process sessile with two entirely separate lobes, each sulcate posteriorly (Pl. 4, fig. 20), with myophore lobes sometimes approaching each other on posterior face, forming deep median sulci; posterior platform strongly thickened; cardinal ridges distinct, obliquely joining base of cardinal process, laterally extending across ears; ear baffles low; lateral ridges prominent (Pl. 4, fig. 19); anterior ridge comparatively indistinct; breviseptum distinct through its extent, extending beyond muscle field but not reaching midlength, terminating with prominent swelling; adductor scars poorly differentiated, tear-shaped or suboval, anteriorly strongly elevated with well rounded margins, not elevated from valve floor posteriorly but encircled by distinct loop-shaped ridges (Pl. 4, fig. 20), marked by weak posteriorly convex ridges; shallow antron-like trough present between inner parts of loop-shaped ridges, V-shaped, presumably filled by secondary material; brachial ridges obscure; endospines prominent on anterior half of valve floor, arranged in irregular rows parallel to anterior margin, recumbent to suberect, two to three in 1 mm (Pl. 4, fig. 19).

Dimensions (in mm).

Specimen	Valve	Length	Width	Height	Hinge width
GSC 97090	DOR	10.0	11	1.5	10
GSC 97092	CON	+8.5	12	4.5	—
GSC 97095	VEN	12.0	12	7.0	10
GSC 97097	VEN	13.0	15	5.5	10

Comparisons. As shown in synonymy, a number of figured specimens from Russia appear identical with the Canadian species. Most were referred to *Fimbrinia cristatotuberculata* (Kozolowski, 1914, p. 43, Pl. 2, figs. 61, 62) from the Asselian Copacabana Formation of Bolivia. The types of this species differ in being larger in size, more transverse in outline, and having larger, well defined ears. Kozlowski figured two specimens, both of which are very small, less than 8 mm in width, and elongate in shape, with small ears.

Fimbrinia? *gracilis* Abramov and Grigor'yeva (1983, p. 78, Pl. 3, figs. 10–14) from the Upper Carboniferous of the southern Verchoyan Mountains, Siberia, is similar in size and general outline, but is distinguished by its more closely spaced concentric ridges and finer spines. *Fimbrinia gijigensis* (Zavodovskiy) of Zavodovskiy and Stepanov (1970, p. 91, Pl. 35, figs. 1–3) from the Sakmarian Irbichan Suite of the Kolyma-Omolon Massif, Siberia, is large, and the ventral valve possesses broad, flattened concentric ridges with spines along their anterior slopes. Specimens from the Upper Carboniferous lower Kigiltas Suite of the western Verchoyan Mountains, identified as *F. gijigensis* by Abramov and Grigor'yeva (1983, p. 77, Pl. 3, figs. 15–17), appear to be closer to the present species in overall appearance, but differ in their elongate shape and elongate ventral spine bases.

Fimbrinia kolymaensis (Zavodovskiy) of Zavodovskiy and Stepanov (1970, p. 90, Pl. 37, figs. 8–10) from the probably Sakmarian Yasachnin Horizon of the Kolyma-Omolon Massif, resembles the new species in general appearance, but is distinguished by having more numerous and closely spaced concentric ridges.

Fimbrinia plummeri (King) from the Asselian Gaptank and Neal Ranch formations of west Texas (Cooper and Grant, 1975, p. 965, Pl. 311, figs. 5–14) is close in overall external features. Differences lie in the concentric ridges and spines on the ventral valve, which are evenly spaced and of equal size from the umbonal region to the anterior margin in the American species. *Fimbrinia ovata* Cooper and Grant (1975, p. 964, Pl. 310, figs. 1–31) from the Sakmarian lower Bone Spring and Skinner Ranch formations is moderately close and differs only in being conspicuously elongate in outline and having a rather narrow hinge line, and lower concentric ridges bearing more delicate spine bases.

Occurrence. In northern Yukon Territory, the new species occurs in the Ey, Eog, and Ej zones of the Jungle Creek Formation and the lowermost unit of the Tahkandit Formation. Outside the Yukon Territory, the new species has been previously described as *F. cristatotuberculata* from the Lower Permian strata of the Pechora Basin and Pai Hoi Range, north Urals (Mironova, 1960); the Asselian to Sakmarian upper Turuzov Horizon of central and western Taimyr, northern Russia (Ustritskiy and Chernyak, 1963); the probably Asselian Paren Horizon of the Kolyma-Omolon Massif (Zavodovskiy and Stepanov, 1970); and the Upper Carboniferous to Lower Permian Kigiltas Suite in the Verchoyan Mountains (Kashirtsev, 1959; Solomina, 1970).

Subfamily TUBERSULCULINAE Waterhouse, 1971

Genus *Krotovia* Frederiks, 1928

Type species. (OD) *Productus spinulosus* Sowerby, 1814.

Krotovia pustulata (Keyserling, 1853)

Plate 4, figures 21–23

1902 *Productus pustulatus* Keyserling; Chernyshev, p. 617, Pl. 30, figs. 1, 2; Pl. 53, figs. 5, 6.
1928 *Krotovia pustulata* (Keyserling); Chao, p. 52, Pl. 5, figs. 18–20.
1957 *Krotovia pustulata* (Keyserling); Cooper, p. 53, Pl. 8A, figs. 1–5.
1968 *Krotovia pustulata* (Keyserling); Sarytcheva et al., p. 79, Pl. 5, fig. 9.
1970 *Krotovia pustulata* (Keyserling); Zavodovskiy and Stepanov, p. 81, Pl. 12, fig. 4; Pl. 26, figs. 10, 11.
1971 *Krotovia pustulata* (Keyserling); Waterhouse *in* Bamber and Waterhouse, Pl. 15, fig. 21; Pl. 16, fig. 2.

Neotype. A specimen with valves conjoined, figured by Chernyshev (1902, Pl. 30, fig. 2) from the Sakmarian Stage of the Ufa Plateau, south Urals, kept at the CNIGR Museum, St. Petersburg.

Diagnosis. Large transverse shell with small tubercles arranged in quincunxial order over umbonal region and in almost concentric rows anteriorly in ventral valve.

Material. One dorsal external mould from GSC loc. 53951; one ventral external mould from JBW loc. 109; one ventral valve from JBW loc. 113.

Description. Shell large for genus, transverse in outline, moderately concavo-convex; widest along midlength or behind it; anterior commissure rectimarginate.

Ventral umbo prominent, moderately extended, strongly incurved; umbonal slopes low, gently concave in profile; umbonal angle close to 90°; ears small, not clearly separated from umbonal slopes; cardinal extremities obtusely rounded at about 120°; no sulcus. Ventral ornament of small rounded tubercles bearing fine suberect spines, tubercles about 0.5 to 1 mm in diameter, 0.8 to 1 mm apart, arranged in quincunxial pattern in umbonal region, anteriorly becoming irregular and in almost concentric rows toward anterior margin.

Dorsal valve moderately deep, not geniculate; ears flat, small, gradually merging with visceral region; no fold. Dimples distinct on dorsal valve; spines more delicate and less dense than in ventral valve, arranged in well defined concentric rows along growth increments.

Comparisons. Productus pustulatus was proposed by Keyserling (1853, p. 247; cited in Sarytcheva et al., 1968, p. 79) without illustration. This species was first formally described and figured by Chernyshev (1902), based on one specimen from the Schwagerina Limestone of the Urals; Chernyshev attributed this species to Keyserling.

Krotovia parva Cooper (1957, p. 53, Pl. 2B, figs. 5-12) from the Coyote Butte Formation of central Oregon is smaller and less transverse than *K. pustulata* and has a higher and more strongly incurved umbo.

Occurrence. Krotovia pustulata is found in the Ey and Ej zones of the Jungle Creek Formation in northern Yukon Territory. Elsewhere, the species has been reported from the Asselian to Sakmarian stages of the Urals (Miloradovich, 1949); the probably Asselian Paren Horizon of the Kolyma-Omolon Massif, northeastern Siberia (Zavodovskiy and Stepanov, 1970); the Sakmarian to ?Kungurian Coyote Butte Formation of central Oregon (Cooper, 1957); the Upper Carboniferous (Gshelian) to Lower Permian (Asselian) Cokpecten Complex of eastern Kazakhstan (Sokolskaya, 1968); and the Sakmarian to Artinskian fauna of the lower Qixia Formation or equivalents in southwestern China (Chao, 1928).

Genus *Tubersulculus* Waterhouse *in* Bamber and Waterhouse, 1971

Type species. (OD) *Tubersulculus maximus* Waterhouse (*in* Bamber and Waterhouse, 1971).

Discussion. This genus is allied to *Krotovia* Frederiks, discussed above, from which it is distinguished by its normally elongate outline, prominent tubiform trail, and the presence of a prominent sulcus. The same is also true of *Stictozoster* Grant (1976), which may be further distinguished in possessing alternating concentric spinose bands and smooth interspaces.

Tubersulculus maximus Waterhouse, 1971

Plate 4, figures 24-29; Plate 5, figures 1-9

?1888 *Productus pseudoaculeatus* Krotov, p. 409, Pl. 1, fig. 8.
1902 *Productus pseudoaculeatus* Krotov; Chernyshev, p. 615, Pl. 30, fig. 7; Pl. 53, figs. 10-12.
1934 *Productus pseudoaculeatus* Krotov; Stepanov, Pl. 3, figs. 1-7.
1971 *Tubersulculus maximus* Waterhouse *in* Bamber and Waterhouse, p. 209, Pl. 23, figs. 1-11.

Holotype. GSC 26393 from JBW loc. 24, Ettrain Creek, northern Ogilvie Mountains; Ey zone, Jungle Creek Formation, figured in Bamber and Waterhouse (1971) in Plate 23, figures 7, 10.

Diagnosis. Moderately large, subquadrate to elongate shell with deep sulcus and high fold, narrow umbo, and fine tubercles arranged in quincunxial pattern.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53999	3	2	
GSC loc. 56917	16	8	
GSC loc. 57052	7	4	
GSC loc. 57053	5	4	7
GSC loc. 57275	8		7
JBW loc. 9	1(im)		
JBW loc. 24	3, 2(im)	1	

JBW loc. 54	3	1(em)	
JBW loc. 60	1(im)	1(em)	
JBW loc. 63	1(em)		
JBW loc. 88	6, 4(im)	1, 1(em)	2
JBW loc. 89	9, 3(em)	1(em), 1(im)	1
JBW loc. 113	5	4	
JBW loc. 508	1		

Description. External. Shell of medium size; strongly concavo-convex in profile (Pl. 4, fig. 27), subquadrate to slightly elongate in outline; maximum width near midlength.

Ventral valve strongly curved in profile with short, moderately convex visceral disc and long, elongate trail; geniculation area strongly rounded with geniculation angle about 80° to 90° (Pl. 5, fig. 2); umbo prominent, moderately extended and incurved beyond hinge line by 1 or 2 mm (Pl. 5, fig. 6); umbonal angle between 60° to 100°, usually at 80°; umbonal slopes moderately high and gently convex in section; hinge line narrower than maximum width; ears small and poorly segregated from visceral disc; cardinal extremities rounded at 130°; trail twice as long as visceral disc, flatly convex in lateral profile, abruptly reduced into narrow tube at front (Pl. 5, fig. 4); flanks narrowly arched in section with vertical, parallel lateral slopes; sulcus well pronounced (Pl. 5, figs. 3, 4), commencing at about 5 to 7 mm from beak with sulcal angle at 15° to 20°, initially shallow and indistinct, narrow and deep over geniculation area where it is deeply incised dorsally, V-shaped in section, becoming shallower and narrower on posterior trail, disappearing on middle and anterior portions of trail, and finally replaced on frontal tubiform extension by low, broad swelling (Pl. 5, fig. 4). Ventral ornament of fine distinct tubercles (Pl. 5, figs. 1, 2), five to six in 5 mm at 5 mm from umbo, arranged in rough quincunxial pattern, slightly elongate, not particularly concentrated on ears or umbonal slopes; small erect spines arising from tubercular crests; tubercles in close-set concentric rows over anterior trail, seven in 5 mm.

Dorsal valve deeply concave without abrupt geniculation (Pl. 4, fig. 26), approximately following curvature of ventral valve in profile, delimiting narrow visceral cavity; fold as distinct as ventral sulcus, well pronounced over midlength of valve, diminishing anteriorly and replaced on tubiform trail by low, narrow median sulcus (Pl. 4, fig. 29). Dorsal ornament similar to that on ventral valve, but tubercles smaller and more close-set, arranged in better defined concentric rows over entire valve (Pl. 4, fig. 26), surface strongly lamellose anteriorly in some specimens.

Internal. Ventral adductor scars placed on slightly elongated platform, bisected by low myophragm (Pl. 4, fig. 24), transversely marked by faint ridges in some specimens; diductor scars weakly impressed, radially striate; cardinal ridges short, diverging slightly from hinge line; valve floor marked by fine pits and relatively large tubercles, the former arranged in two to three irregular rows around anterior margin; tubercles concentrated thickly just in front of muscle field (Pl. 5, fig. 4), up to 1.5 mm in diameter, diminishing in size forward.

Within dorsal valve, low, thin median septum extends over posterior half of shell length (Pl. 5, fig. 5), less than 1 mm in diameter; adductor scars tear-shaped (Pl. 4, fig. 27), anteriorly sited on low platform, posteriorly flattened and well outlined, poorly differentiated, mostly smooth; cardinal ridges distinct, about 1 to 2 mm in diameter, low, rounded, arising from base of cardinal process, diverging slightly from hinge, crossing inside ears as low baffles, disappearing before reaching anterolateral margins; brachial ridges with distinct loops, recurved at front; fine pustules in front of adductor scars, two to three in 1 mm, larger toward anterior margin, disappearing on trail.

Dimensions (in mm).

Specimen	Valve	Length	Width	Height	Hinge width
GSC 96903	VIM	+17	26	8	20
GSC 96904	DEM	+26	34	12	28
GSC 96906	VEN	23	25	11	20
GSC 96907	DEM	+22	31	13	25
GSC 96908	DEM	+19	31	?6	25
GSC 96909	VEN	20	25	10	20
GSC 96910	DEM	20	25	9	20
GSC 96911	DEM	18	24	9	20
GSC 96912	DIM	27	30	12	26

Comparisons. Waterhouse (*in* Bamber and Waterhouse, 1971) noted that *Tubersulculus maximus* was very close to *Productus pseudoaculeatus* Krotov (1888), a species originally described from the Lower Permian of the Urals. The type specimen of *P. pseudoaculeatus* is slightly smaller than most of the Yukon material, but it shows a similar spine pattern and density (with fine tubercles arranged on the ventral valve in quincunxial pattern; about five to six in 5 mm over ventral umbonal region), as well as a deep sulcus; but no tubiform trail can be observed from the type specimen, which was presumably damaged. Specimens attributed by Chernyshev (1902) and Stepanov (1934) to *Productus pseudoaculeatus* Krotov are possibly conspecific with the Yukon species. These shells are also characterized by numerous fine tubercles, five to seven in 5 mm on posterior ventral valve; they have a distinct sulcus and a well defined tubiform trail at front, as in the Yukon material. The size of the Russian species ranges from 20 to 24 mm wide and 20 to 25 mm long and is compatible with small specimens of the Yukon species. The slight size variation is considered of little specific significance; it may have resulted from different ecological adaptation or ontogenetic variation.

Specimens with a distinct tubiform trail and tubercular spinose ornament from the Sakmarian beds at Tastuba, southern Urals, were described as *Productus tastubensis* (Möller) by Chernyshev (1902, p. 615, Pl. 53, figs. 7-9). Its sulcus, tubiform trail, and tubercular spinose ornament appear to suggest *Tubersulculus*, but the species may be distinguished from *T. maximus* in having well defined concentric spinose bands separated by narrow, flat, smooth interspaces.

Productus tundrae Frederiks (1926, p. 87, Pl. 3, figs. 7-9) from the Sakmarian beds in Kejim–Terovey River, northern Urals, also approaches the Yukon species in having a distinct sulcus and a tubiform trail, but appears to differ in possessing more distinct concentric rugae, especially over the umbo.

Occurrence. Tubersulculus maximus occurs in Ey, Eog and Ej biozones in northern Yukon Territory. Outside the Yukon Territory, it was described as *Productus pseudoaculeatus* by Chernyshev (1902) from the Sakmarian beds in the southern Urals and Timan; and by Stepanov (1934) from the Sakmarian Bryozoa Limestone in Kolva River area, north Urals.

Family PLICATIFERIDAE Muir-Wood and Cooper, 1960

Subfamily PLICATIFERINAE Muir-Wood and Cooper, 1960

Genus *Jakutoproductus* Kashirtsev, 1959

Type species. (OD) *Marginifera verchoyanica* Frederiks (1931).

Diagnosis. Subquadrate to subrectangular in outline, moderately concavo-convex, short geniculate trail at front in some species; hinge line equal to, or slightly narrower than, maximum width; ventral valve strongly and irregularly rugose with elongate tubercles bearing small spines in roughly quincunxial pattern, larger spines in row near hinge line; dorsal valve lamellose with large elongate dimples, no spines. Ventral interior with low elongate nondendritic adductor ridge in contact with relatively large, flabellate, and longitudinally striate diductors; cardinal and lateral ridges prominent. Dorsal interior with small, sessile, trilobate cardinal process; lanceolate adductors; posteriorly bifurcated median septum; distinct brachial ridges; and prominent cardinal and lateral ridges.

Discussion. The two publications of Kashirtsev over the 1959 to 1960 period were both dated 1959 in their title pages and both contained the description of *Jakutoproductus* as a new genus without making reference to one another. Kashirtsev (1960, as used herein in the references), although dated as 1959 on the title page of the periodical volume, was actually released or published on February 22, 1960, as indicated in the last page of the periodical volume, and confirmed by Sarytcheva (*in* Sarytcheva et al., 1968, p. 85) in her synonymy list of "*Jakutoproductus*" *cheraskovi* Kashirtsev. *Jakutoproductus* Kashirtsev (1959) was published in October, 1959, and hence provided the first publication of the generic name. Most researchers (Muir-Wood, 1965; Kotlyar *in* Kotlyar and Popeko, 1967; Doescher, 1981; Abramov and Grigor'yeva, 1983, 1988; Ganelin, 1991) who have referred to *Jakutoproductus* attributed the genus to Kashirtsev (1960).

There has been a varied opinion among brachiopod workers over the familial position of *Jakutoproductus*. Kashirtsev (1959, 1960) originally compared the genus to *Avonia* Thomas, 1914 and *Plicatifera* Chao, 1927 and placed *Jakutoproductus* in the family Avoniidae Sarytcheva, 1960. This designation was followed by Sarytcheva and Likharev (1960), Ustritskiy and Chernyak (1963), Sarytcheva (*in* Sarytcheva et al., 1968), Abramov (1970), Zavodovskiy and Stepanov (1970), and Solomina (1981). Ching (1963) and Kotlyar (*in* Kotlyar and Popeko, 1967) pointed out the flaws in assigning *Jakutoproductus* to the Avoniidae, noting that *Jakutoproductus* and *Plicatifera* differed from members of the Avoniidae in their extended shell, presence of geniculated trail, narrow visceral disc, ornament of distinct concentric rugae and sparse spinose tubercles, and different internal structure. In his study of *Urushtenia* Likharev, 1935, Ching (1963) placed a high value on the presence of concentric rugae on the umbonal region and of a bilobate cardinal process, and thus classed *Plicatifera* and *Jakutoproductus* with *Urushtenia* in his new family Urushtenidae (correctly, Urushteniidae). No comments were made of Ching's classification scheme by Kotlyar (*in* Kotlyar and Popeko, 1967) when she upgraded the subfamily Plicatiferinae Muir-Wood and Cooper to family rank, in which she included *Jakutoproductus* and *Plicatifera*. Muir-Wood (1965), followed by Li and Gu (1976, 1980), on the other hand, assigned *Jakutoproductus* to the family Leioproductidae Muir-Wood and Cooper, 1960. Still another classification scheme was expressed by Abramov and Grigor'yeva (1983, 1988), Pavlova (1988), and Ganelin (1991), who referred *Jakutoproductus* to the family Overtoniidae Muir-Wood and Cooper, 1960. Lazarev (1990) recognized the Plicatiferidae and included in the family five subfamilies, in which *Jakutoproductus* was separated from the Plicatiferinae and classed with *Levipustula* Maxwell (1951) in the subfamily Levipustulinae Lazarev, 1985.

The question thus is which if any of the above classification schemes is more appropriate as far as the phenetic characteristics of *Jakutoproductus* are concerned? Or is another scheme needed? As a criterion in the following discussion, we agree with Muir-Wood and Cooper (1960, p. 65) that the external ornament pattern, especially the arrangement of spines, plays a primary role in familial and subfamilial classification of productids. The dorsal interior is also significant, but it is noted that genera classed in the same family or even subfamily with relatively homogeneous external morphology may vary in details of the cardinal process (bilobate to trilobate with minute median lobe) and adductor scars (slightly dendritic to nondendritic).

Jakutoproductus is characterized most distinctly by its subquadrate to subrectangular outline, low convexity, normally strongly and irregularly rugose ventral and dorsal valve; a short, sharply geniculated trail around the frontal margin of ventral valve; sparsely and approximately quincunxially arranged tubercles on the ventral valve and dimples on the dorsal valve; usually well distinguished ventral sulcus and dorsal fold; a small, sessile bilobate cardinal process; small, lanceolate, weakly to nondendritic adductors; distinct brachial ridges given off horizontally from the median septum; and a posteriorly bifurcated dorsal median septum. The combination of these characteristics, especially external morphology, suggests a relatively closer relationship to *Plicatifera* than to any other productid genus. *Verchojania* Abramov, 1970, *Spinorugifera* Roberts, 1976, *Aseptella* Martínez Chacón and Winkler Prins, 1977, *Ferganoproductus* Galitskaya, 1977, and *Rugoconcha*, Jin and Sun, 1981 are also related and, with *Jakutoproductus*, are here classified together under the subfamily Plicatiferinae within the family Plicatiferidae.

Among the genera that have been previously compared to *Jakutoproductus* in relation to their familial relationships, *Plicatifera* is perhaps closest, as noticed by Kashirtsev (1959, 1960) and Kotlyar (*in* Kotlyar and Popeko, 1967). Chao (1927a, p. 25) originally defined *Plicatifera*, type species *Productus plicatilis* Sowerby, 1824, on the basis of its "prominent concentric wrinkles and a few irregularly distributed spines" on the shell surface. As pointed out by Muir-Wood and Cooper (1960), this generalized definition permitted the inclusion of many concentrically wrinkled species that were previously included in *Pustula* Thomas (1914), regardless of their internal structures. *Plicatifera* was redefined by Muir-Wood and Cooper (1960, p. 202) as follows: "Shell subrectangular to subquadrate in outline, pedicle valve slightly convex on visceral disc, with shallow sulcus, geniculated, with curved medianly sulcate trail, . . . Pedicle-valve ornament of even, prominent, subangular rugae, crossing visceral disc; trail smooth or with growth lines, appearing finely costellate when decorticated; spine bases rare, arranged, (1) on rugae, (2) scattered on trail, (3) row of erect spines near hinge. Brachial valve with similar ornament, . . . spines rare, of small diameter. Interior of brachial valve with trilobate cardinal process, median lobe narrow, developed posteriorly between two sulcate lateral lobes; median septum with swollen base supporting cardinal process, tapering anteriorly and extending two thirds of valve length; lateral ridges diverging slightly from hinge, not reaching cardinal extremities; adductors trigonal, dendritic, posteriorly placed; brachial ridges not observed." From this definition it is clear that *Plicatifera* is particularly close to *Jakutoproductus* in shell outline (subquadrate to subrectangular), the overall pattern of the external ornament (concentric rugae and sparsely distributed spine bases on the ventral valve), and the presence of a sulcus and fold and a geniculated trail. It should be noted that although the cardinal process in *Plicatifera* was said to be trilobate, the median lobe is only a minute structure developed posteriorly between the two distinct lateral lobes. Because this median lobe is minute, the cardinal process of *Plicatifera plicatilis* Sowerby appears to be bilobate in posterior view (see *Plicatifera plicatilis* Sowerby figured by Muir-Wood and Cooper, 1960, Pl. 56, figs. 18–21).

There are two major distinctions between *Plicatifera* and *Jakutoproductus* in that the geniculated trail of *Plicatifera* is smooth (except for fine growth lines and lamellae) and its dorsal median septum is posteriorly massive and not bifurcated. Both distinctions are considered to be of generic, not familial significance.

Overtonia Thomas, 1914 and *Avonia* Thomas, 1914 may be compared with *Jakutoproductus* because all share a bilobate cardinal process and are variably ornamented by concentric lamellae. *Overtonia*, type species *Producta fimbriata* Sowerby, 1824, is characterized externally by broad, regularly spaced concentric wrinkles, bearing elongate spine ridges on the ventral valve and quincunxially arranged erect spines on the dorsal valve. The concentric wrinkles first suggest a relationship to *Jakutoproductus*, but detailed comparison between the two shows considerable differences, even in the concentric ornament. The concentric wrinkles on the ventral valve of *Overtonia* are broad, convex, angular bands separated by relatively concave growth lines. These are clearly distinct from the rugae on the ventral valve of *Jakutoproductus*, which are lamellose, irregular, and discontinuous across the visceral disc. Moreover, in addition to large dimples, the dorsal valve of *Overtonia* is distinguished by the possession of numerous, quincunxially distributed spines, unlike that of *Jakutoproductus*, which is characterized by dimples only. *Avonia*, type species *Productus youngianus* Davidson, 1860, is similar to *Overtonia* in many respects. The concentric wrinkles in *Avonia* are much weaker and less regularly spaced compared to those in *Overtonia*, thus suggesting closer similarity to *Jakutoproductus*, but the spine ridges on the ventral valve of *Avonia* are much more prominent and often extend across concentric lamellae, forming costae. Both *Avonia* and *Overtonia* are circular to, more commonly, elongate in shape and usually strongly convex; their dorsal median septa are not bifurcated at the posterior end.

Ching (1963) compared *Plicatifera* and *Jakutoproductus* with *Urushtenia* principally on the grounds that they all have concentric rugae over the umbonal region (i.e., at the juvenile stage), strong geniculation at maturity, and the presence of a bilobate cardinal process. The Urushteniidae Ching, 1963, in which *Plicatifera* and *Jakutoproductus* were included, was characterized as "Shell small to medium sized, both valves geniculated; ornament at juvenile stage like that of *Plicatifera* (i.e., rugose over umbonal region), but consisting of costae on anterior visceral disc and trail; dorsal interior with variably developed marginal ridges, cardinal process bilobate or slightly trilobate (i.e., trilobate with a minute median lobe)" (Ching, 1963, p.11). According to this definition, both *Plicatifera* and *Jakutoproductus* are not likely to be allied to the Urushteniidae because they lack any costae; instead they are characterized by strongly developed concentric rugae on the entire visceral disc (*Plicatifera*) or entire shell (*Jakutoproductus*).

When we compare *Plicatifera* and *Jakutoproductus* with *Urushtenia* itself, the differences are even more striking. *Urushtenia*, type species *Productus pseudomedusa* Chernyshev, 1902, appears to be a unique genus that has characteristics of not only the productaceans [absence of an interarea, see Ching (1963)], but also of the strophalosiaceans, especially the chonostegid (a strongly developed anterior rim around the margin of the ventral valve bearing long spine ridges, a dorsal marginal fence also bearing long spines, coarse and simple costae on the trail, and the presence of cicatrix of attachment). *Urushtenia* was classed with the Aulostegidae by Muir-Wood and Cooper (1960) and Muir-Wood (1965), but it ranks as a separate family.

The placement of *Jakutoproductus* in the Leioproductidae by Muir-Wood (1965) and Li and Gu (1976, 1980) was presumably based principally on the fact that the dorsal median septum of *Leioproductus* Stainbrook, 1947, type species *Productella coloradoensis* Kindle, 1909, is also posteriorly bifurcated and the cardinal process bilobate. The external ornament of *Leioproductus*, however, is remarkably different from that of *Jakutoproductus* in that the former lacks the rugae that characterize *Jakutoproductus*. In addition, *Leioproductus* possesses numerous coarse spines in a regular pattern: in a row near the hinge margin, in a curved row up the umbonal slopes, and in a median longitudinal row often on a ridge up the venter (Muir-Wood and Cooper, 1960, p. 169). This pattern is not seen in *Jakutoproductus*.

Classification of *Jakutoproductus* with *Levipustula* Maxwell (1951) in the subfamily Levipustulinae of the family Plicatiferidae by Lazarev (1990) is not accepted herein because of the great dissimilarity in external morphology between the two genera. Apart from fine growth lines, *Levipustula*, type species *Levipustula levis* Maxwell (1951; see also Campbell, 1961) from the Upper Carboniferous of eastern Australia, lacks the rugae of *Jakutoproductus*. Instead it possesses numerous long, closely and quincunxially spaced spine ridges on both valves, unlike the sparsely, approximately quincunxially distributed tubercles only on the ventral valve of *Jakutoproductus*. Moreover, *Levipustula* is nonsulcate, nongeniculate or only very weakly so, and rarely has well developed brachial or marginal ridges.

In view of these comparisons, it is proposed that *Jakutoproductus* be placed in the subfamily Plicatiferinae of the family Plicatiferidae.

Two genera are particularly allied to *Jakutoproductus*. *Spinorugifera* Roberts, 1976, p. 50, type species *S. chichesterensis* Roberts, 1976 from the Viséan of New South Wales, Australia, is also characterized by strong, irregular rugae on both valves, small, widely spaced tubercles, and a bilobate cardinal process. But the Australian genus is well distinguished, as noted by Roberts (1976), by the absence of a ventral sulcus and dorsal fold, absence of marginal ridges within the dorsal valve, smaller and sparser tubercles, and well differentiated dorsal adductor scars.

Verchojania Abramov (1970, p. 112) was proposed for *Jakutoproductus cheraskovi* Kashirtsev, 1959, a species that is widely distributed in the Upper Carboniferous in northeast Siberia (Zavodovskiy and Stepanov, 1970; Solomina, 1978; Abramov and Grigor'yeva, 1983), east Zabaikal (Kotlyar and Popeko, 1967), northeast China (Li and Gu, 1976), and east Kazakhstan (Sarycheva *in* Sarycheva et al., 1968). The genus has been recently suppressed by Ganelin (1991) but recognized by Pavlova (1988) and Lazarev (1990). The genus is regarded as valid on the basis of its distinction from *Jakutoproductus* in the absence or only incipient development of concentric rugae on the visceral disc of the ventral valve, relatively large tear-shaped dorsal adductor scars, and a posteriorly thickened, rather than bifurcated dorsal median septum (Abramov and Grigor'yeva, 1983; Pavlova, 1988).

Jakutoproductus verchoyanicus (Frederiks, 1931)

Plate 5, figures 10-23; Figures 19, 20

1931 *Marginifera verchoyanica* Frederiks, p. 211, Pl. 1, figs. 3, 11-13.

1939 *Productus (Avonia?) verchoyanicus* (Frederiks); Likharev and Einor, p. 30, Pl. 3, figs. 4-6.

1946 *Productus (Avonia?) verchoyanicus* (Frederiks); Einor, p. 31, Pl. 2, figs. 6, 7; Pl. 4, fig. 9.

1946 *Productus (Plicatifera?) verchoyanicus* (Frederiks); Stepanov, p. 201, Pl. 2, figs. 2-9.

1959 *Jakutoproductus verchoyanicus* (Frederiks); Kashirtsev, p. 35, Pl. 13, figs. 9-10; Pl. 13, figs. 9-10.

1960 *Jakutoproductus verchoyanicus* (Frederiks); Kashirtsev, p. 28, Pl. 3, fig. 16.

1963 *Jakutoproductus verchoyanicus* (Frederiks); Ustritskiy and Chernyak, p. 75, Pl. 5, figs. 1-4; Pl. 28, figs. 2, 3.

1967 *Jakutoproductus verchoyanicus* (Frederiks); Kotlyar and Popeko, p. 103, Pl. 18, figs. 1-8.

1970 *Jakutoproductus verchoyanicus* (Frederiks); Solomina, p. 76, Pl. 3, figs. 10, 11.

1970 *Jakutoproductus verchoyanicus* (Frederiks); Zavodovskiy and Stepanov, p. 82, Pl. 40, figs. 5-10; Pl. 4, figs. 2-4.

1971 *Jakutoproductus* sp. Waterhouse *in* Bamber and Waterhouse, Pl. 15, figs. 18-20.

1974 *Jakutoproductus verchoyanicus* (Frederiks); Abramov, p. 79, Pl. 1, figs. 3, 4.

1981 *Jakutoproductus verchoyanicus* (Frederiks); Solomina, p. 61, Pl. 5, figs. 1-3.

1988 *Jakutoproductus verchoyanicus* (Frederiks); Abramov and Grigor'yeva, p. 111, Pl. 4, figs. 4, 7, 8, 13, 14; Pl. 5, fig. 20.

1991 *Jakutoproductus verchoyanicus* (Frederiks); Ganelin, p. 51, Pl. 3, figs. 10, 11.

1994 *Jakutoproductus verchoyanicus* (Frederiks); Shi, p. 115, Fig. 4A-J.

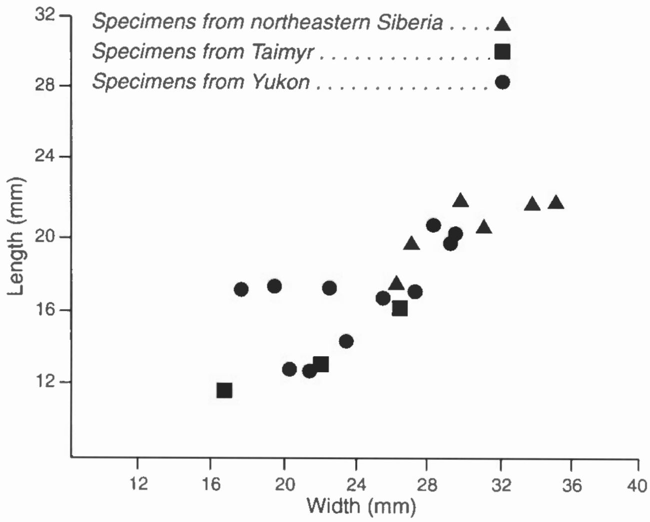


*Figure 19. Relation of length to width in **Jakutoproductus verchoyanicus** (Frederiks) from different localities.*

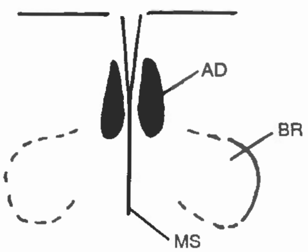


*Figure 20. **Jakutoproductus verchoyanicus** (Frederiks) showing dorsal interior (GSC 96916, x3). Abbreviations as in Figure 17. BR, brachial ridge.*

Lectotype (selected by Solomina, 1981). CNIGR Museum 2320/1, figured by Frederiks (1931, Pl. 1, fig. 3) from the Early Artinskian lower Echii Suite of northern Verchoyan Mountains, Siberia.

Diagnosis. Moderately large, subrectangular shell at maturity, with short, strongly geniculate trail and small ears; sulcus narrow and deep with angular floor; ventral valve gently to moderately convex; ventral concentric wrinkles distinct, not anastomosing.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53718	8, 1(im)	1, 1(im)	2
GSC loc. 53774	1		
GSC loc. 56922	2		

Description. External. Shell slightly variable in size and outline (Fig. 19): immature specimens usually subquadrate to elongate in outline (Pl. 5, fig. 11), mature shell subrectangular (Pl. 5, fig. 21); moderately concavo-convex; hinge line normally slightly narrower than maximum width, at or slightly behind midlength at maturity.

Ventral valve gently to moderately convex, most inflated at midlength; lateral and anterior margins abruptly geniculate in maturity (Pl. 5, figs. 19, 22). Trail short, up to one quarter of shell length; umbo small, low, not extended beyond hinge line; umbonal slopes low, straight or gently convex in profile, umbonal angle between 90° and 95°; ears small to moderately large, not well differentiated from umbonal slopes, flatly convex, triangular in shape; cardinal extremities bluntly rounded between 85° and 130°, commonly at 105°; anterolateral margins broadly rounded; sulcus distinct (Pl. 5, figs. 13, 21), commencing about 5 to 6 mm from umbo with sulcal angle between 25° and 40°, narrow and deep with angular floor over midlength, slightly broader and shallower toward anterior margin; flanks flatly convex, spreading to lateral margins. Ventral surface ornamented by irregular concentric wrinkles and many swollen bases bearing small spines (Pl. 5, fig. 13); wrinkles continuous or broken off, low and ill defined or prominent, stronger on umbonal slopes and near anterior margin; lamellae sometimes developed at late growth stage, most prominent on anterior third of valve length; spines arising from small, often elongated tubercular bases, moderately differentiated: finer, suberect spines clustered over umbonal region, 0.5 mm across, two to three in 5 mm, arranged in rough quincunxial pattern; larger spines elsewhere (Pl. 5, fig. 13), about 1 mm in diameter, in single row along hinge line (Pl. 5, fig. 10) with three or four on each side of umbo, projecting outward at 15° to hinge, and in broad set and rough quincunxial pattern over flanks and anterior part of valve, 2 to 3 mm apart; usually 3 to 4 spines on ears at or near cardinal extremities.

Dorsal valve with slightly to moderately concave visceral disc and short, broadly geniculate trail (Pl. 5, fig. 20); fold beginning about 4 mm from dorsal umbo (Pl. 5, fig. 17), well pronounced on disc and trail, approximately 4 mm wide and 2.5 mm high in front, crest angular posteriorly and broadly rounded in front. Dorsal valve conspicuously lamellose and pitted, lamellae stronger than those on ventral valve; pits elongate and arranged in rough quincunxial pattern, about 1 mm in diameter; no spines.

Internal. Ventral adductor ridge narrow and elongate, divided by thin median myophragm (Pl. 5, figs. 15, 23), smooth; comparatively large diductor scars to each side, weakly impressed, marked by few radial grooves; cardinal ridges distinct, diverging at low angle (about 15°) from hinge, short, not crossing ears.

Dorsal median septum prominent, about 1 mm across, alveolate at posterior end (Pl. 5, fig. 14; Fig. 20), anteriorly thin between adductor scars, extending beyond midlength; adductor scars distinct, long and narrow, lanceolate in shape, slightly raised; brachial ridges well formed with prominent distal loops, proximal parts obscure; lateral ridges not known.

Dimensions (in mm).

Specimens	Valve	Length (L)	Width (W)	Height	Hinge width (HW)	W/L	W/HW
GSC 96914	VEN	17	26	6	22	1.53	1.18
GSC 96915	VEN	18	28	7	26	1.55	1.08
GSC 96916	VEN	13	22	5	20	1.69	1.1
GSC 96917	DOR	20	30	?5	28	1.5	1.07
GSC 96918	DOR	15	24	5	23	1.6	1.04
GSC 96919	DEM	20	30	+4	?26	1.5	1.15
GSC 96921	VEN	13	21	4	18	1.62	1.16
GSC 96922	VEN	18	18	5	18	1.00	1.00
GSC 96924	VEN	18	20	6	20	1.10	1.00
GSC 96925	VEN	18	23	7	21	1.28	1.1
GSC 96926	VEN	21	29	7	24	1.38	1.21
Average	17.36	24.64	5.54	22.36	1.43	1.1	

Comparisons. The Yukon material appears to be conspecific overall with *Jakutoproductus* *verchoyanicus* (Frederiks, 1931) from the Early Artinskian lower Echii Suite of the Verchoyan Mountains. Internal structures were not described in detail by Frederiks but are well shown in the material figured by Solomina (1981), with which the Yukon material can be closely compared. Though this species varies in size from different localities (Fig. 19), its shape, convexity, development of sulcus, and short geniculate trail consistently distinguish it from other species. *Jakutoproductus protoverchoyanicus* Kashirtsev, 1959, as redescribed by Solomina (1981, p. 65, Pl. 5, figs. 9–12) and Abramov and Grigor'yeva (1983, p. 114, Pl. 5, figs. 10–14) from the Asselian–Sakmarian upper Kigiltas Suite of the Verchoyan Mountains, is larger and less transverse and has a broader and deeper sulcus than in the Yukon species. *Jakutoproductus tatjanae* Abramov and Grigor'yeva (1983, p. 67, Pl. 1, figs. 19–26) from the Upper Carboniferous to Lower Permian strata in the Verchoyan Mountains is comparable in size, outline, and convexity, but differs in having a wider hinge line at the maximum width and shows less conspicuous concentric wrinkles. *Jakutoproductus terechovi* Zavodovskiy of Zavodovskiy and Stepanov (1970, p. 83, Pl. 23, fig. 10; Pl. 27, figs. 5–9) from the probably Asselian Paren Horizon of the Kolyma–Omolon Massif is close in general appearance but distinguished by its strong, anastomosing concentric ridges crossing the entire ventral valve. Comparatively large specimens with similar ornament and outline have been referred to *J. crassus* Kashirtsev (1959, p. 36, Pl. 13, figs. 11, 12) from the Upper Carboniferous lower Kigiltas Suite of the Verchoyan Mountains, also recorded by Solomina (1981, p. 62, Pl. 5, figs. 4, 5). This species lacks the geniculate trail of *J. verchoyanicus* and is also larger than the Yukon material.

Ganelin (1991) recently described 15 species (including 12 new species) under the name of *Jakutoproductus* from the Carboniferous and Permian strata of northeastern Siberia, but if *Verchojania* is accepted as being distinguishable from *Jakutoproductus*, as discussed above, only seven (*J. mirandus* Ganelin, *J. irreprensis* Ganelin, *J. expositus* Ganelin, *J. verchoyanicus* Frederiks, *J. rugosus* Ganelin, *J. immemoratus* Ganelin, and *J. burgaliensis* Ganelin) may be attributable to *Jakutoproductus*. The remaining eight species are assigned to *Verchojania*. *Jakutoproductus burgaliensis* Ganelin (1991, p. 52, Pl. 3, figs. 15, 16) from the Lower Permian (probably Aktastinian) upper Munugudgak Horizon of the Verchoyan Mountains and the Kolyma–Omolon Massif is particularly close to *J. verchoyanicus* in size and development of sulcus and rugae, but it differs in being quadrate to subquadrate in outline and is less convex in profile.

Jakutoproductus excellens Li and Gu (1976, p. 240, Pl. 157, fig. 4) from the probably Lower Artinskian Gegenhongbao Formation of northeastern Inner Mongolia, northeastern China, resembles *J. verchoyanicus* in overall appearance and dorsal interior, but is distinguished by possessing a rather narrow, deep sulcus and two concentric rugae crossing the trail of the ventral valve.

Occurrence. In northern Yukon Territory, Bamber and Waterhouse (1971) reported the present Yukon species as *Jakutoproductus* sp. from GSC localities 53812–53818, 53946–53951, 54000, 54001, 56917, 57052, 57275. The species is confined to the Ej zone (of Early Artinskian age) in northern Yukon Territory. Elsewhere, this species appears to be most common in the Sakmarian and especially in Early Artinskian faunas. It has been described from the Lower Artinskian lower Echii Suite or equivalents in the Verchoyan Mountains, northeastern Siberia (Solomina, 1981); the Lower Artinskian Munugudjak Horizon in the Kolyma–Omolon Massif, northeastern Siberia (Zavodovskiy and Stepanov, 1970); the uppermost Sakamrian uppermost Turuzov Horizon and the Lower Artinskian lower Birrang Horizon in west Taimyr, northern Russia (Ustritskiy and Chernyak, 1963); and the Lower Artinskian Hipkhoshin Suite of east Zabaikal, southern Siberia (Kotlyar and Popeko, 1967).

Superfamily MARGINIFERACEA Stehli, 1954

(nom. transl. herein ex MARGINIFERIDAE Stehli, 1954)

Families included. Marginiferidae Stehli, 1954; Paucispiniferidae Muir-Wood and Cooper, 1960; Costispiniferidae Muir-Wood and Cooper, 1960 [ex Costispiniferinae, uplifted to family rank by Waterhouse (1983a)].

Discussion. The Family Marginiferidae Stehli is herein elevated to superfamily rank to include the above three families. It is well distinguished from other superfamilies of the Productidina (e.g., Productellacea Schuchert and LeVene, Productacea Waagen, and Linoproductacea Stehli) by its generally small size; generally few, coarse, regularly placed ventral body spines, well developed marginal ridges in both valves or in the dorsal valve only, and the usually well defined zygidium.

Family PAUCISPINIFERIDAE Muir-Wood and Cooper, 1960

Subfamily PAUCISPINIFERINAE Muir-Wood and Cooper, 1960

Genus *Kozlowskia* Frederiks, 1933

Type species. (OD) *Productus capacii* d'Orbigny, 1842.

Discussion. *Kozlowskia* is characterized, as revised by Grant (1976), by a row of small spines along the hinge line, one or two stout but short spines from the end of each ear, one on each lateral slope, and one or two straight transverse rows of strut spines crossing the middle section of the trail.

The placement of *Kozlowskia* in the Paucispiniferinae is provisional, as indicated by Sarytcheva (1977d). It lacks the single row of large spines over the posterolateral slopes as in *Paucispinifera* Muir-Wood and Cooper and allies such as *Liosotella* Cooper and *Anemonaria* Cooper and Grant.

Kozlowskia sp.

Plate 5, figures 24–29

Material. Two ventral valves from JBW loc. 57; two ventral valves from JBW loc. 109; one ventral valve from JBW loc. 545.

Description. Shell small, 20 mm wide, 15 mm long, and 11 to 12 mm high, slightly transverse in outline; widest along hinge line.

Ventral valve narrowly arched in lateral profile with geniculation angle at about 80° to 90°; visceral disc low and massive, gently to moderately swollen; umbo low and broad, slightly extended and incurved, umbonal angle at 80° to 90°; umbonal slopes low and broad, gently sloping toward ears, not well demarcated from the latter, gently convex in section; ears small and moderately defined, strongly curved in section; cardinal extremities rounded, approximately at right angles; trail slightly longer than visceral disc, moderately convex, and strongly curved in section to steep lateral slopes; no distinct sulcus. Ventral surface almost smooth, faintly costate (Pl. 5, figs. 25, 27), costae low and well rounded, three in 2 mm on anterior disc, slightly stronger on trail; rugae even weaker or not developed. Seven large spines present on ventral valve, generally 0.5 to 0.8 mm in diameter, three located approximately on middle trail in front (Pl. 5, fig. 26), one over each lateral slope (Pl. 5, figs. 27, 28), and one from each cardinal extremity, no hinge row or umbonal slope row of spines. Ventral interior not known.

Dorsal external features not known. Dorsal marginal ridge well shown in partly exposed dorsal internal mould (Pl. 5, fig. 24), crossing anterior edge of dorsal visceral disc, 2 mm in diameter, rounded.

Comparisons. The small size, transverse outline, and large ventral spines of the Yukon material first recall the type species *Kozlowskia capacii* (d'Orbigny) from the Asselian Copacabana Formation of Bolivia, redescribed and illustrated by Kozlowski (1914, p. 22, Pl. 2, figs. 1-15) and Samtleben (1971, p. 48, Pl. 1, figs. 20–36). But the Bolivian species has larger, pointed ears, stronger costae, and well defined rugae on the visceral disc. Stepanov (1934, p. 60, Pl. 4, fig. 23) recorded the Bolivian species from the probably Sakmarian Bryozoa Limestone of the Kolva River, northern Urals. Not enough features can be seen from the poorly preserved Russian ventral valve to tell if it is conspecific with the Bolivian types, but it seems to have stronger costae on the trail and a well defined sulcus, compared with the types of *K. capacii*. The same characteristics also distinguish the Russian specimen from the Yukon material.

Kozlowskia schellwieni (Chernyshev, 1902, p. 825, Pl. 58, figs. 9-12; Kalashnikov, 1980, p. 58) from the Sakmarian faunas in the Urals is distinguished by its pointed ears and stronger costae.

Occurrence. Ey, Eog, and Ej zones, Sakmarian to Early Artinskian.

Genus *Liosotella* Cooper, 1953

Type species. (OD) *Liosotella rugosa* Cooper, 1953.

Diagnosis. Shell of small to medium size, strongly concavo-convex with sulcate trail, widest at hinge; shell costate, strongest on trail; spines only on ventral valve, in curved row on each lateral slope; hinge spines rare, few (usually three or more) strut spines arranged in irregular transverse rows crossing trail, and smaller halteroid spines scattered over visceral disc and trail. Ventral interior with variably developed ear baffles. Dorsal interior with strongly developed zygidium and poorly developed marginal ridges.

Discussion. *Liosotella* differs from *Paucispinifera* Muir-Wood and Cooper, 1960 in its normally subquadrate to elongate outline, small ears and strongly, coarsely costate ventral trail.

Anemonaria Cooper and Grant (1969) is usually transverse in outline with fine subdued costae on the trail and two, rarely more, strut spines over the ventral trail.

Both *Hystriculina* Muir-Wood and Cooper, 1960 and *Azygidium* Waterhouse, 1983b lack a zygidium. The latter is closer to *Liosotella* in its paucity of ventral spines, but differs in possessing faint costae only, and at times more than one row of spines over the umbonal slopes. *Hystriculina* is distinguished further by its more transverse outline, weakly or nonsulcate, weakly costate ventral trail, and more numerous finer ventral spines.

Waterhouse (*in* Waterhouse and Briggs, 1986) considered that no large strut spines were present in *Liosotella* and *Anemonaria* and accordingly assigned the two genera to the Marginiferidae. Yet a few large ventral strut spines are clearly shown in the type species of both genera. Two strut spines that are as coarse as the spines over the umbonal slopes are well shown in *Anemonaria sublaevis* (King) (see Cooper and Grant, 1975, Pl. 408, figs. 1, 24), and three large spines in a row crossing the ventral trail are also present in *Liosotella rugosa* Cooper (1953, Pl. 11, fig. 15). Most species ascribed to *Liosotella* from west Texas have a few large strut spines across the venter, as in *Paucispinifera*, notably *Liosotella tetragonalis* Cooper and Grant (1975, Pl. 413, figs. 1, 15, 18) and *L. spinumbona* Cooper and Grant (1975, Pl. 14, figs. 1, 13).

Liosotella compacta n. sp.

Plate 5, figures 30–31; Plate 6, figures 1–9;
Figure 21

Etymology. Latin *compactus*, thick, firm.

Holotype. GSC 96944 from JBW loc. 2, Ettrain Creek, northern Ogilvie Mountains (Fig. 4); Ej zone; Jungle Creek Formation (Pl. 6, figs. 4–6).

Diagnosis. Small, elongate shell with narrow, deep sulcus and low costae on trail; one or two strut spines over the ventral trail and a few smaller spines scattered over the visceral disc.

Material.

Locality	Ventral	Dorsal
GSC loc. 53858	1	
JBW loc. 2	6, 4(im)	2(em)
JBW loc. 57	1(im)	
JBW loc. 545	1	

Description. External. Shell small for genus, elongate in outline, width equal to, or slightly shorter than, length; strongly concavo-convex; widest along hinge line; anterior commissure emarginate (Pl. 6, fig. 6).

Ventral valve strongly arched in lateral profile with short visceral disc and narrow, long trail (Pl. 6, fig. 5), geniculation angle about 90°; visceral disc strongly inflated; umbo prominent, strongly incurved with short, suberect beak that slightly protrudes beyond hinge, umbonal angle about 50°; umbonal slopes high and steep; ears small and clearly discriminated from high lateral walls of visceral disc (Pl. 6, fig. 6), triangular in shape, flatly convex; cardinal extremities rounded at about 85°; lateral margins almost parallel to each other; trail long, moderately to strongly convex, about twice as long as visceral disc; sulcus distinct, commencing from near umbo with sulcal angle measured from umbo at 10° to 15° (Pl. 6, fig. 4), generally rather narrow and deep, deepening over frontal disc, approximately 5 mm wide and 4 mm deep over trail, sulcal sides parallel to each other, floor narrowly U-shaped in section; flanks high and well rounded on crests; lateral slopes high and steep. Ventral umbonal region smooth, except for occasional small spines, trail usually moderately costate; costae low and narrowly rounded, generally 1 mm in diameter, separated by slightly wider interspaces. Spines in distinct, curved row on umbonal slopes

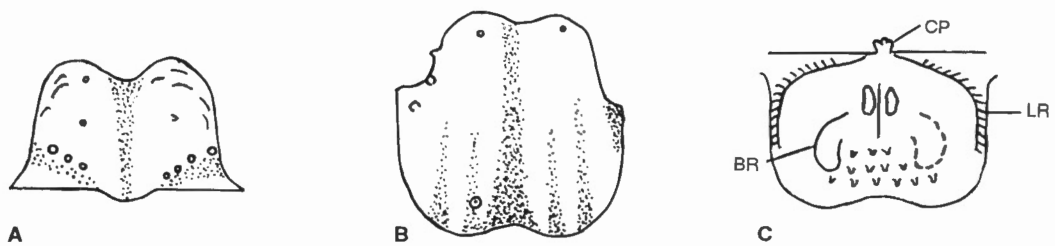


Figure 21. Liosotella compacta *n. sp. A–B, ventral spine pattern (GSC 96944, x2); C, dorsal interior (GSC 96950, x2). Abbreviations as in Figure 17. BR, brachial ridge; LR, lateral ridge.*

overhanging ears (Fig. 21A, B), diminishing in size toward hinge line, up to 1 mm in diameter, 0.7 to 1 mm apart, about four each side; strut spines rare, one observed on anterior trail in holotype (Fig. 21B) where it arises from a single costa, and in GSC 96953 (Pl. 6, fig. 7), one strut spine also observed on middle section of flank in front in GSC 96952 (Pl. 5, fig. 31), generally 1 mm in diameter; additional smaller spines occasionally present over visceral disc, three seen in holotype (Fig. 21A, B) and rare on trail and ears, generally less than 0.5 mm in diameter.

Dorsal valve with large, rounded flat disc and broadly geniculate trail approximately as long as visceral disc; geniculation abrupt with angle close to 90°; fold beginning 2 to 3 mm from dorsal umbo (Pl. 6, fig. 2), about 4 to 5 mm wide and 3 to 4 mm high on anterior disc, slightly higher on trail, crest narrowly rounded. Costae prominent on anterior disc and trail (Pl. 6, figs. 1, 2); no spines.

Internal. Ventral adductors small, elevated, narrow, elongate (Pl. 6, fig. 7), each 2 mm wide and 4 mm long, smooth; larger diductor scars on each anterolateral side, weakly impressed, marked by a few faint radial grooves. Cardinal process small, sessile, trilobate in posterior view, joined at base by cardinal ridges (Pl. 6, fig. 9; Fig. 21C); zygidium obscure; median septum weak between adductors, thin anteriorly, not extending beyond midlength; adductor scars elevated, narrow, elongate, and smooth; brachial ridges distinct, proximal parts oblique to the horizontal, loops narrow; cardinal ridges prominent, about 1 mm in diameter, highest across ears; lateral ridges not extending to anterior margin; floor marked by small granules posterolaterally; prominent endospines present in front of median septum.

Dimensions (in mm).

Specimens (Ventral valves)	Length	Width	Height	Disc length	Trail length
GSC 96944	16	16	10	7	15
GSC 96946	18	17	11	8	17
GSC 96947	16	15	11	9	16
GSC 96949	14	16	8	6	13
GSC 96952	16	16	12	9	16

Comparisons. The small size, elongate outline, narrow and deep sulcus, moderately developed costae, and sparse ventral spines over visceral disc and trail distinguish the Yukon species from other representatives of *Liosotella*. *Liosotella parva* Cooper and Grant (1975, p. 1110, Pl. 416, figs. 26–54) from the Word Formation of west Texas, U.S.A., has a somewhat similar size and shape, but differs considerably in its strongly spinose ventral umbonal region and shallow sulcus.

Several species have been reported from Kungurian strata of central-east Greenland. *Liosotella grandicosta* Dunbar (1955, p. 78, Pl. 6, figs. 1–33) is close in general outline but differs in its more strongly costate or plicate surface and larger size. *Liosotella spitzbergiana* (Toula) described by Dunbar (1955, Pl. 5, figs. 1–13) has weak costae similar to those of the new species, but is transverse and has a broader sulcus. *Liosotella vadosisinuata* Dunbar (1955, p. 77, Pl. 5, figs. 14–22) is distinguished in possessing large, extended, pointed ears and an ill defined sulcus.

Probolionia elongata Cooper (1957, p. 29, Pl. 8B, figs. 6–12) from the Sakmarian to Lower Kungurian Coyote Butte Formation of central Oregon is externally very close to the Yukon material, but it has a clearly reticulate dorsal visceral disc and a "long and prominent flange around the margin of visceral disc" (Cooper, 1957, p. 29) in the dorsal interior.

Occurrence. Ey, Eog and Ej zones, Sakmarian to Early Artinskian.

Genus *Anemonaria* Cooper and Grant, 1969

Type species. (OD) *Marginifera sublaevis* King, 1931.

Diagnosis. Small to moderately large, nearly smooth, with variably developed sulcus; ventral spines in distinct row over umbonal slopes and few strut spines on trail in front, rare over visceral disc and ears; costellae absent or very faint.

Discussion. The above diagnosis is expanded from that of Cooper and Grant (1975, p. 1103). The number of coarse spines over the umbonal slopes in *Anemonaria* varies from two to four, but the number of similarly coarse spines on the trail appears to be less variable in the figured specimens of the type species (Cooper and Grant, 1975, Pl. 408); there are usually two, one on each flank bounding the sulcus.

Azygidium Waterhouse (1983b) has the nearly smooth appearance of *Anemonaria,* but lacks a zygidium and has a less well defined sulcus and more ventral spines.

Anemonaria auriculata n. sp.

Plate 6, figures 10–28; Figures 22–24

1971 *Anemonaria* sp. Waterhouse *in* Bamber and Waterhouse, Pl. 16, fig. 3.

Etymology. Latin *auris*, ear; *latus*, wide.

Holotype. GSC 96932 from GSC loc. 53947, section 116C-1; Ej zone, Jungle Creek Formation; Plate 6, figures 17–19, 23.

Diagnosis. Small, with alate ears, broad, deep sulcus, well developed lateral ridges, and weak, poorly defined brachial ridges.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53946	4, 1(em), 1(im)		
GSC loc. 53947	1		1
GSC loc. 53999	1		
GSC loc. 56917	31	15, 2(im)	20
GSC loc. 56937	1		
GSC loc. 57052	6		
GSC loc. 57154	1		
JBW loc. 63	4	2(em), 1(im)	
JBW loc. 88	6	1	
JBW loc. 113	4		1
JBW loc. 512	4, 1(im)		

Description. External. Shell small, usually 15 to 20 mm wide, occasionally up to 26 mm in width (Figs. 22, 23); transverse in outline; strongly concavo-convex in profile; widest at hinge line; anterior commissure strongly emarginate (Pl. 6, fig. 22).

Ventral valve strongly arched in profile, most inflated at midlength; geniculate at about 10 to 12 mm behind anterior commissure with geniculation angle between 80° and 90° (Pl. 6, fig. 16); visceral disc small, short, strongly convex, triangular; umbo prominent, pointed, strongly extended and incurved beyond hinge line by 0.5 to 1 mm (Pl. 6, fig. 17); umbonal angle between 80° and 100°; umbonal slopes gently convex, broadly rounded in section, steeply sloping to ear bases; hinge line extended by large, alate, moderately convex, and well delineated ears (Pl. 6, figs. 20, 24, 26); cardinal angles acute, usually at 65° to 70°; lateral margin converging toward anterior margin; trail approximately twice as long as visceral disc, moderately convex in profile; lateral slopes high and steep; sulcus beginning near umbo with sulcal angle at 45°, widening and deepening over midlength and continuing to anterior margin, occupying over one third of width of trail in front, deeply indenting dorsal valve, floor angular, broadly V-shaped in section; due to deep incision of sulcus, venter divided into two

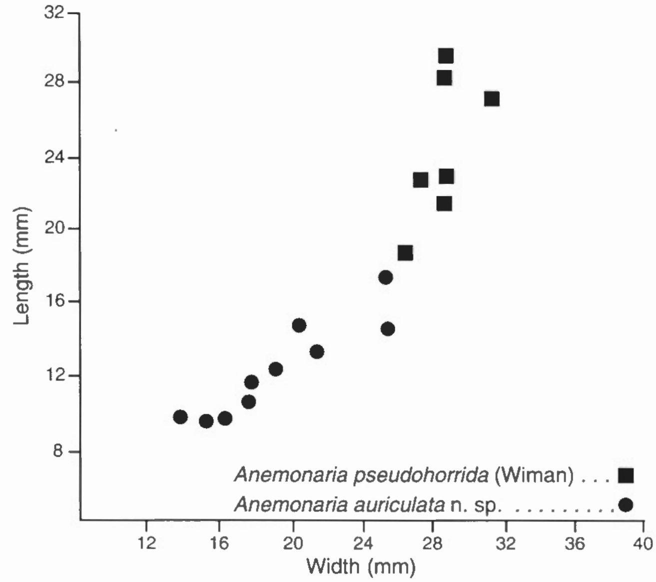


***Figure 22.** Relation of length and width in **Anemonaria auriculata** n. sp. and **A. pseudohorrida** (Wiman); the latter is shown to be normally much larger and less transverse than the Yukon species.*

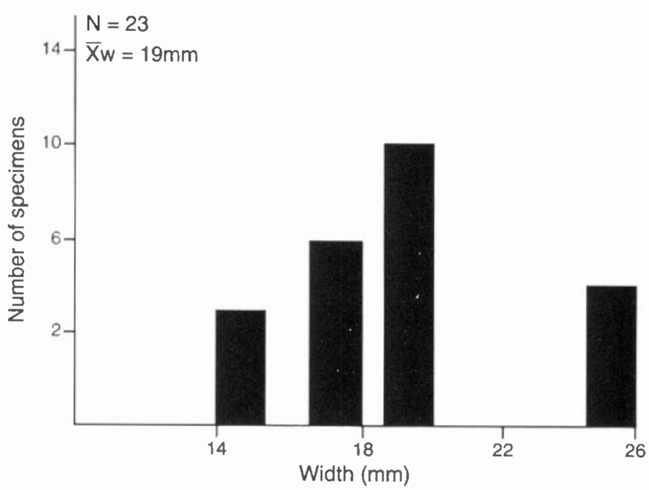


***Figure 23.** Size-frequency plot of **Anemonaria auriculata** n. sp.*

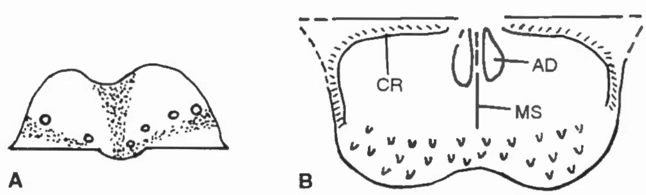


***Figure 24. Anemonaria auriculata** n. sp. A, ventral pattern (GSC 96932, x2); B, dorsal interior (GSC 96941, x3). Abbreviations as in Figure 17.*

prominent humps; flanks slightly narrower than sulcus, high and narrowly to angularly rounded on crests. Ventral surface nearly smooth except for very faint costellae on trail, strongest toward anterior margin and over sulcus in some specimens, indistinct on lateral slopes, four to five in 5 mm. Ventral spines in distinct row on umbonal slopes over ears (Pl. 6, fig. 25; Fig. 24A), about four on each side, increasing in strength toward lateral margin, up to 0.8 mm in diameter; usually one pair of similarly coarse spines present on middle section of trail, rising on each side of sulcus (Pl. 6, fig. 15); one or two additional smaller spines occasionally observed from cardinal extremities, less than 0.5 mm in diameter, rare over visceral disc.

Dorsal valve with large, gently concave visceral disc and short, broadly geniculate trail (Pl. 6, fig. 17); fold beginning at 5 to 8 mm from dorsal umbo, low and broadly rounded over anterior disc, higher and narrowly rounded over geniculation and trail. Dorsal valve smooth, except for fine, concentric lamellae in some specimens, no spines.

Internal. Ventral adductor ridge narrow, approximately 2 mm wide and long; diductor scars slightly impressed with faint radial markings; floor covered with fine endospines and pits, two to three in 1 mm (Pl. 6, fig. 16). Dorsal adductors small, tear-shaped (Fig. 24B), weakly impressed, smooth; median septum faint between adductor scars, rather thin in front, reaching midlength of visceral disc; brachial ridges poorly or not developed; cardinal ridges prominent, 0.5 mm in diameter, parallel to hinge margin, obliquely crossing ears and continuing as lateral ridges, disappearing before reaching anterior margin; visceral disc floor posteriorly smooth, anteriorly bearing two to three rows of endospines (Fig. 24B).

Dimensions (in mm).

Specimens	Valve	Length	Width	Height	Umbonal angle	Cardinal angle
GSC 96932	CON	12	16	8	87°	–
GSC 96937	VEN	17	26	11	85°	65°
GSC 96942	DOR	10	18	–	–	65°
GSC 96943	VEN	15	26	10	80°	70°

Comparisons. The new species appears to be close to *Anemonaria pseudohorrida* (Wiman, 1914, p. 74, Pl. 17, figs. 1–11) from the Kungurian to Kazanian upper Kapp Starostin Formation in Spitsbergen, also recorded by Gobbett (1964) and Sarytcheva (1977d). The lectotype of the Spitsbergen species (Wiman, 1914, Pl. 17, figs. 8–10, selected by Gobbett, 1964) and other syntypes and hypotypes are normally less transverse and larger than the Yukon material (Fig. 24). Other differences between the two species include the size of ears and the development of lateral ridges in the dorsal valve. Ears are comparatively small and less alate in *A. pseudohorrida,* irrespective of its large size, with hinge line usually equal to midwidth. Its outline, therefore appears to be less transverse and more often elongate. The dorsal interior of *A. pseudohorrida* was clearly shown by Gobbett (1964, Pl. 3, fig. 23) and Sarytcheva (1977d, Fig. 72). Its brachial ridges are distinct and cardinal ridges are short and do not extend across the ears as lateral ridges. In the Yukon species, the brachial ridges are poorly defined even in the well preserved dorsal interiors (Pl. 6, figs. 10–12, 28); but cardinal ridges are distinct, crossing ears as ear baffles, and continuing forward as prominent lateral ridges (Fig. 24B).

Anemonaria pinegensis (Likharev, 1931, p. 26, Pl. 3, figs. 24, 25) from the Kungurian strata in Kanin Peninsula, northwestern Russia, redescribed by Sarytcheva (1977d, p. 123, Pl. 18, figs. 5–14; Figs. 73, 74), is close in size but differs in possessing a longer trail and a narrower, much shallower sulcus.

Occurrence. Ey, Eog and Ej zones, Sakmarian to Early Artinskian.

Subfamily RETIMARGINIFERINAE n. subfam.

Diagnosis. Paucispiniferidae usually with well defined reticulation over disc of both valves; costae and concentric rugae normally strong; strut spines usually in one to three transverse rows of four to eight spines across the ventral valve, one to two pairs of large spines over the umbonal slopes, as well as occasional smaller halteroid spines scattered over the venter; marginal ridges in both valves or in dorsal valve only, usually strongest across the hinge and ear areas; cardinal process trilobate.

Genera included. *Rugivestis* Muir-Wood and Cooper, 1960, *Alifera* Muir-Wood and Cooper, 1960, *Retimarginifera* Waterhouse, 1970b, *Uraloproductus* Ustritskiy, 1971, *Caricula* Grant, 1976, and *Transennatia* Waterhouse, 1975c, (objective synonyms: *Gratiosina* Grant, 1976 and *Asioproductus* Zhan, 1977), and *Minispina* Waterhouse, 1982d.

Discussion. The diagnosis is mainly based on *Retimarginifera* studied by Waterhouse (1970b), Grant (1976), and Archbold (1984). Reticulation of the posterior part of the shell is prominent in all genera mentioned above although it varies in strength. The new subfamily resembles the Paucispiniferinae

Muir-Wood and Cooper in the paucity and coarseness of the spines as well as in the internal structures, but differs in possessing a prominent radial and concentric ornament, which usually forms a distinct reticulation over the posterior shell. Probolioniinae Muir-Wood and Cooper, 1960, classified within the Marginiferidae by Muir-Wood and Cooper (1960), is also reticulate on the posterior shell and has a few ventral strut spines, but it may be distinguished by as many as 40 to 50 multiple trails arising from the dorsal marginal ridge.

Genus *Uraloproductus* Ustritskiy, 1971

Type species. (OD) *Productus stuckenbergianus* Krotov, 1885.

Diagnosis. Shell small to medium in size, transverse, strongly concavo-convex without abrupt geniculation; dorsal valve closely following ventral valve in curvature, delimiting very narrow visceral cavity; costae weak over visceral disc, strong on trail; rugae confined to umbonal region of both valves; reticulation distinct; sulcus and fold normally prominent; spines confined to ventral valve, one from each ear tip, one or two pairs over umbonal slopes, one to two pairs on trail in front, with a few additional smaller spines scattered over visceral disc; no distinct hinge row or curved row of spines over umbonal slopes; dorsal valve pitted. Dorsal interior unknown.

Discussion. The name *Uraloproductus* was proposed by Ustritskiy (1971, p. 21), in a footnote, for *Productus stuckenbergianus* Krotov, 1885. Abramov and Grigor'yeva (1983, p. 83) first described the genus. The spines were poorly figured in the type specimens of *Productus stuckenbergianus* (Krotov, 1885, Pl. 4, figs. 4-6). Abramov and Grigor'yeva did not indicate the number and distribution pattern of the spines, but these were shown in the illustrations of the type species figured by Ifanova (1972, Pl. 6, figs. 10-14). The few strut spines consist of one pair on the ears, one pair on the posterolateral slopes, and one pair on the trail anteriorly, as well as a few smaller halteroid spines over the umbonal region. The large pair of auricular spines was also shown in *Uraloproductus bilobatus* Abramov and Grigor'yeva (1988). One large specimen, here identified as *Uraloproductus* sp. B, has two pairs of strut spines on the trail.

Uraloproductus is externally very close to *Retimarginifera* Waterhouse (1970b), as pointed out by Ustritskiy (1974), from which it may be distinguished by its coarser costae, a more transverse outline, a less concave dorsal valve, and a broader visceral cavity.

Uraloproductus sp. A

Plate 6, figures 40-42; Figure 25A

Material. One specimen with valves conjoined from GSC loc. 53951.

Description. Shell 20 mm wide, 16 mm long, and 7 mm high; strongly concavo-convex (Fig. 27A); hinge line at maximum width and approximately equal to midwidth.

Ventral valve strongly convex, most inflated at about posterior third of shell length; visceral disc small and short, strongly swollen; umbo narrow and pointed, strongly incurved and projecting beyond hinge for about 1 mm; umbonal angle at 45°; umbonal slopes high and vertically set off, gently concave or rounded in outline; ears partly damaged, generally small, slightly convex, moderately defined by depression separating ears from umbonal slopes; cardinal extremities rounded at about 90°; trail approximately twice as long as visceral disc, moderately convex; sulcus prominent, commencing at 5 to 7 mm from umbo with sulcal angle measured from umbo at 20°, generally broad and shallow, floor well rounded. Costae distinct on trail, weak or absent over umbonal region and ears, low and rounded, six in 5 mm at midlength, occasionally increasing anteriorly by intercalation; rugae strong over umbonal region where costae are ill defined, 11 in total, diminishing forward in strength, crossing costae on anterior disc; reticulation moderately distinct (Pl. 6, fig. 42). Spines few, one seen from flank bounding sulcus, one from umbonal slope, about 0.5 mm in diameter, with additional smaller spines located near umbo, 0.3 mm in diameter (Fig. 25A).

Dorsal valve deeply concave (Pl. 6, fig. 40), closely following curvature of opposite valve; visceral cavity narrow, 2 to 3 mm deep at maximum depth (Fig. 25A); fold beginning about 5 mm in front of tip of dorsal umbo, extending to anterior margin as low median swelling. Dorsal ornament similar to that on ventral valve but costae more prominent over visceral disc and

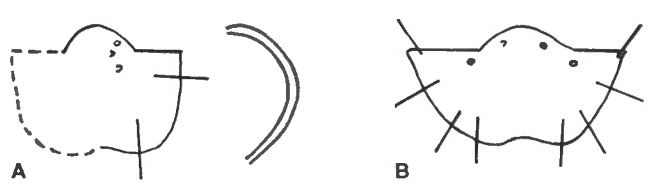


Figure 25. *A ventral spine pattern and lateral profile of **Uraloproductus** sp. A (GSC 96980, x1.5); B, ventral spine pattern of **Uraloproductus** sp. B (GSC 96981, x1).*

reticulation better defined, lacking spines, occasionally pitted.

Comparisons. This single shell resembles in size and ornament *Uraloproductus stuckenbergianus* (Krotov, 1885, p. 267, Pl. 4, figs. 4–6), also recorded by Frederiks (1915a) and Ifanova (1972), from the Sakmarian faunas of the Urals, but differs in possessing a narrower and more incurved umbo, smaller, less well defined ears, and a more strongly curved lateral profile. The spine pattern is poorly known in the Russian species.

Occurrence. Ej zone, Early Artinskian.

Uraloproductus sp. B

Plate 6, figure 43; Figure 25B

Material. One ventral valve with damaged trail from GSC loc. 57266.

Description. Specimen 30 mm wide, 15 mm long, and 10 mm high; strongly convex; hinge line greatly extended by large ears, marking maximum width; visceral disc strongly inflated, broad, and moderately delimited from ears through broad depression; umbo prominent, strongly extended and incurved beyond hinge line; ears large, well discriminated, moderately convex in profile, with cardinal extremities pointed at about 50°; sulcus prominent, beginning at 7 mm from umbo with sulcal angle close to 35°, generally broad and shallow, slightly widening and deepening forward, floor broadly concave. Costae distinct on anterior disc and trail, faint posteriorly, generally low and rounded, seven in 5 mm on anterior disc; rugae strong in umbonal region, diminishing forward, 11 in total, round-crested; reticulation indistinct in umbonal region, moderately formed on anterior disc; ears lack costae and rugae. Spine bases arranged in regular pairs (Fig. 25B), one pair from cardinal extremities, one pair on posterolateral slopes, two pairs on trail in front, generally 0.6 to 0.8 mm in diameter, with additional smaller spines over umbonal region.

Comparisons. The single ventral valve is similar in known respects to *Uraloproductus bilobatus* Abramov and Grigor'yeva (1988, p. 121, Pl. 7, figs. 2, 3, 5) from the Upper Carboniferous lower Akatchan Suite of the Verchoyan Mountains, but the spines in the Russian species are poorly known. The species was said to have one pair of auricular spines and some small spines scattered on the venter, so that the present form has one more spine pair.

The Yukon specimen resembles *U. stuckenbergianus* in generic respects but differs in its large size, extensive ears, and, possibly, one more pair of large spines on trail.

Productus (*Marginifera*?) *himalayensis* Stepanov (1934, p. 53, Pl. 4, figs. 15–18) (not Diener) from the Sakmarian Bryozoa Limestone in Kolva River, northern Urals, was previously considered to be conspecific with *U. stuckenbergianus* (Solomina, 1960; Ifanova, 1972). The Russian species is large and possesses more extensive ears, approaching the Yukon material, but it seems to have a deeper sulcus with an angular floor. *Productus himalayensis* Diener, 1899, the type species of *Lamnimargus* Waterhouse, 1975, from the Late Permian *Lamnimargus himalayensis* Zone in the Himalayas, is clearly distinguished by its multiple trails in the dorsal valve.

Occurrence. Eog zone, Late Sakmarian.

Genus *Rugivestis* Muir-Wood and Cooper, 1960

Type species. (OD) *Proboscidella*? *carinata* Muir-Wood and Cooper *in* Cooper (1957).

Diagnosis. Small to medium-sized shell, ventral trail carinate with incipient tube; cincture present on both valves, flattened marginal rim extending around to hinge; ventral internal submarginal rim distinct; costae irregular, crossed by rugae in posterior shell, reticulation variably developed; spines confined to ventral valve, two pairs on posterolateral slopes, one pair on flanks bounding sulcus, with few additional smaller spines scattered over umbo, no rows near hinge or on umbonal slopes.

Rugivestis arctica n. sp.

Plate 8, figures 9–14; Figure 26

1959 *Marginifera peregrina* (Frederiks); Kashirtsev (partim.), p. 47, Pl. 19, figs. 4, 5, non *cet.*

Etymology. After the Arctic.

Holotype. GSC 96976 from JBW loc. 109, Ettrain Creek, northern Ogilvie Mountains; Ey zone, Jungle Creek Formation; Plate 8, figure 12.

Diagnosis. Small shell with distinct sulcus and fold, weak costae and strong rugae.

Material. One ventral internal mould from GSC loc. 53951; four ventral valves and one dorsal valve from JBW loc. 109; two ventral valves and two dorsal valves from JBW loc. 113.

Description. External. Shell small, moderately to strongly concavo-convex; widest along hinge line. Ventral valve with strongly convex venter and flattened marginal rim (Pl. 8, figs. 11, 12, 14); umbo prominent, extended, and slightly incurved beyond hinge; umbonal slopes moderately high and steep, straight or gently convex toward hinge; umbonal angle close to 90°; ears large, triangular, flatly convex, clearly separated from venter (Pl. 8, fig. 13); cardinal extremities acute between 70° and 80°; cincture short, deep; marginal rim approximately 0.2 of shell length, extending around to hinge with prominent nasute and carinate trail in front (Pl. 8, figs. 12, 14); sulcus commencing at 2 to 3 mm from umbo with sulcal angle between 10° and 15°, narrow and deep over venter, broad V-shaped in section, replaced over carinate trail by gentle fold. Ventral ornament of costae and rugae (Pl. 8, figs. 10, 13), absent from ears; costae low and rounded, generally indistinct, extending from umbo to anterior margin, five to six in 5 mm at midlength; rugae high and narrowly rounded, much stronger than costae, separated by deep, narrow interspaces, fading toward cincture, crossing costae but not forming distinct reticulate pattern. Spines few and slightly differentiated (Fig. 26), six large spines symmetrically arranged, two pairs on umbonal slopes, one pair on flanks bounding sulcus in front, generally 0.8 to 1 mm in diameter; in addition, few smaller spines observed over umbo, 0.3 to 0.5 mm in diameter.

Dorsal valve moderately to strongly concave in visceral region; fold low and rounded, beginning 3 to 4 mm in front of umbo, anteriorly flattened. Dorsal costae indistinct; rugae well defined, stronger than those on opposite valve; reticulation indistinct. No dorsal spines.

Internal. Ventral submarginal ridge distinct (Pl. 8, fig. 11), corresponding to external cincture; muscle field obscure.

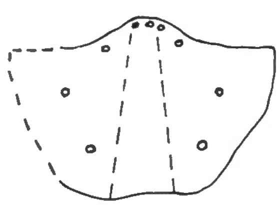


***Figure 26.** Ventral spine pattern in **Rugivestis arctica** n. sp. (GSC 96978, x2).*

Dimensions (in mm).

Specimens (Ventral valves)	Length	Width	Height
GSC 96974	17	25	?6
GSC 96975	15	20	+3
GSC 96976	17	+20	+3
GSC 96978	+14	22	6.5

Comparisons. Two ventral valves from the western Verchoyan Mountains that are likely conspecific with the new species were referred by Kashirtsev (1959, Pl. 19, figs. 4, 5) to *Marginifera peregrina* (Frederiks), a species originally described from the Upper Permian of the Russian Far East (Frederiks, 1925, Pl. 1, figs. 41–44) and clearly distinguished from the Verchoyan material by its large size, fine, distinct reticulation, and ill defined sulcus. The Verchoyan species comes from the Asselian–Sakmarian upper Kigiltas Suite and appears to be slightly larger than the Yukon species (30 mm wide), but other details are comparable. Another two specimens included in the same species by Kashirtsev (1959, Pl. 19, figs. 6, 7) from the same horizon are probably not conspecific because they have a much deeper sulcus.

Rugivestis is a rare Permian genus known so far only from three species: *R. carinata* (Muir-Wood and Cooper) (Cooper, 1957, p. 36, Pl. 3B, figs. 10–17; Fig. 2B) from the Coyote Butte Formation of central Oregon; *R. kutorgae* (Chernyshev, 1902, p. 643, Pl. 59, figs. 1–3) from the Asselian and Sakmarian faunas of the Urals; and *R. pangjiaoensis* Jin and Sun (1981, p. 135, Pl. 1, figs. 14–16) from the Upper Permian Gaqoi Limestone of east Xizang (Tibet). The first of these is small and has a moderately developed sulcus and fold resembling those of the new species, but its sulcus is broader and shallower, and its costae and rugae are equally strong, producing distinct reticulation in the umbonal region of the ventral valve. Like *R. carinata*, *R. kutorgae* has strong costae and distinct reticulation, and its sulcus is very weak. *Rugivestis pangjiaoensis* is nonsulcate and its ventral valve is more convex; but its ornament and short carinate trail are similar to the features of *R. arctica*.

Occurrence. In northern Yukon Territory, the new species is found in the Ey and Ej zones of the Jungle Creek Formation. Elsewhere, the new species was incorrectly described as *Marginifera peregrina* (Frederiks) by Kashirtsev (1959) from the Asselian to Sakmarian upper Kigiltas Suite of the Verchoyan Mountains, Siberia.

Family COSTISPINIFERIDAE Muir-Wood and Cooper, 1960

Genus *Costispinifera* Muir-Wood and Cooper, 1960

Type species. (OD) *Costispinifera costata* (King, 1931).

Diagnosis. Small subquadrate to slightly elongate Costispiniferidae distinguished by rugose umbonal region and conspicuously costate trail at maturity, numerous ventral spines over venter as well as on ears and along hinge margin, and sparse and delicate spines over dorsal valve.

Discussion. Echinauris Muir-Wood and Cooper, 1960 is distinguished from *Costispinifera* by its noncostate shell surface, unwrinkled umbonal region, and coarser and longer halteroid spines on posterolateral slopes of the ventral valve. The presence of fine dorsal spines serves to distinguish *Costispinifera* from *Hystriculina* Muir-Wood and Cooper, *Elliotella* Stehli, 1954, and *Liosotella* Cooper; *Costispinifera* may be further distinguished from *Liosotella* by its more numerous halteroid spines over the posterolateral slopes, and weaker costae on the trail.

Costispinifera paucispinosa n. sp.

Plate 6, figures 29-39

Etymology. Latin *paucus*, few; *spinosus*, spiny.

Holotype. GSC 96955 from GSC loc. 57053, section 116F-16; Ey zone, Jungle Creek Formation; Plate 6, figures 32, 33, 39.

Diagnosis. Small elongate shell with weakly costate ventral trail and lamellose, strongly dimpled dorsal valve; sulcus very shallow or not defined; concentric wrinkles weakly developed over umbonal region of ventral valve; relatively few ventral spines.

Material. Two specimens with valves conjoined, six ventral valves, and two dorsal external moulds from GSC loc. 57053.

Description. External. Shell small, less than 15 mm in width; slightly longer than wide; elongate in outline; strongly concavo-convex; widest in front of hinge line; anterior commissure slightly and broadly deflected dorsally in some specimens.

Ventral valve strongly enrolled longitudinally with short visceral disc and long trail (Pl. 6, fig. 37), geniculation angle close to 90°; visceral disc occupying approximately posterior third or less of shell curvature length; umbo prominent, strongly incurved with short, suberect beak that projects beyond hinge by about 0.5 mm; umbonal angle at 45° in holotype; umbonal slopes high and steep, straight, or gently concave in outline; ears very small (Pl. 6, fig. 32), but clearly differentiated from high visceral disc; cardinal extremities broadly rounded between 90° and 100°; lateral margins nearly parallel to each other; trail elongate, moderately to strongly convex in profile, twice as long as visceral disc; sulcus indistinct (Pl. 6, fig. 39), varying from low median depression to being absent. Ventral umbonal region weakly rugose (Pl. 6, figs. 32, 33), smooth except for very fine concentric growth increments in some specimens; costae arising from geniculation and extending to anterior margin (Pl. 6, fig. 39), generally low and rounded, three costae in 4 mm, separated by slightly wider interspaces. Spines distinct, generally 0.5 to 0.8 mm in diameter, in one or two rows along hinge line, in tufts on umbonal slopes (Pl. 6, figs. 31, 34), where they point laterally to posterolaterally, and loosely scattered on venter (Pl. 6, figs. 36, 39), where they arise from costae without swollen bases; occasional finer spines over visceral disc.

Dorsal valve with large, subrounded, and flat or gently concave visceral disc, and short, broadly geniculate trail (Pl. 6, fig. 33); geniculation angle close to 90°; fold ill defined or absent. Dorsal valve finely and conspicuously lamellose, lamellae consisting of very fine concentric growth increments, seven to nine in 1 mm; dimples large, rounded, arranged in rough quincunxial pattern; hairlike spines sparse, scattered between dimples (Pl. 6, fig. 38); costae obscure.

Internal. Details not known except for well defined lateral and anterior ridges of dorsal interior observed from one fragment (Pl. 6, fig. 30).

Dimensions (in mm).

Specimens	Valve	Length	Width	Height	Hinge width
GSC 96954	CON	15	14	8	11
GSC 96955	CON	16	14.5	9	12
GSC 96956	VEN	13	13	8.5	–

Comparisons. These small elongate shells are distinct in their external appearance, as they lack the prominent wrinkles seen in the umbonal region of the type *Costispinifera*. The type species, *C. costata* King, 1931 (see also Cooper and Grant, p. 1975, Pl. 320, figs. 1-44; Pl. 321, figs. 10-29) chiefly from the Willis Ranch Member of the Word Formation of west Texas, resembles the Yukon species in overall appearance, but differs in its larger size, larger ears, stronger costae, and more numerous ventral spines.

Occurrence. Ey zone, Early Sakmarian.

Superfamily ECHINOCONCHIDAE Stehli, 1954

Family ECHINOCONCHIDAE Stehli, 1954

Subfamily CALLIPROTONIINAE Lazarev, 1985

Genus *Calliprotonia* Muir-Wood and Cooper, 1960

Type species. (OD) *Calliprotonia renfrarum* Muir-Wood and Cooper, 1960.

Diagnosis. Echinoconchid shell distinguished by flat concentric bands fully covered by undifferentiated spines on posterior shell and by two series of spines on anterior shell, and by highly elevated concentric ridges.

Discussion. Lazarev (1985, p. 64-69) discussed the genus and its distinctions from allied genera *Echinoconcha* Weller, 1914 and *Karavankina* Ramovs, 1966. From both *Calliprotonia* is distinguished by its raised concentric ridges and well defined concentric bands bearing undifferentiated spines in the posterior of the ventral valve and two series of spines anteriorly.

Calliprotonia inexpectum (Cooper, 1957)

Plate 8, figures 15-26; Figure 27

1957 *Echinoconchus inexpextus* Cooper, p. 48, Pl. 8C, figs. 13-26.

Holotype. USNM 125551 figured by Cooper (1957) in Plate 8C, figures 24-26 from the Coyote Butte Formation of central Oregon, United States.

Diagnosis. Moderately large, slightly elongate *Calliprotonia* with broad umbo and long dorsal median septum; each concentric band on anterior ventral valve bearing three to five rows of coarse spines and one to two rows of smaller spines.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53858	2	3	4
GSC loc. 53999		2(em)	
GSC loc. 56917	4	1	
GSC loc. 56922	3		
GSC loc. 57052	2		1
GSC loc. 57053	3	2	2
GSC loc. 57141	2		
GSC loc. 57154	1		
GSC loc. 57275	1	1(em)	
JBW loc. 2	1(im)		
JBW loc. 24	1(em), 6(im)	1, 1(im)	3
JBW loc. 88	2(em)	2(em), 1(im)	
JBW loc. 109			2
JBW loc. 508	2	2	

Description. External. Shell of medium size, ovate to slightly elongate with length nearly equal to width; widest at midlength or in front.

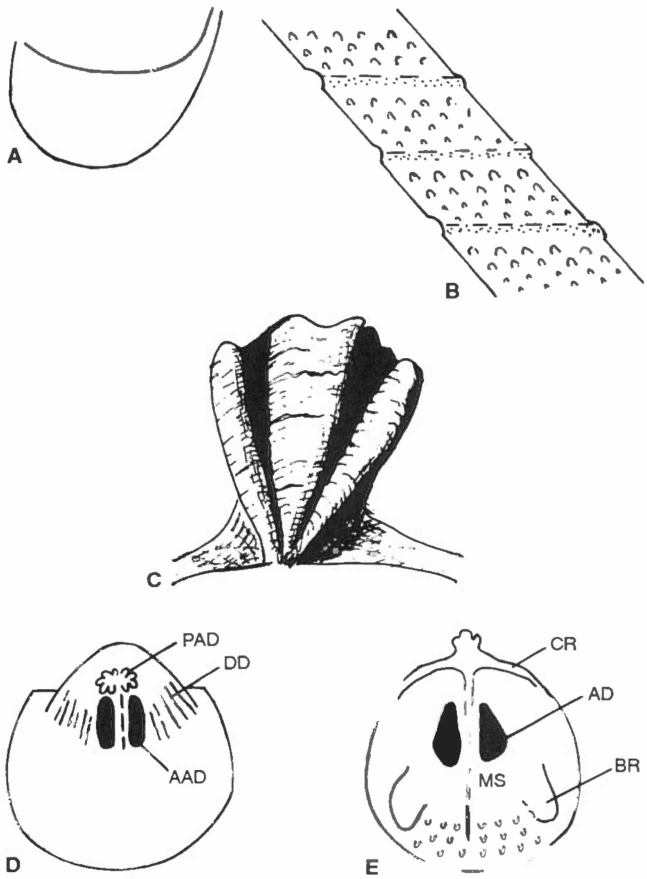


Figure 27. Calliprotonia inexpectum *(Cooper). A, lateral profile (GSC 97665, x1); B, ventral spine pattern (GSC 96983, x2.5); C, cardinal process (GSC 96984, x5); D, ventral muscle scars (GSC 96982, x1); E, dorsal interior (GSC 96987, x1). AAD, anterior adductor; AD, adductor; BR, brachial ridge; CR, cardinal ridge; DD, diductor; MS, median septum; PAD, posterior adductor.*

Ventral valve strongly convex, most inflated at posterior third and behind midlength of shell (Fig. 27A); visceral disc strongly swollen and delimited by high umbonal slopes, triangular in shape; umbo prominent, strongly extended and incurved with beak overhanging hinge line and extending beyond it by about 3 mm (Pl. 8, fig. 19); umbonal slopes high and steep, straight or only gently convex in outline; umbonal angle between 50° and 60°; hinge line about half shell width; ears rather small or not defined; cardinal extremities well rounded at 115°; flanks rounded, lateral slopes high and steeply sloping to lateral margins, conspicuously flared forward; no sulcus except for very shallow median deflection in some specimens (Pl. 8, fig. 20). Flat concentric bands distinct, extending from umbonal region to anterior margin (Pl. 8, fig. 17), 3-4.5 mm in diameter at maximum, slightly decreasing in diameter toward lateral margins and umbo, more closely spaced over umbonal and lateral slopes and toward anterior margin where they may overlap and become lamellose in some specimens, separated by elevated concentric ridges (Fig. 27B); concentric ridges 0.8-1 mm high, approximately symmetrical in section and sharp-crested in some specimens; each concentric band almost fully covered by fine, long, prostrate spines, arranged in irregular rows; spines not differentiated in posterior half of valve where there are three to five rows of spines along each band; anteriorly, spines clearly differentiated into two series within each band: three to five rows of large spines located on posterior portion of concentric band, about 0.5 mm in diameter, and one to two rows of smaller spines, 0.3 mm across, on anterior portion (Fig. 27B); spines over umbo small and arranged in rough quincunxial order (Pl. 8, fig. 19).

Dorsal valve moderately and evenly concave without prominent geniculation, trapezoidal in shape; no distinct fold. Concentric bands about 2 mm in diameter on average (Pl. 8, fig. 22); concentric ridges less distinct than those in opposite valve, appearing more like concentric lines; each concentric band with four to six rows of more delicate spines, weakly differentiated.

Internal. Ventral adductor scars elevated, narrow-elongate in shape (Fig. 27D), anteriorly bisected by prominent median groove, each measuring 2 mm wide and 7 mm long; posterior adductor scars small and weakly dendritic, anterior scars strong, raised prominently, smooth; diductors moderately impressed, relatively large, flabellate, strongly marked by radial ridges; dorsal floor covered with distinct small endospines in concentric rows (Pl. 8, fig. 21).

Cardinal process trilobate in dorsal and posterior views (Pl. 8, fig. 22; Fig. 27C), supported at base by cardinal ridges and median septum (Fig. 27E); median septum extending over two thirds of shell length and ending without swelling; adductor scars moderately raised, tear-shaped, smooth; brachial ridges distinct, about 45° to horizontal, anterior loop distinct; cardinal ridges about 2 mm in diameter, slightly diverging from hinge, crossing ears, continuing forward as lateral ridges, which fade away before reaching anterior margin; three to four concentric rows of coarse endospines at 5-7 mm in front of adductors (Pl. 8, fig. 26), up to 1 mm in diameter, 1-2 mm apart, absent within brachial loops (Pl. 8, fig. 25).

Dimensions (in mm).

Specimens	Valve	Length	Width	Height	Hinge width
GSC 96982	VIM	20	21	16	14
GSC 96983	VIM	21	23	+11	18
GSC 96987	CON	27	30	-	16
GSC 96990	CON	24	27.5	-	16

Comparisons. The specimens are conspecific with *Calliprotonia inexpectum* (Cooper) from the Sakmarian to Lower Kungurian Coyote Butte Formation of central Oregon. The internal structure was not known from the type material but is well shown in the present specimens. Logan and McGugan (1968, p. 1132, Pl. 141, figs. 4-6) described as *Echinoconchus inexpectus* Cooper several slightly larger and more elongate specimens from the Kungurian Ranger Canyon Formation of southeastern British Columbia. These specimens also exhibit more rows of spines within concentric bands of the ventral valve, and more distinct dorsal spines.

Muir-Wood and Cooper (1960) assigned *Echinoconchus pelliceus* Chronic, 1949 from the Asselian Copacabana Formation of Peru to *Calliprotonia*. The Peruvian species, as redescribed and figured by Chronic (*in* Newell et al., 1953, p. 85, Pl. 15, figs. 1a-3c) is smaller and more elongate in outline than *C. inexpectum*, more attenuate in posterior portion, and has a much shorter median septum that does not reach midlength.

Calliprotonia sterlitamakensis (Stepanov, 1934, p. 26, Pl. 3, fig. 13) from the Sakmarian Bryozoa Limestone of north Urals, is poorly preserved, precluding detailed comparison. In his synonymy list, Stepanov included *Productus fasciatus* (not Kutorga) of Chernyshev (1902, p. 631, Pl. 31, fig. 7; Pl. 34, fig. 5; Figs. 72-74) from the Sakmarian beds at

Sterlitamak, south Urals. The ventral interior of the Sterlitamak specimens is identical to that of *Calliprotonia inexpectum*. Externally, the Sterlitamak material differs in being larger, more elongate, and in having a longer, narrower and more attenuate umbo.

Occurrence. *Calliprotonia inexpectum* occurs in the Ey, Eog, and Ej zones of Sakmarian to Early Artinskian age in northern Yukon Territory. Outside the Yukon Territory, this species is known only from its type locality, the Coyote Butte Formation, in central Oregon, United States.

Family WAAGENOCONCHIDAE Muir-Wood and Cooper, 1960

Genus *Waagenoconcha* Chao, 1927a

Type species. (OD) *Productus humboldti* d'Orbigny, 1842.

Discussion. *Septiconcha* Termier and Termier (*in* Termier et al., 1974, p. 125), type species *S. taeniosa* Termier and Termier, differs from *Waagenoconcha* by means of a massive dorsal median septum arising from an antron. The antron indicates the possible presence of buttress plates.

Waagenoconcha parvispinosa Cooper, 1957

Plate 9, figures 1–3

1957 *Waagenoconcha parvispinosa* Cooper, p. 47, Pl. 4C, figs. 8–12.

Holotype. USNM 125353 figured by Cooper (1957, Pl. 4C, figs. 9–10) from the Coyote Butte Formation, central Oregon, United States.

Diagnosis. Shell small and moderately convex, lacking sulcus and fold.

Material. One dorsal internal mould from GSC loc. 57053; two dorsal external moulds and one internal mould from JBW loc. 88; one dorsal external mould from JBW loc. 109; and one dorsal external mould from JBW loc. 113.

Description. Shell small for genus; subquadrate in outline; widest at midlength; cardinal extremities broadly rounded at 100°; dorsal visceral disc flat, trail short and geniculate at 130°; fold not developed. Fine, short spine ridges regularly arranged quincunxially, close-set, bearing fine, prostrate spines. Cardinal process rests on long shaft; cardinal ridges 1–1.5 mm thick, well rounded, not extending across ears; median septum posteriorly massive, anteriorly thin, extending beyond midlength; muscle scars obscure; numerous fine ridges covering disc floor, arranged in quincunxially; small pustules over trail, irregularly arranged.

Comparisons. This small *Waagenoconcha* agrees in all observable features with *W. parvispinosa* Cooper (1957). The Yukon specimens are slightly larger than the holotype but identical to other syntypes.

Occurrence. This species is known from the Early Sakmarian (Tastubian) Ey zone in northern Yukon Territory and from the Sakmarian to Kungurian Coyote Butte Formation of central Oregon.

Waagenoconcha permocarbonica Ustritskiy 1963

Plate 9, figures 4–15; Plate 10, figures 1–4

1963 *Waagenoconcha permocarbonica* Ustritskiy *in* Ustritskiy and Chernyak, p. 79, Pl. 7, fig. 6; Pl. 8, figs. 1–3.

1988 *Waagenoconcha wimani* (Frederiks); Abramov and Grigor'yeva, p. 121, Pl. 6, fig. 6; Pl. 7, fig. 1.

Holotype. A ventral valve figured by Ustritskiy and Chernyak (1963, Pl. 8, fig. 2) from the Late Carboniferous Makarov Horizon of western Taimyr, northern Russia, kept at the CNIGR Museum.

Diagnosis. Large, subquadrate to subrounded shell with strongly convex ventral valve and moderately developed sulcus; spine ridges fine, short, and well rounded on crests, five to eight ridges in 5 mm over umbonal region, 20–25 in 5 mm near anterior margin.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53703	1		
GSC loc. 53710	1(em)	2	
GSC loc. 53710	1(em)		
GSC loc. 53723	2	3(em)	4
GSC loc. 53774	3		
GSC loc. 53775			4
GSC loc. 53776	1(em)	1	
GSC loc. 53999	1		

JBW loc. 14		1(em)	
JBW loc. 54	1	1(em)	1
JBW loc. 109	1(em)		2(im)
JBW loc. 113	1		
JBW loc. 546		1	

Description. External. Shell large, subrounded to subquadrate in outline, width usually equal to length; widest at midlength or in front of it.

Ventral valve strongly inflated both transversely and longitudinally (Pl. 9, fig. 5), most convex at midlength; umbo prominent, moderately extended and strongly incurved with beak overhanging and protruding beyond hinge line by about 2 mm; umbonal slopes concave in outline, high and steep; umbonal angle between 75° and 85°; flanks steeply sloping to lateral margins; hinge line slightly narrower than midwidth with inconspicuous ears; cardinal extremities rounded at 110° to 115°; sulcus moderately developed (Pl. 10, fig. 1), commencing at about 8–15 mm from umbo with sulcal angle between 30° and 45°, initially indistinct, strongest over midlength, sulcal sides almost parallel to each other, floor broadly V-shaped in section, becoming shallower toward anterior margin (Pl. 9, fig. 6). Five to eight short spine ridges in 5 mm in umbonal region and 20–25 in 5 mm at anterior margin where a marginal band of close-set, fine spine ridges is present. Concentric growth increments indistinct over median portion of valve, strongest on umbonal slopes, about 2–3 mm apart.

Dorsal valve with moderately concave, rounded visceral disc and short, broadly geniculate trail; geniculation angle between 130° and 140°; fold indistinct (Pl. 9, fig. 11), commencing about 5 mm from dorsal umbonal tip, very low and broadly swollen on disc, weak on trail. Dorsal ornament of small elongate tubercles bearing hair like spines and small shallow pits, both closely set on anterior marginal band (Pl. 9, fig. 15).

Internal. Ventral adductor platform elongate (Pl. 9, fig. 13), bisected by low myophragm, each adductor scar measuring 2.5 mm wide and 13 mm long, posteriorly smooth, anteriorly slightly dendritic; large flabellate diductors weakly impressed, marked by radial ridges.

Cardinal process with moderately high shaft and approximately equally high myophore (Pl. 9, fig. 12), trilobate with deep median groove; median septum thick, 1.5 mm in diameter at origin, arising from base of cardinal process, tapering anteriorly and extending as far as visceral disc; cardinal ridges prominent, extending along hinge, 2–3 mm across, rounded in section, not crossing ears; adductors posteriorly placed, elongate and subrounded (Pl. 9, fig. 14), each 7 mm wide and 12 mm long, dendritic on posterior portions, relatively smooth anteriorly; brachial ridges given off horizontally from anterolateral edges of adductors, anteriorly recurved to form large loops; two to three distinct concentric rows of large endospines present just in front of median septum, 1 mm in diameter, 2–3 mm apart (Pl. 10, fig. 3). Dorsal valve not conspicuously thickened (Pl. 10, fig. 3).

Dimensions (in mm).

Specimens	Valve	Length	Width	Height	Hinge width	Umbonal angle
GSC 96991	CON	+55	65	+15	–	85°
GSC 96992	CON	50	52	+14	44	88°
GSC 96994	VEN	48	50	24	46	87°
GSC 96995	VEN	36	40	+11	32	73°

Comparisons. Specimens from the Verchoyan Mountains of Siberia strikingly similar to *Waagenoconcha permocarbonica* were probably incorrectly identified as *Waagenoconcha wimani* (Frederiks), the type species of *Wimaniconcha* Waterhouse, 1983a. *Wimaniconcha wimani*, as originally described and figured by Wiman (1914, p. 68, Pl. 14, figs. 8, 9; Pl. 15, figs. 1, 2; Pl. 16, figs. 1–4) from Kungurian-Kazanian strata in Spitsbergen, differs from the Verchoyan material considerably in being very large and mostly elongate and in having a flat, strongly thickened dorsal valve, as noted by Waterhouse (1983a).

Sarytcheva et al. (1968, p. 104) synonymized *Waagenoconcha permocarbonica* with *W. sarychevae* (Benedictova, 1962), a species described from the "Middle Carboniferous" Keregetas Suite of eastern Kazakhstan (see Sarytcheva et al., 1968, p. 104, Pl. 8, figs. 1–10). But later, Sarytcheva (1984, p. 123) recognized *W. permocarbonica* and pointed out that the Kazakhstan species could be distinguished by its more elongate outline and longer, coarser spine ridges. One additional difference is that the Kazakhstan species has a less convex ventral valve.

Waagenoconcha piassinaensis Einor (1939, p. 42, Pl. 7, fig. 2; Ustritskiy and Chernyak, 1963, p. 78, Pl. 7, fig. 1) from the Late Carboniferous Makarov Horizon of western Taimyr, north Russia, shares many characteristics with *W. permocarbonica,* but is distinguished by its longer, sharp-crested spine ridges that often terminate with slight anterior swelling (see also Sarytcheva, 1984, Pl. 13, fig. 5).

Occurrence. Waagenoconcha permocarbonica is found in the Ey, Eog, and Ej zones in northern Yukon Territory, ranging in age from Sakmarian to Early Artinskian. Elsewhere, this species is known from the Late Carboniferous Makarov Horizon and Late Carboniferous to Early Permian Turuzov Horizon of Taimyr, north Russia (Ustritskiy and Chernyak, 1963), and the Early Artinskian lower Echii Suite of the west Verchoyan Mountains, northeastern Siberia (Abramov and Grigor'yeva, 1988).

Family BUXTONIIDAE Muir-Wood and Cooper, 1960

Subfamily KOCHIPRODUCTINAE Lazarev, 1985

Genus *Kochiproductus* Dunbar, 1955

Type species. (SD by Muir-Wood and Cooper, 1960) *Productus porrectus* Kutorga (1844).

Discussion. Gemmulicosta Waterhouse (*in* Bamber and Waterhouse, 1971) is common in the Upper Carboniferous (Lazarev, 1984). It is distinguished from *Kochiproductus* in having strong, sometimes anastomosing costae interrupted by large ramp-like swellings on the ventral valve.

In his revision of the classification of buxtoniids and echinoconchids, Lazarev (1985) placed a high value on the presence or absence of buttress plates and used this feature for discriminating the Buxtoniidae from the Echinoconchidae, the former with buttress plates, the latter without. Accordingly, he classified the Kochiproductinae with the Echinoconchidae.

However, buttress plates are highly variable features even within a genus, as demonstrated by both Likharev (1938) and Lazarev (1985). Likharev (1938) stated that the median septum (and the buttress plates) in buxtoniids could be built differently in different specimens even from the same locality and that this variation of buttress plates and median septum "induces us to regard the medial septum in *Buxtonia* as an unhomogeneous formation; the posterior part of the septum, generally bifurcated, appears to be, in my opinion, nothing else as the ridges developed in connection with the base of the cardinal process and only as the last resort coalescing with one another and with the medial septum" (Likharev, 1938, p. 290). Lazarev (1985) pointed out that the buttress plates were distinct in Carboniferous species of *Waagenoconcha* but obsolete in Permian representatives. For the familial classification, therefore, it seems preferable to emphasize external ornament, particularly the spines and pattern of costae. Accordingly, the Kochiproductinae is here transferred back to the Buxtoniidae where it was placed as a genus by Muir-Wood and Cooper (1960).

Kochiproductus porrectus (Kutorga, 1844)

Plate 10, figures 5-12; Plate 11, figures 1-6; Figure 28

1844 *Productus porrectus* Kutorga, p. 26, Pl. 10, fig. 3.
1902 *Productus porrectus* Kutorga; Chernyshev, p. 634, Pl. 32, fig. 4; Pl. 55, fig. 1; Pl. 56, fig. 4; Pl. 62, fig. 2; Figs. 75-77.
1953 *Productus* aff. *P. porrectus* Kutorga; Gerasimov et al., p. 57, Pl. 7, fig. 4.
1957 *Kochiproductus* cf. *K. porrectus* (Kutorga); Cooper, p. 47, Pl. 4B, fig. 7.
1959 *Buxtonia* cf. *B. porrecta* (Kutorga); Kashirtsev, p. 38, Pl. 15, figs. 1-2.
1960 *Kochiproductus porrectus* (Kutorga); Muir-Wood and Cooper (1960), p. 260-261.
1963 *Kochiproductus* n. sp. Yole, Pl. 1, figs. 4, 5.

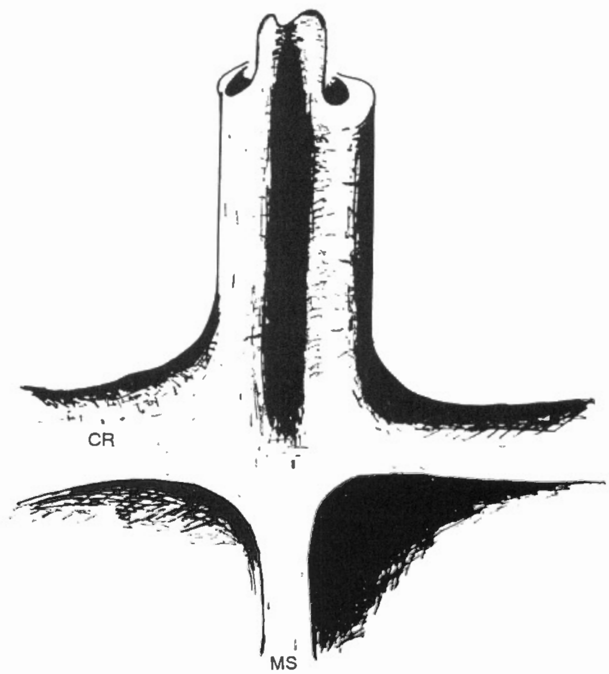


Figure 28. *Ventral view of cardinal process of **Kochiproductus porrectus** (Kutorga) (GSC 97004 approx. x7). CR, cardinal ridge; MS, median septum.*

1970 *Kochiproductus porrectus* (Kutorga); Solomina, p. 82, Pl. 5, fig. 1.
1971 *Kochiproductus* cf. *K. porrectus* (Kutorga); Waterhouse *in* Bamber and Waterhouse, Pl. 13, fig. 9.
1976 *Kochiproductus porrectus* (Kutorga); Li and Gu, p. 253, Pl. 168, figs. 2, 3; Pl. 183, figs. 2–4.
1980 *Kochiproductus porrectus* (Kutorga); Kalashnikov, p. 40, Pl. 7, figs. 3–4.

Holotype. The specimen figured by Kutorga (1844, Pl. 10, fig. 3) from the Sakmarian Sterlitamak Limestone near Sterlitamak, southern Urals, kept at the CNIGR Museum, St. Petersburg.

Diagnosis. Large, subquadrate to slightly elongate shell with broad, shallow sulcus and mostly simple, radiating costae interrupted by thin, elongate ramps.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53710	2		
GSC loc. 53714		1	1
GSC loc. 53951	2		
GSC loc. 53954	1		
GSC loc. 53999		1(em)	
GSC loc. 57053			
JBW loc. 24		1(im)	
JBW loc. 63		1(em), 1(im)	
JBW loc. 88		3(em)	1
JBW loc. 89	1(im)	1(im)	
JBW loc. 109	1(em)	1, 1(em)	
JBW loc. 110		1	
JBW loc. 113	1(em)	2	1
JBW loc. 508	1		
JBW loc. 537	1(em)		
JBW loc. 541		1(em), 1(im)	1
JBW loc. 545	1	1	
JBW loc. 559			1(im)

Description. External. Shell large, up to 80 mm in width; subquadrate to slightly elongate in outline; widest at midlength.

Ventral valve moderately to strongly convex without abrupt geniculation, most inflated at midlength or slightly behind it; umbonal region strongly swollen, umbo low and massive, strongly incurved, overhanging and protruding beyond hinge line by 1 to 1.5 mm (Pl. 10, fig. 10), umbonal angle between 60° and 75°; umbonal slopes high and almost vertically set; hinge approximately three quarters of shell width; ears small, triangular, flatly convex, well separate from venter; sulcus variably developed, generally ill defined, commencing at varying distances (ranging from 8 to 15 mm) from umbo, expressed as broad, shallow median deflection in most specimens (Pl. 10, fig. 7; Pl. 11, fig. 5), poorly differentiated from flanks, strongest over middle trail and toward anterior margin. Ventral ornament of distinct costae and inconspicuous rugae (Pl. 10, fig. 7); seven to nine costae in 10 mm at midlength, narrowly rounded, separated by interspaces of equal or, more often greater, width, straight, continuing from umbo to anterior margin, occasionally increasing in front by intercalation, regularly and repeatedly interrupted by thin elongate ramps (Pl. 10, figs. 7, 12); rugae strongest on umbonal and lateral slopes, ill defined over median portion, usually 2–4 mm wide, broadly rounded or sharp crested, slightly crossing costae; reticulation indistinct. Ventral spines arise from elongate ramps that are as wide as costae (Pl. 11, fig. 1), projecting forward at 70° to 80° to the surface; ramps swollen, 0.5 mm in diameter, 7 to 10 mm apart along costae (Pl. 10, fig. 7).

Dorsal valve with large, flat, rounded to slightly elongate or subquadrate visceral disc, and short, broadly geniculate trail with geniculation angle at 125°; anterior and lateral margins fringed by broad rim, which is recurved dorsally around to hinge (Pl. 10, fig. 9), clearly separated from trail through sharp, narrow trough; fold indistinct. Pattern of costae similar to that on ventral valve but lacking distinct ramps; rugae higher and narrower than over opposite valve, more closely spaced and conspicuously crossing costae to produce stronger reticulation (Pl. 10, fig. 10). Spines hair-like, arising from intersections of costae and rugae.

Internal. Ventral adductors small, dendritic (Pl. 11, fig. 5); myophragm indistinct, no median septum or ridge; diductors obscure.

Cardinal process with high shaft, bilobate with deep median sulci in ventral view (Fig. 28), conspicuously trilobate in dorsal and posterior views, myophore of median lobe dorsally curved; buttress plates fused with posterior end of median septum; antron filled with secondary material (Pl. 10, fig. 11); median septum massive, slightly tapering anteriorly, continuously extending near to anterior margin of disc; cardinal ridges extending along hinge (Pl. 10, fig. 6), 1.5 mm thick, rounded, not crossing ears; adductors elongate-oval in outline (Pl. 10, fig. 9), posterior scars large and dendritic, anterior scars comparatively small, smooth; brachial ridges obscure.

Dimensions (in mm).

Specimens	Valve	Length	Width	Height	Hinge width
GSC 97003	CON	53	54	23	40
GSC 97004	CON	64	+58	-	42

Comparisons. The Yukon shells are large with generally weak sulci, low and mostly simple radiating costae, and thin, elongate ramps that are as wide as the costae. These characteristics strongly suggest material commonly referred to as *Kochiproductus porrectus* (Kutorga, 1844). Other material cited above also appears to be conspecific, judging by the external morphology and internal structures.

Among the many reported occurrences of *K. porrectus*, some seem to embrace merely large sulcate productid shells with more or less repeatedly ramped costae bearing fine spines. For example, Ustritskiy and Chernyak (1963, p. 81, Pl. 9, figs. 4, 5) figured as *K. porrectus* two large specimens from the Late Carboniferous Makarov Horizon of central Taimyr, northern Russia. These specimens have a deeper, more distinct sulcus and broader, higher costae than the type material of *K. porrectus*. Kulikov (1974) identified as *K. porrectus* a single incomplete ventral valve from the Kungurian beds of the Urals, which appears to be distinguished by coarser costae, stronger rugae, and an indistinct sulcus. Reed (1925, p. 30, Pl. 5, figs. 12–14) ascribed to this species a few large, strongly costate, reticulate specimens from the Lower Permian in Chitral, Pakistan. Not enough features can be seen on these specimens to say whether or not they belong to *Kochiproductus*, but they appear to be much more strongly costate and reticulate than typical *K. porrectus* from the Urals, and have indistinct ramps and sulcus. Mansuy (1913, p. 42, Pl. 3, fig. 10) figured under *Productus porrectus* Kutorga a rather small fragmentary specimen from a Lower Permian outcrop in north Vietnam. This specimen seems to be too small to allow adequate comparison with the type material of *Kochiproductus porrectus*, and it is more strongly reticulate posteriorly. Solomina (1960, p. 41) referred *Productus* (*Buxtonia*) *lesnikowae* Stepanov (1934, p. 24, Pl. 2, figs. 8–10) to *Kochiproductus porrectus*. This species was described from the Sakmarian fauna of the Kolva River, northern Urals. It is much smaller and has a narrower, deeper sulcus than the type material of *K. porrectus*.

Kochiproductus peruvianus (d'Orbigny), from the Asselian Copacabana Formation of Bolivia, was sometimes considered to be a synonym of *K. porrectus* (Kozlowski, 1914; Frederiks, 1915a; King, 1931). But the Bolivian species, as redescribed and illustrated by Kozlowski (1914, p. 38, Pl. 4, figs. 1–4) and Samtleben (1971, p. 61, Pl. 3, figs. 1–3), has more conspicuous ramps, which are strongly swollen, elongate, and coarser than the costae. In addition, a thin, long median groove bisecting the adductors in the ventral interior was clearly shown in *K. peruvianus*, a feature not present in the Yukon material.

Occurrence. *Kochiproductus porrectus* is present in the Ey, Eog, and Ej zones in northern Yukon Territory, of Sakmarian to Lower Artinskian age. Elsewhere, this species has been reported from the Sakmarian faunas of the Urals (Kalashnikov, 1980); the Lower Artinskian lower Echii Suite and equivalents in the Verchoyan Mountains, northeastern Siberia (Solomina, 1970); the Sakmarian fauna of "Formation B" in Vancouver Island (Yole, 1963); the Sakmarian to Kungurian Coyote Butte Formation of central Oregon (Cooper, 1957); and the Sakmarian fauna in northeastern China (Li and Gu, 1976).

Kochiproductus saranaeanus (Frederiks, 1933)

Plate 11, figures 7–10, 12

1902 *Productus longus* Chernyshev (not Meek), p. 637, Pl. 27, fig. 2; Pl. 34, fig. 4; Pl. 35, fig. 2.
1933 *Buxtonia saranaeana* Frederiks, p. 37, Pl. 5, fig. 1.
1939 *Productus* (*Buxtonia*) *saranaeanus* (Frederiks); Likharev and Einor, p. 37, Pl. 5, fig. 1.
1986 *Kochiproductus saranaeanus* (Frederiks); Kalashnikov, Pl. 118, fig. 5.

Lectotype (here selected). The ventral valve figured by Chernyshev (1902, Pl. 34, fig. 4), from the ?Asselian Cora Horizon of the southern Urals, kept at the CNIGR Museum, St. Petersburg.

Diagnosis. Very large, elongate *Kochiproductus* with well defined sulcus; ventral costae repeatedly slightly swollen into indistinct radial ramps and subdivided on anterior trail; spines small and abundant, crowded on anterior trail.

Material. A single ventral valve and a fragment of a dorsal external mould from GSC loc. 53723.

Description. Shell 80 mm wide (excluding damaged ears), over 70 mm long, and 48 mm high; slightly elongate in appearance; probably widest at hinge.

Ventral valve strongly enrolled in lateral profile with geniculation occurring at about posterior third of shell curvature length (Pl. 11, fig. 10), geniculation angle between 90° and 100°; visceral disc strongly convex, triangular in outline, delimited by high, almost vertical umbonal slopes; umbo prominent, moderately extended, strongly incurved beyond hinge line for approximately 5 mm; umbonal angle close to 70°; ears mostly broken, probably small to moderately large; trail trapezoidal in shape, gently convex; sulcus distinct (Pl. 11, fig. 12), commencing 23 mm from umbo, extending to anterior margin as broad, moderately deep median depression, floor broadly rounded. Ventral costae low, rounded, repeatedly slightly swollen into indistinct radial ramps (Pl. 11, fig. 9), especially over visceral disc, seven in 10 mm over midlength, irregularly subdivided and intercalated over anterior portion of trail (Pl. 11, fig. 8), 12 in 10 mm at 15 mm from anterior margin, further subdivided and intercalated at front where costae start fading away toward anterior margin; rugae ill defined, strongest on umbonal slopes, almost absent over median portion; reticulation very weak. Spines numerous, small, arising from slightly rounded, little swollen nodes on costae (Pl. 11, fig. 9), spine bases 0.3 mm in diameter, 2 to 3 mm apart along costae; hair-like spines crowded over anterior third of trail, as many as 2 to 3 per mm (Pl. 11, figs. 8, 9), arising from both costae and interspaces.

Dorsal valve with flat visceral disc and broadly geniculate trail, geniculation angle about 110°. Costae stronger than on ventral valve, well rounded, eight to nine in 10 mm on disc and seven in 10 mm on posterior trail; concentric rugae distinct, crossing costae to produce prominent reticulation; visceral disc pitted; small spines arising from nodes at intersections of costae and rugae.

Comparisons. The ventral costae, which are frequently and irregularly subdivided over the frontal trail and are only slightly swollen into indistinct radial ramps, are most distinctive. The Yukon shell shares these characteristics with *Productus longus* Chernyshev, 1902 from the Cora Limestone of the Urals. This species was later found to be a homonym of *Productus longus* Meek, 1887 and renamed *P. saranaeanus* (Frederiks, 1933)

Occurrence. *Kochiproductus saranaeanus* is found in the Ey zone of Early Sakmarian age (Tastubian) in northern Yukon Territory. In the southern Urals, *K. saranaeanus* occurs in Asselian to Artinskian faunas. Elsewhere, this species has been found in the Late Asselian Nenets Horizon of Timan, northern Russia, and Early Permian (probably Sakmarian) exposures on the western coast of north Island, Novaya Zemlya, northern Russia.

Superfamily PRODUCTACEA Waagen, 1883

Family RETARIIDAE Muir-Wood and Cooper, 1960

Genus *Kutorginella* Ivanova, 1951

Type species. (OD) *Kutorginella mosquensis* Ivanova, 1951.

Discussion. *Kutorginella* is closely allied to *Thamnosia* Cooper and Grant, 1969 and *Thuleproductus* Sarytcheva and Waterhouse, 1972. From both, *Kutorginella* is distinguished primarily by lacking a thick brush of spines on the posterolateral slopes. *Retaria* Muir-Wood and Cooper, 1960 was referred to the synonymy of *Kutorginella* by Sarytcheva (1971).

Kutorginella yukonensis Sarytcheva and Waterhouse, 1972

Plate 7, figures 1–19

1971 *Kutorginella* sp. Waterhouse *in* Bamber and Waterhouse, Pl. 14, fig. 14; Pl. 16, fig. 16.
1972 *Kutorginella yukonensis* Sarytcheva and Waterhouse, p. 501, Pl. 7, figs. 1, 2.
1972 *Kutorginella triangulata* Sarytcheva and Waterhouse, p. 505, Pl. 7, figs. 3–8.

Holotype. GSC 26353, Ey zone, Jungle Creek Formation; GSC loc. 53722, section 116H-1B, figured by Sarytcheva and Waterhouse (1972, Pl. 7, fig. 1).

Diagnosis. Moderately large shell with well defined sulcus and broad umbo; seven to nine costae in 10 mm at midlength.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53703	1		
GSC loc. 53713	1		2
GSC loc. 53720			1
GSC loc. 53722			3
GSC loc. 53856	2		
GSC loc. 53946			1
GSC loc. 54001	1(em)		
GSC loc. 56917	6		
GSC loc. 56922	5		

GSC loc. 57049			1
GSC loc. 57052			1(im)
GSC loc. 57266	1	1	
JBW loc. 24	6	3(em)	
JBW loc. 54	1		
JBW loc. 58	1(em)		
JBW loc. 64	1		
JBW loc. 88	7, 5(im)	5(em)	2
JBW loc. 89	2, 2(em), 3(im)		
JBW loc. 109		6	
JBW loc. 508	2	2(em)	1

Description. External. Shell of medium to moderately large size; transverse in outline; widest along hinge.

Ventral valve strongly convex, most inflated at near midlength or slightly behind it; visceral disc convex, subtriangular to subrectangular in shape (Pl. 7, fig. 11), delimited by moderately high, steeply sloping umbonal slopes; umbonal angle between 90° and 120°; ears mostly broken off, well segregated from visceral disc; trail probably as long as visceral disc or slightly longer, moderately convex, slightly flared laterally; no tubiform extension developed at front; lateral slopes high and steep; sulcus beginning from anterior third of visceral disc with sulcal angle between 45° and 65° (Pl. 7, figs. 7, 16), strongest over midlength where the valve is most inflated, slightly shallower forward in some specimens, generally broad and shallow with well rounded floor, occupying less than one third of frontal width of trail, gradually merging with flanks. Seven to nine in 10 mm at midlength (usually eight or nine), low and well rounded, not extending to ears, increasing anteriorly by intercalation, separated by interspaces approximately as wide as costae, crossed by usually less distinct rugae (Pl. 7, figs. 6, 11); reticulation low, best developed on umbonal slopes, weak or not developed over median portion. There are three different arrangements of spines: 1) fine, suberect to erect spines arising from costae (Pl. 7, fig. 7), evenly distributed over entire valve, about 0.5 to 0.8 mm across, generally 3 mm apart, pointing anteriorly (Pl. 7, fig. 6); 2) in single row along hinge margin (Pl. 7, figs. 11, 15), as coarse as ventral spines, approximately three to four on each side; 3) coarser spines in curved row over posterolateral slopes (Pl. 7, fig. 15), diminishing in strength away from hinge margin (Pl. 7, fig. 15).

Dorsal valve with large, flat, triangular to subrectangular visceral disc and short, strongly geniculate trail, geniculation abrupt with angle close to 90°; fold not defined over visceral disc in most specimens, but arising as rather low median swelling from anterior disc in others, generally low and broad over trail. Dorsal costae and rugae similar to those on ventral valve. Spines more delicate and fragile; small, rounded dimples also prominent.

Internal. Ventral adductor ridge raised and weakly striated (Pl. 7, figs. 13, 18); large flabellate diductors well impressed, marked by deep radiating ridges and grooves.

Cardinal process with well defined trilobate myophore supported by long shaft (Pl. 7, figs. 5, 12), which is in turn supported by prominent median septum and well developed cardinal ridges; lateral ridges thin but well defined, crossing inside ears; anterior marginal ridge thin and low; median septum distinct between posterior adductors, very thin between anterior scars, and subdivided into two or three ridges in some specimens just in front of muscle field (Pl. 7, fig. 5); posterior adductor scars slightly impressed, elongate, weakly dendritic, anterior scars comparatively small, ovate, and smooth (Pl. 7, fig. 17); brachial ridges well defined with prominent loops and anteriorly recurved portions; floor densely pitted over posterior portion, about three pits in 1 mm.

Dimensions (in mm).

Specimens (ventral valves)	Length	Width	Height	Umbonal angle	Number of costae (in 10 mm at midlength)
GSC 26354	+38	+54	+22	120°	9
GSC 96958	+32	+42	+20	100°	8
GSC 96959	+31	+46	+16	110°	9
GSC 96961	–	+40	–	120°	9
GSC 96963	+29	+38	+20	105°	–

Comparisons. Sarytcheva and Waterhouse (1972) recognized two species of *Kutorgi nella* from the Ey zone based on a limited number of specimens. Their *K. yukonensis* was named for material from GSC loc. 53720, distinguished by large shells with a broad umbonal angle that defines a large, transverse visceral disc, a broad, shallow sulcus, and fine costae (seven to nine in 10 mm at midlength). Their *K. triangulata* was named for smaller shells from GSC loc. 53720 in the same section (116H-1B); these shells were said to have a narrower umbo, triangular visceral disc, better defined sulcus, and coarser costae (five to six in 10 mm at midlength, but from the illustrations there appears to be seven to eight in 10 mm at midlength). Measurements from a few comparatively well preserved specimens, including the two holotypes, syntypes, and additional material, indicate that there appears to be no clear differentiation of the two species in terms of either shell size, density of costae, or umbonal angle, as recognized by Sarytcheva and Waterhouse. *Kutorginella triangulata* is here regarded as a junior synonym of *K. yukonensis*, which has page priority.

Kutorginella orientalis (Frederiks, 1915a, p. 46, Pl. 2, figs. 5, 8; Pl. 3, figs. 6, 8, 10, 11) from the Sakmarian beds of the southern Urals and northern Timan has the overall morphology of the Yukon species, but is smaller and more strongly geniculate with a distinct tubiform trail at front. *Kutorginella neoinflatus* Likharev (1939, p. 90, Pl. 21, fig. 2) from the Upper Carboniferous of the Donets Basin, Russian Platform, and the Lower Permian of the Pechora Basin (Mironova, 1964), northern Urals, is also close in general appearance but has stronger rugae, particularly over the median portion of the ventral visceral disc.

Occurrence. Sarytcheva and Waterhouse (1972) described the present species from GSC locs. 53720 and 53722 from section 116H-1A, Peel River area. In northern Yukon Territory, *K. yukonensis* is found in the Ey, Eog, and Ej zones of the Jungle Creek Formation to the lowermost Tahkandit Formation, ranging in age from Sakmarian to Early Artinskian.

Genus *Thamnosia* Cooper and Grant, 1969

Type species. (OD) *Thamnosia anterospinosa* Cooper and Grant, 1969.

Diagnosis. Like *Kutorginella* in overall appearance, but with more numerous spines over the entire ventral valve, a thick brush of stout spines on the posterolateral slopes, and thickly concentrated spines on the anterior portion of the ventral trail.

Discussion. *Thuleproductus* Sarytcheva and Waterhouse is distinguished from *Thamnosia*, as summarized by Sarytcheva (1977a, p. 73), by its very large, elongate, and strongly enrolled ears, and to a lesser extent by its large size, and the less numerous, but more evenly distributed, spines on the ventral valve.

Thamnosia spinosa n. sp.

Plate 7, figures 20–22; Plate 8, figures 1–8

Etymology. Latin *spinosus*, spiny.

Holotype. GSC 96968 from GSC loc. 53712, section 116H-1A; Ey zone, Jungle Creek Formation; Plate 8, figures 6, 8.

Diagnosis. Moderately large shell with long elongate trail and weak sulcus; ventral spines usually in two to four rows on posterolateral slopes and thickly concentrated on anterior and middle portions of trail.

Material. One ventral valve from GSC loc. 53712; 10 ventral valves, six dorsal valves, and three conjoined shells from GSC loc. 57053; six ventral valves, one dorsal valve, two dorsal internal moulds, and nine conjoined shells from JBW loc. 63; one ventral valve from JBW loc. 113.

Description. External. Shell of average size for genus; subquadrate to elongate in shape; widest along hinge or slightly in front.

Ventral valve strongly arched in profile; geniculation occurring at about middle curvature length of valve or slightly behind it (Pl. 8, figs. 5–6), geniculation angle between 80° and 90°; visceral disc large, triangular in shape, moderately inflated with well distended and slightly incurved umbo; umbonal slopes straight or gently convex in outline, high and steep; umbonal angle between 85° and 95°; ears mostly broken off, ear bases well segregated from visceral disc; trail approximately one and a half to twice as long as visceral disc, gently flared anterolaterally; sulcus ill defined, beginning from anterior visceral disc, rather shallow on trail (Pl. 8, figs. 7, 8), not well discriminated from flanks. Seven to nine in 10 mm on trail, crests narrowly rounded, separated by interspaces as wide as costae or slightly narrower, increasing principally by intercalation, becoming thinner and frequently subdivided on anterior trail in holotype (Pl. 8, fig. 8), crossed over visceral disc by weak rugae; reticulation low and indistinct; fine growth increments well developed. Spines very characteristic, abundant, generally 1 mm in diameter, usually in three (ranging from two to four) rows on posterolateral slopes where they point laterally (Pl. 8, figs. 4–6), and thickly concentrated on middle and anterior portions of trail (Pl. 7, figs. 20–21) where they arise from costae with bases slightly wider than costae (Pl. 8, fig. 7), two to three spines in 5 mm along costae, projecting forward approximately at 80° to surface; few additional similar sized spines scattered over visceral disc and along hinge; smaller spines occasionally present among above mentioned coarser halteroid spines, less than 0.5 mm in diameter.

Dorsal valve with large, flat, subtriangular visceral disc and abruptly geniculate trail approximately as long as visceral disc; geniculation angle between 80° and 95°; fold indistinct, originating from anterior visceral disc, very low or flattened on trail. Dorsal ornament similar to that on ventral valve, but spines much more delicate, hair-like, sparse, accompanied by common dimples on visceral disc.

Internal. Ventral adductor ridge narrow and raised, slightly dendritic (Pl. 8, fig. 3); diductor scars large, flabellate, weakly impressed, marked by fine radial ridges and grooves.

Cardinal process with strong shaft, joined at base by massive cardinal ridges and median septum (Pl. 7, fig. 22); ear baffles prominent, lateral ridges thin but distinct, marginal ridge poorly developed; median septum distinct between posterior adductor scars where it may reach 2 mm in diameter, nearly disappearing between anterior scars, and becoming distinct again (about 0.5 mm in diameter) beyond muscle field, extending near anterior margin of visceral disc, ending with elongate swelling (Pl. 7, fig. 22); posterior adductors obscure, anterior scars small and raised as narrow elongate ridges; brachial ridges well developed with distinct horizontal and anteriorly recurved portions, arising from conjunction of posterior and anterior adductor scars; posterior disc floor densely pitted, anteriorly reflecting external costae.

Comparisons. Spines are the most distinctive characteristic of the new species. Their distribution pattern strongly suggests that of the type species, *Thamnosia anterospinosa* Cooper and Grant (1969, p. 10, Pl. 9, figs. 26, 27; 1975, p. 1032, Pl. 348, figs. 1-19; Pl. 349, figs. 1-5) from the Upper Artinskian Cathedral Mountain Formation of west Texas, but the Texas species is more strongly enrolled longitudinally with a shorter trail and more numerous, closely spaced spines, as well as the almost total lack of sulcus. No other species is particularly comparable.

Occurrence. Ey zone, Early Sakmarian.

Family DICTYOCLOSTIDAE Stehli, 1954

Subfamily DICTYOLCOSTINAE Stehli, 1954

Genus *Reticulatia* Muir-Wood and Cooper, 1960

Type species. (OD) *Productus huecoensis*, King, 1931.

Discussion. *Callytharrella* Archbold (1985, p. 19) differs from *Reticulatia* in possessing a broadly and deeply sulcate trail, costate ears, and irregularly branching costae on the trail and converging costae in the sulcus.

Reticulatia uralica (Chernyshev, 1902)

Plate 11, figure 11; Plate 12, figures 1-11;
Plate 13, figures 1, 2; Plate 32, figure 1

1902 *Productus uralicus* Chernyshev, p. 612, Pl. 32, fig. 1; Pl. 33, fig. 1; Pl. 62, fig. 1.
1915a *Productus moelleri* var. *uralicus* Chernyshev; Frederiks, p. 44, Pl. 2, figs. 1-2.
1934 *Productus uralicus* Chernyshev; Stepanov, p. 152, Pl. 14, figs. 7, 8.
1938 *Productus* (*Dictyoclostus*) *uralicus* (Chernyshev); Kulikov, p. 152, Pl. 2, figs. 1-2.
1939 *Productus* cf. *P. uralicus* (Chernyshev); Likharev and Einor, p. 49, Pl. 9, fig. 1.
1960 *Dictyoclostus uralicus* (Chernyshev); Volgin, p. 91, Pl. 11, fig. 3.
1960 *Dictyoclostus* cf. *D. uralicus* (Chernyshev); Solomina, p. 60, Pl. 11, figs. 1-6.
1964 *Reticulatia* cf. *R. moelleri* (Stuckenberg); Gobbett, p. 89, Pl. 8, figs. 10-11; Pl. 9, fig. 8.
1967 *Reticulatia uralica* (Chernyshev); Yanagida, p. 54, Pl. 16, figs. 7, 8; Pl. 17, figs. 1-4; Textfig. 5.
1971 *Reticulatia* cf. *R. uralica* (Chernyshev); Waterhouse *in* Bamber and Waterhouse, Pl. 13, fig. 4.
1986 *Reticulatia uralica* (Chernyshev); Kalashnikov, Pl. 115, fig. 1.

Lectotype (selected by Volgin, 1960, p. 91). The specimen with valves conjoined figured by Chernyshev (1902) in Plate 33, figure 1 from the Sakmarian Stage of the Urals, kept at the CNIGR Museum, St. Petersburg.

Diagnosis. Large shell with strongly enrolled ventral valve, large, transverse ears, weak sulcus, six to seven coarse costae in 10 mm over midlength of ventral valve, and strong, regular reticulation over posterior third of shell length.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53704		1(em)	5
GSC loc. 53950			1
GSC loc. 56917			1
JBW loc. 24		1(em), 1(im)	
JBW loc. 54	1		
JBW loc. 56	1		
JBW loc. 57		1(em), 1(im)	1
JBW loc. 59	1		
JBW loc. 109		1	
JBW loc. 113	2		

Description. External. Shell usually large, width varying from 60 to 120 mm; transverse in outline; widest along hinge.

Ventral valve strongly enrolled in lateral profile (Pl. 12, fig. 3), geniculation occurring at posterior third of shell curvature length with geniculation angle of 80° to 90°; visceral disc short and strongly convex, delimited by high, steep umbonal slopes, triangular in shape; umbo prominent, low, massive, slightly extended and incurved; umbonal angle between 70° and 90°; umbonal slopes gently convex in outline; ears large and well defined (Pl. 12, fig. 4), transversely extended, triangular in shape, strongly convex in section with pointed cardinal extremities at about 50°, separated from rest of valve by deep, well rounded depression just below high umbonal slopes; trail subquadrate to slightly elongate in shape, approximately one and a half to twice as long as visceral disc; lateral margins diverging slightly forward, anterior margin broadly rounded; anterior commissure emarginate (Pl. 13, fig. 1); sulcus generally weak, but variable in specimens even from the same locality: in GSC 97016 (Pl. 12, figs. 3, 10), sulcus moderately defined, commencing at about 20 mm from umbo, shallow on anterior disc, and slightly widening on trail, not well demarcated from flanks; in specimens from JBW loc. 57 (Pl. 13, figs. 1, 2) and some specimens from GSC loc. 53704 (Pl. 12, fig. 6), sulcus very weak, discernable only at midlength where it is best expressed as shallow median depression, disappearing forward on anterior trail or persisting to anterior margin as very shallow median deflection; flanks bounding sulcus broad and flatly convex in transverse direction, with nearly vertical lateral slopes. Costae and rugae equally strong (Pl. 12, fig. 5), distinct; nine costae in 10 mm at 10 mm from umbo, six to seven costae in 10 mm at about midlength, and five to six in 10 mm on middle section of trail, well rounded, increasing anteriorly by intercalation, not converging in sulcus; rugae covering posterior third of shell, five to six in 10 mm at 10 mm from umbo, crossing costae to form distinct, regular reticulation; no costae on ears (Pl. 12, fig. 10), but rugae may extend to anterior portions of ears. Spines few, moderately differentiated; coarse spines in row along hinge line, on ears, and as well as scattered over trail; finer spines clustered on visceral disc and umbonal slopes; hinge spines strong, up to 2 mm in diameter, approximately four each side of umbo, projecting posterolaterally at 65° to 75° to hinge; one or two similarly coarse spines on ear tips; approximately four to six large halteroid spines scattered on trail, 2 to 2.5 mm in diameter, arising from single or double costae, erect; finer spines arising from nodose swellings on reticulation of visceral disc and umbonal slopes (Pl. 12, figs. 5, 10), 0.5 to 0.8 mm in diameter.

Dorsal valve generally deeply concave; visceral disc large and flattened; trail about as long as visceral disc (Pl. 12, fig. 11); geniculation abrupt with angle between 90° and 100°; ears flat or slightly concave; fold variable as ventral sulcus, generally low and indistinct, occasionally prominent on trail in some specimens. Dorsal ornament similar to that on ventral valve, but lacks spines, growth increments more prominent (Pl. 12, fig. 11), three to five in 1 mm.

Internal. Ginglymus distinct in both valves (Pl. 12, fig. 6), extending along hinge as low band, not reaching cardinal extremities. Large flabellate ventral diductor scars observed in broken ventral valve, marked by prominent radial grooves and ridges.

Cardinal process high, massive (Pl. 32, fig. 1), trilobate in posterior and dorsal views, median lobe high and robust, joined at base by two lower, weaker lateral lobes on anterior face, myophore dorsally curved; median septum arising from base of cardinal process, posteriorly massive, 1.5 mm across, extending over two thirds of visceral disc, gradually tapering anteriorly; adductor scars strongly raised (Pl. 12, fig. 8), narrow-elongate in shape, each scar 5 mm wide and 10 mm long, conspicuously differentiated (Pl. 12, fig. 8): anterior scars small and highly elevated over disc floor, smooth; posterior scars relatively large, elongate, and dendritic; brachial ridges distinct (Pl. 13, fig. 2), proximal parts obscure, distal loops prominent and strongly recurved; cardinal ridges well developed, 1.5 mm across and well rounded, slightly diverging from hinge, extending laterally but not crossing ears to lateral margins; endospines numerous on floor of anterior disc just in front of median septum, as well as on trail, in irregular rows.

Dimensions (in mm).

Specimens (Ventral valves)	Length	Width	Height	Curvature length	Disc length	Trai length
GSC 97016	66	+76	50	133	40	+65
GSC 97021	+75	120	–	–	–	–

Comparisons. The described material appears conspecific with *Reticulatia uralica* (Chernyshev, 1902) from the Sakmarian Stage of the Urals.

Chao (1927a, p. 40, Pl. 1, figs. 5-9) assigned to *R. uralica* some shells from the Asselian Taiyuan Formation of north China. The Chinese material is comparable in size and some other external respects, but has a thick brush of spines of up to 1 mm in diameter on its extensive ears.

Reticulatia moelleri (Stuckenberg, 1898), as figured by Chernyshev (1902, p. 613, Pl. 34, fig. 1) from the Lower Permian of the Urals, is close in ornament but distinguished in being much smaller, less convex in ventral valve, and in having a broader area of reticulation that extends over two thirds of shell length, and in having finer costae, especially on the trail where there are 10 to 11 in 10 mm.

Reticulatia magna Sarytcheva (1977b, p. 101, Pl. 14, fig. 5; Pl. 15, fig. 1) from the Upper Carboniferous of northern Pai-Hoi Range, north Urals, resembles *R. uralica* in its large size, strong costae and rugae, but differs in having a broader umbo and less convex ventral visceral disc.

Reticulatia huecoensis (King, 1931, p. 68, Pl. 11, figs. 56, 57; Cooper and Grant, 1975, p. 1088, Pl. 378, figs. 14–17) from the Hueco, Gaptank, and Neal Ranch formations of Texas, United States, also recorded from the Russian Arctic and Spitsbergen (Sarytcheva, 1977b, p. 94, Pl. 12, figs. 1–6; Pl. 13, fig. 1; Figs. 56, 57), is similar in size and sulcus but has finer costae (8 to 10 in 10 mm at frontal margin), and more closely spaced reticulation.

Cooper (1957, p. 34, Pl. 3A, figs. 1–9) identified several large shells as *Antiquatonia reticulata* from central Oregon. No curved ridge-bearing spines over the ears was reported from the Oregon species, nor can it be seen from the illustrations. The Oregon species is large and strongly and regularly reticulate in the posterior third of the shell. It differs from *Reticulatia uralica* in possessing finer costae, probably has a more rounded outline, and a more prominent and consistent sulcus.

Occurrence. In northern Yukon Territory, *R. uralica* is found in the Ey, Eog, and Ej zones of the Jungle Creek Formation, of Sakmarian to Early Artinskian age. In the southern Urals, this species is known to be one of the characteristic species for the Sakmarian faunas (Stepanov, 1951), though it may also range into the Artinskian faunas. Elsewhere, it has been described from the Sakmarian to Artinskian Karachatyr Horizon in southern Fergana (Volgin, 1960); the Sakmarian strata in northern Timan, north Russia; the Upper Artinskian to Kungurian Talatin Suite in the Pechora Basin and the Pai-Hoi Range, northern Urals; the Asselian Tham Nam fauna in north central Thailand; the possibly Sakmarian beds in Novaya Zemlya; and the Asselian to Sakmarian Wordiekammen Limestone of Spitsbergen.

Genus *Antiquatonia* Miloradovich, 1945

Type species. (OD) *Productus antiquatus* Sowerby, 1821.

Diagnosis. Dictyoclostinid with strongly, regularly reticulate visceral disc, usually medium to large in size, subquadrate to slightly transverse in outline, and with large extended ears; trail long and strongly sulcate; a curved ridge bearing long, stout spines around and over bases of ears.

Antiquatonia cooperi Shi, 1990

Plate 13, figures 3–11

non 1822 *Antiquatonia sulcata* (Sowerby), p. 17, Pl. 319, fig. 2.
1957 *Antiquatonia sulcata* Cooper, p. 35, Pl. 5C, figs. 18–22.
1963 *Antiquatonia sulcata* Cooper; Yole, Pl. 2, fig. 18.
1990 *Antiquatonia cooperi* Shi, p. 490.

Holotype. USNM 125327 figured by Cooper (1957, Pl. 5C, figs. 18–21) from the Sakmarian to Kungurian Coyote Butte Formation of central Oregon, United States.

Diagnosis. Large *Antiquatonia* with short, strongly convex visceral disc and long, elongate, deeply sulcate trail; ears large and well defined.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53713			1
JBW loc. 14	1		
JBW loc. 24		1(em)	1
JBW loc. 113	1		

Description. Shell large for genus, slightly elongate in overall appearance, widest at hinge line.

Ventral valve strongly arched longitudinally with geniculation angle between 80° and 95° (Pl. 13, fig. 3); visceral disc approximately one third of shell curvature length, strongly and evenly convex, triangular, with high, nearly vertical umbonal slopes; umbo prominent, moderately extended, well incurved beyond hinge line approximately by 1.5 mm (Pl. 13, fig. 6); umbonal angle close to 60°; ears large, extending laterally well beyond venter (Pl. 13, fig. 4), triangular in shape, clearly delineated from venter through well defined umbonal depression, strongly enrolled in section; cardinal extremities pointed at 55°; trail narrow and conspicuously elongate in shape (Pl. 13, fig. 4), curvature length approximately twice as long as visceral disc, strongly convex in profile, with lateral slopes nearly parallel to each other; sulcus prominent, commencing from anterior disc with sulcal angle at 45°, slightly widening and deepening over geniculation area, deeper on trail but not widening much to anterior margin; flanks bounding sulcus broadly rounded in section. Costae distinct and narrowly rounded (Pl. 13, fig. 5), not extending to ears, 11 to 14 costae in 10 mm at 10 mm from umbo, seven to nine in 10 mm on middle trail, anteriorly increasing by intercalation, crossed by distinct concentric rugae over posterior 25 mm of shell curvature length (Pl. 13, fig. 6), forming prominent reticulation. Spines in single row along hinge, two or three spines on ears, about four spines arranged in low discontinuous curved ridge around and over ears (Pl. 13, figs. 3, 11), generally 1 mm in diameter; a few other spine bases are scattered on trail.

Dorsal valve with large flat visceral disc and approximately equally long trail; geniculation abrupt at 80° (Pl. 13, fig. 8); ears moderately concave; fold arising at about 10 to 16 mm from umbo, distinct over geniculation area and trail, crest broadly rounded. Costation similar to that on ventral valve, but rugae stronger and more regular; distinct and regularly defined reticulation extending over entire visceral disc; no spines.

Internal. Partly preserved dorsal interior (Pl. 13, fig. 7) shows low, dorsally trilobate cardinal process, median lobe large and high; cardinal ridges short, not crossing ears. Otherwise interior not shown.

Dimensions (in mm).

Specimens	Valve	Length	Width	Height	Curvature length	Disc length	Trail length
GSC 97011	VEN	64	+62	38	97	30	+56
GSC 97012	CON	55	60	30	100	28	+55

Comparisons. The large transverse ears, long, elongate, and strongly sulcate trail, and moderately strongly reticulate visceral disc of the Yukon material are identical to aspects of *Antiquatonia sulcata* Cooper, 1957 (not Sowerby) from the Coyote Butte Formation of central Oregon. *Productus sulcatus* Sowerby (1822, p. 17, Pl. 319, fig. 2) from the Lower Carboniferous (Viséan) of England possesses a distinctive row of spines over the ear bases and has been assigned to *Antiquatonia* (Sarytcheva, 1949; Litvinovich, 1962; Muir-Wood and Cooper, 1960; Zakowa, 1988). It differs from the Oregon species in having smaller ears and a shallower sulcus. Consequently, the Early Carboniferous British species becomes a homonym of the Oregon species. Shi (1990) renamed the latter *A. cooperi*.

Antiquatonia is common mostly in the Carboniferous, especially in its lower division (Sarytcheva, 1949). Few Permian representatives have been recorded, most from North America. *Antiquatonia hessensis* (King) as redescribed and figured by Cooper and Grant (1975, p. 1090, Pl. 391, figs. 6-9) from the Skinner Ranch Formation of western Texas is also a deeply sulcate form, but conspicuously transverse in outline with a large transverse trail and finer costae. *Antiquantonia planumbona* Stehli (1954, p. 316, Pl. 20, figs. 1-5) from the Bone Spring Formation of western Texas, also figured by Cooper and Grant (1975, Pl. 390, figs. 8-22), resembles *A. cooperi* in the presence of a well defined sulcus, but differs in its large transverse visceral disc and relatively short trail bearing numerous halteroid spines.

Productus aff. *P. multistriatus* Likharev and Einor (1939, p. 51, Pl. 9, fig. 4) (not Meek) from the Lower Permian on the western coast of the southern Island, Novaya Zemlya, has similar external characteristics but a curved ridge bearing spines over the ears is not known, and its generic position is thus uncertain.

Occurrence. Apart from its occurrence in the Ey zone in northern Yukon Territory and at the type locality in central Oregon, where it occurs in the Sakmarian to Kungurian Coyote Butte Formation, *Antiquatonia cooperi* is known also from Formation B, probably of Early Sakmarian age, on Vancouver Island.

Genus *Chaoiella* Frederiks, 1933

Type species. (OD) *Productus grunewaldti* Krotov, 1888.

Chaoiella sp.

Plate 13, figures 12-17

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53947			1
GSC loc. 53951	2		
GSC loc. 53954		1(em)	
JBW loc. 9		1(em)	

Description. Shell over 40 mm wide, 30 mm long, and 19 mm high; subquadrate in outline, strongly concavo-convex in profile; hinge line at maximum width.

Ventral valve strongly enrolled in lateral profile with geniculation angle close to 90°; visceral disc short and strongly inflated; umbonal slopes gently convex in profile, broadly rounded in section, high and steep; ears distinct, moderately extended, convex in section, clearly discriminated from steep umbonal slopes; trail approximately twice as long as visceral disc, slightly flared laterally and anteriorly; sulcus distinct, commencing at anterior third of visceral disc with sulcal angle about 40°, broad and moderately deep on trail, floor well rounded; flanks bounding sulcus broadly rounded in section. Costae fine and low, rounded, strongest on visceral disc, fading over anterior disc and trail (Pl. 13, fig. 15), evenly spaced, six in 5 mm at anterior disc, separated by wider interspaces; concentric rugae restricted to visceral disc, moderately strong on umbonal slopes and ears, indistinct over median portion, approximately 10 in total, slightly crossing costae; reticulation indistinct and irregular (Pl. 13, fig. 12), better defined on umbonal slopes. Spines few, in single row along hinge, 0.8 mm in diameter; four similarly coarse spines observed on trail, rare on visceral disc.

Dorsal valve with moderately concave disc and strongly and abruptly geniculate trail, geniculation angle 120° to 130°; fold distinct over anterior disc and trail, crest well rounded. Ornament similar to ventral valve, but lacking spines; concentric lamellae prominent on anterior trail.

Thin ginglymus well preserved along hinge of conjoined specimen (Pl. 13, fig. 17); other internal structures not seen.

Comparisons. These few poorly preserved specimens seem comparable to *Chaoiella grunewaldti* Krotov (1888, Pl. 1, figs. 9–11) from the Sakmarian strata of the Urals in all respects except for the weaker costae in the Yukon material. However, hypotypes of *C. grunewaldti* from a Lower Permian exposure at Gikash Siding of the Ural, figured by Muir-Wood and Cooper (1960, Pl. 54, figs. 1–11), strongly resemble the present material in possessing comparably weak costae, though they have stronger rugae and are larger.

Occurrence. Ey and Ej zones, Early Sakmarian to Early Artinskian.

Family HORRIDONIIDAE Muir-Wood and Cooper, 1960

Subfamily HORRIDONIINAE Muir-Wood, 1960

Genus *Sowerbina* Frederiks, 1928

Type species. (OD) *Productus timanicus* Stuckenberg, 1875.

Diagnosis. Horridoniinids with dorsal hinge spines and one or two large dorsal auricular spines; ventral valve lacking hinge spines but with one to three irregular radial rows of large halteroid spines over venter; micro-ornament of fine granules on both valves.

Discussion. *Sowerbina* appears to be very similar externally to *Horridonia* Chao, 1927a, and both were previously considered to be synonymous by some workers (Gobbett, 1961; Stepanov, 1961; Logan, 1966). But *Horridonia* is restricted to horridoniinids possessing a distinct row of ventral hinge spines, distinguished from *Sowerbina*, which lacks these spines (Dunbar, 1955; Sarytcheva, 1977c; Sarytcheva et al., 1960; Kalashnikov, 1980; Waterhouse, 1982a).

Praehorridonia Ustritskiy, 1962, was proposed for medium to large productid shells with faint costae and lack of ventral spines. *Bailliena* Nelson and Johnson, 1968 was erected for large Late Carboniferous horridoniinids with numerous ventral spines (both along the hinge and on the venter), but lacking dorsal hinge spines and possessing a microornament of fine concentric lamellae.

Burovia Ustritskiy (1980, p. 25) was named for three Late Permian horridoniinid species from the Arctic, including two previously described species from Greenland: *Burovia maynci* (Dunbar, 1955) and *B. rudis* (Dunbar, 1955). The genus is distinguishable from *Sowerbina* by its characteristic micro-ornament consisting of numerous fine concentric lirae and numerous small pustules, and by its strongly thickened anterior portion of the dorsal valve that may be as much as 12 mm thick.

Sowerbina bullocki (Nelson and Johnson, 1968)

Plate 14, figures 1–21; Figure 29

1963 *Horridonia* sp. Yole, Pl. 2, figs. 11, 12.
1968 *Horridonia bullocki* Nelson and Johnson, p. 726, Pl. 91, figs. 1-12; Textfigs. 3c, d.
1971 *Sowerbina* cf. *S. timanicus* (Stuckenberg); Waterhouse *in* Bamber and Waterhouse, Pl. 13, fig. 8.

Holotype. UA 524 figured by Nelson and Johnson (1968, Pl. 91, figs. 1–3) from the basal Tahkandit Formation, Tatonduk River, northern Yukon Territory.

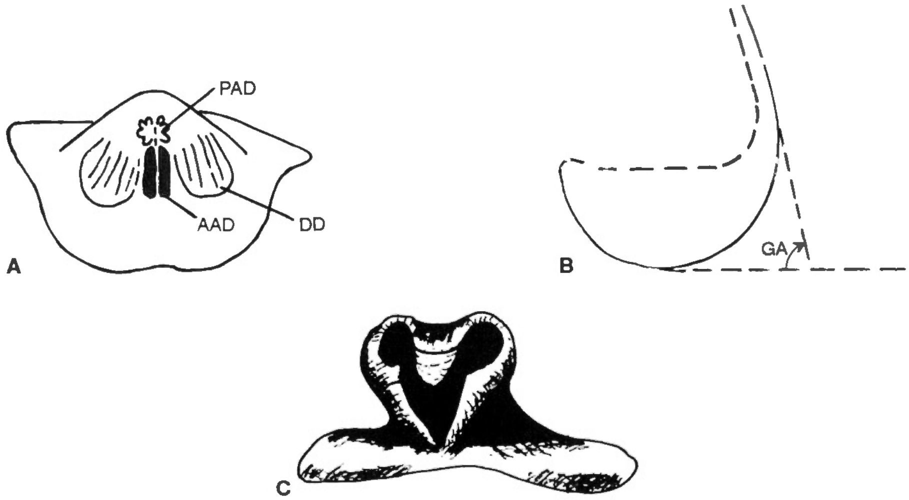


Figure 29. ***Sowerbina bullocki*** *(Nelson and Johnson). A, ventral internal mould (GSC 97027, x1); B, lateral profile illustrating geniculation angle (GSC 97026, x1); C, cardinal process (GSC 97032, x4). GA, ventral geniculation angle, other abbreviations as in Figure 27.*

Diagnosis. Moderately large, strongly enrolled *Sowerbina* with elongate trail and small ears; ventral spines few and irregularly arranged; sulcus distinct throughout ventral valve.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53856	9	2	4
GSC loc. 56937	3, 2(im)	3	2
GSC loc. 57255	2		
JBW loc. 113	3	1	

Description. External. Shell of medium size; slightly wider than long when ears are preserved; subquadrate to slightly elongate in shape (Pl. 14, fig. 15); widest along hinge line; anterior commissure strongly emarginate.

Ventral valve narrowly enrolled longitudinally (Pl. 14, fig. 16; Fig. 29B), geniculation occurring at about the posterior third of shell curvature length, with geniculation angle between 70° and 80°; visceral disc moderately to strongly convex, triangular in shape; umbo low and massive, not well discriminated, moderately extended, slightly if at all protruding beyond hinge line; umbonal angle between 80° and 100°; umbonal slopes broad and moderately high, steeply sloping to ears, gently convex in outline; ears small to moderately large (Pl. 14, fig. 13), clearly delineated from venter, laterally slightly extended by cardinal extremities, triangular, strongly convex in section; hinge line as wide as midwidth or slightly wider; cardinal extremities acute, between 40° and 60°; lateral margins nearly parallel to each other, almost perpendicular to anterior margin; trail one and one half to two times as long as visceral disc, elongate in shape, moderately convex in profile; sulcus prominent (Pl. 14, fig. 4), commencing from umbo with sulcal angle at about 45°, distinct throughout entire valve, floor narrowly to broadly rounded; flanks bounding sulcus well rounded in section with vertical lateral slopes. Ventral valve posteriorly smooth, trail usually irregularly costate, particularly on anterior portion (Pl. 14, fig. 15). A row of large dimples corresponding to coarse dorsal hinge spines clearly present along hinge margin in some well preserved specimens (Pl. 14, fig. 4), no hinge spines; few strut spines scattered on venter (Pl. 14, fig. 8), about three to five on each flank, irregularly arranged, up to 1 mm in diameter; spine bases not swollen. Micro-ornament of rather fine granules, two to three in 1 mm, preserved as fine pits on worn surfaces (Pl. 14, fig. 19).

Dorsal valve with large, subquadrate, and nearly flat visceral disc and short, abruptly geniculate trail, approximately as long as visceral disc or slightly longer, geniculation angle 70°; ears flat or gently concave; fold as distinct as ventral sulcus (Pl. 14, fig. 6), commencing from umbo or at a short distance from it, about 3 to 4 mm high and 7 to 10 mm wide on anterior disc and trail, crest angularly rounded. Dorsal hinge spines, four to five on each side of umbo, 1 to 1.5 mm in diameter, with one or two additional large auricular spines (Pl. 14, figs. 20, 21).

Internal. Ventral adductor platform long, narrow, and elongate (Pl. 14, fig. 3; Fig. 29A), strongly elevated above valve floor for up to 5 mm, extending over posterior half of valve floor, 5 to 7 mm wide and 8 to 10 mm long, crest flat, posteriorly slightly dendritic, bisected by indistinct myophragm; large flabellate diductor scars to each side, moderately depressed, marked by distinctive radial grooves and ridges.

Cardinal process trilobate in dorsal view (Pl. 14, figs. 17-18; Fig. 29C), median lobe high and dorsally curved, supported at base by strong, short cardinal ridges.

Dimensions (in mm).

Specimens	Valve	Length	Width	Height	Curvature length of disc	Curvature length of trail
GSC 97026	VEN	38	48	25	33	41
GSC 97031	DOR	30	40	–	–	–
GSC 97034	VEN	32	+36	20	–	–

Comparisons. *Pleurohorridonia elongata* Cooper (1957, p. 37, Pl. 7C, figs. 30–33) from the Coyote Butte Formation of central Oregon was based on ventral valves only. These ventral specimens are strikingly similar to those of the Yukon species, with narrow, elongate outline, small ears, short, strongly incurved visceral disc, narrow, elongate trail, narrow, deep sulcus; weak costae on anterior trail; and lack of ventral hinge spines. Unfortunately, the lack of dorsal material in the Oregon species hinders detailed comparison with the Yukon species, but the Oregon form may prove to be the senior synonym of *Sowerbina bullocki* (Nelson and Johnson, 1968).

Sowerbina timanica (Stuckenberg) from the Sakmarian faunas in the Urals and northern Timan, as redescribed and figured by Chernyshev (1902, p. 638, Pl. 30, fig. 5; Pl. 57, figs. 1–6; Figs. 78, 79) and Barchatova (1970, p. 129, Pl. 2, figs. 3–7), resembles *S. bullocki* in many respects, but is distinguished by its larger and more transverse ears, which consequently give rise to a transverse outline. In addition, ventral spines of *S. timanica* are more numerous, stronger, and arranged in more regular radial rows.

Occurrence. Nelson and Johnson (1968) described *S. bullocki* from the "Middle Recessive Unit" (i.e., the Jungle Creek Group in this study) and basal Tahkandit Formation in the Peel River area and the northern Ogilvie Mountains. Waterhouse (*in* Bamber and Waterhouse, 1971) figured this species as *S.* cf. *timanica,* a ventral valve from GSC loc. 53856, in the northern Richardson Mountains. *Sowerbina bullocki* was found elsewhere — from the probably Lower Sakmarian "Formation B" on Vancouver Island.

Genus *Tityrophoria* Waterhouse *in* Bamber and Waterhouse, 1971

Type species. (OD) *Tityrophoria nelsoni* Waterhouse (*in* Bamber and Waterhouse, 1971).

Discussion. This genus is distinguished from *Horridonia* Chao, 1927a and *Sowerbina* Frederiks in lacking dorsal spines and having more distinct costae, and from *Praehorridonia* Ustritskiy, 1962 and *Bailliena* Nelson and Johnson, 1968 in the absence of dorsal hinge spines.

Tityrophoria nelsoni Waterhouse, 1971

Plate 14, figures 22–26;
Plate 15, figures 1–8; Figure 30

1971 *Tityrophoria nelsoni* Waterhouse *in* Bamber and Waterhouse p. 216, Pl. 25, figs. 11–15.

Holotype. GSC 26417 from GSC loc. 57052, section 116C-2, figured by Waterhouse (*in* Bamber and Waterhouse, 1971, Pl. 25, figs. 13, 14); Ej zone, basal Tahkandit Formation; kept at Geological Survey of Canada, Ottawa.

Diagnosis. Moderately large shell with well pronounced sulcus and fold; fine and low, but regularly defined costae, especially on visceral disc; spines confined to ventral valve, in a row along hinge line and few scattered over venter.

Material.

Localities	Ventral	Dorsal	Conjoined
GSC 56917	6	1, 1(im)	
GSC 56922	5		1
GSC 57052	21, 7(im)	11, 2(im)	12
GSC 57275	5		
GSC 56	1(em)		

Description. External. Shell moderately large, transverse, strongly concavo-convex; widest along hinge; anterior commissure strongly emarginate (Pl. 15, fig. 7).

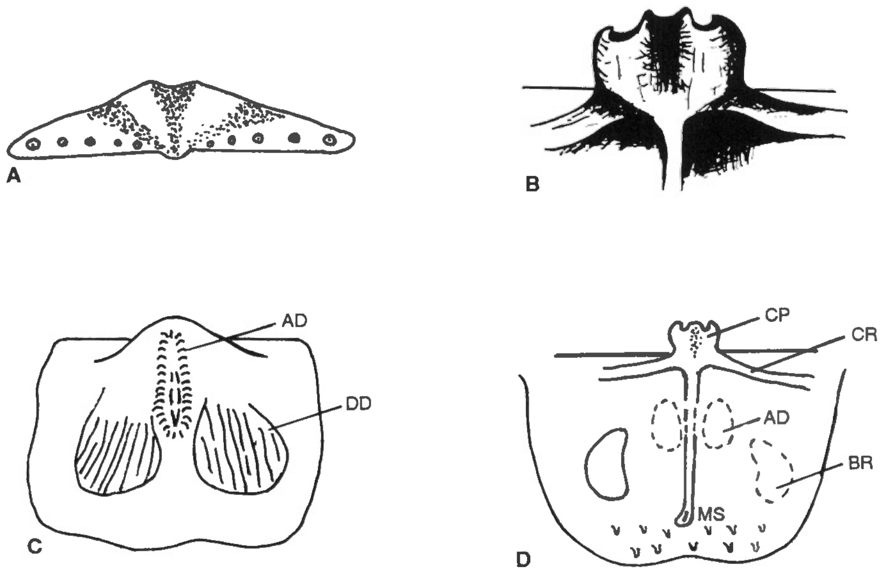


***Figure 30. Tityrophoria nelsoni** Waterhouse. A, posterior view of a ventral valve showing ventral hinge spines (GSC 97043, x1); B, cardinal process (GSC 97042, x4); C, ventral internal mould (GSC 97039, x1); D, dorsal interior (GSC 97042, x1). Abbreviations as in Figure 27. CP, cardinal process.*

Ventral valve strongly enrolled in lateral profile with geniculation angle at about 90°; visceral disc about one third of shell curvature length, moderately to strongly swollen, triangular in shape (Pl. 14, fig. 23), delimited by high and steep umbonal slopes; umbo broad with umbonal angle of about 130°, low and slightly incurved, beak slightly if at all extended beyond hinge line; umbonal slopes straight to very gently convex in outline, broad and moderately steep; ears large and transverse (Pl. 14, fig. 23), well segregated from visceral disc, strongly convex in section with obtuse cardinal extremities; trail about twice as long as visceral disc, elongate in shape; sulcus well pronounced (Pl. 14, fig. 23; Pl. 15, fig. 7), commencing at or very close to umbonal apex with sulcal angle of about 25°, initially weak over posterior half of visceral disc, anteriorly broad and deep with narrowly concave floor over frontal disc and trail where it is clearly separated from hump-shaped flanks. Faint costae clearly present in well preserved specimens (Pl. 15, fig. 1), obscure on worn surfaces, 10 to 12 in 10 mm over visceral disc, indistinct and fading away on trail; 10 to 12 weak concentric rugae present on umbonal slopes and ear bases, slightly crossing costae without defining any observable reticulation on visceral disc (Pl. 14, figs. 23, 24). Spines in single row along hinge line (Pl. 15, fig. 6; Fig. 30A) approximately five each side of umbo, 1 to 1.4 mm in diameter, diminishing in strength toward umbo; similarly coarse spines also present on flanks (Pl. 15, fig. 7), four to five on each side of sulcus, and one or two in sulcus, two to three over visceral disc, not in regular transverse or radial rows, suberect to erect (Pl. 15, fig. 1). Micro-ornament of minute pustules, shown as fine pits on worn surfaces (Pl. 15, fig. 7).

Dorsal valve with moderately concave visceral disc and sharply geniculated trail, delimiting very narrow (up to 5 mm) visceral cavity; geniculation angle between 70° and 90°; fold beginning at 7 to 8 mm from umbo, strongest over geniculation area and trail, crest narrowly rounded. Dorsal ornament similar to ventral valve, but lacking spines.

Internal. Ventral adductor platform strongly raised (Pl. 15, fig. 2; Fig. 30C), elongate-oval in shape, about 6 mm wide and 17 mm long, bisected by low myophragm, dendritic; diductor scars very large, deeply impressed, anterolateral to adductors, about 10 mm wide and 15 mm long, radially marked by distinct ridges; rest of valve floor pitted and marked by fine pustules, pits about two in 1 mm, pustules three to five in 1 mm.

Dorsal interior with sessile cardinal process (Pl. 15, fig. 8; Fig. 30B), trilobate in posterior face (Pl. 15, fig. 4), supported by median septum and cardinal ridges; median septum posteriorly strong, anteriorly almost absent between adductors, but becoming prominent again in front of muscle field (Pl. 15, fig. 8), extending probably to anterior margin of visceral disc; adductor scars slightly raised, small and suboval in shape; brachial ridges distinct with prominent longitudinal loops; cardinal ridges 2 mm across, extending along hinge, not crossing ears to lateral margins; anterior disc covered by two to three rows of large endospines (Fig. 30D); fine pits present between these pustules and muscle scars, absent from adductors and brachial loops.

Dimensions (in mm).

Specimen	Valve	Length	Width	Height
GSC 97038	VEN	?35	46	+18
GSC 97040	VEN	+25	+40	?18
GSC 97041	CON	+25	?42	15

Comparisons. Gobbett (1964, p. 97, Pl. 10, figs. 5–7) recorded a few specimens from the Sakmarian Cora Limestone of Spitsbergen, under the name *Horridonia geniculata* that come moderately close to *Tityrophoria nelsoni*. These specimens are characterized by low but prominent costae on both valves, a single row of spines along ventral hinge line, and few other body spines scattered over venter. No dorsal valves were known to Gobbett and, as a consequence, the generic name is not certain. Judging by its distinct costae crossed by low rugae, the Spitsbergen species appears to be more related to *Chaoiella* than to any horridoniid genus, perhaps except for *Tityrophoria*, which also exhibits weak costae. *Tityrophoria nelsoni* may be distinguished from the Spitsbergen species by its much less conspicuous costae and rugae.

Occurrence. Ej zone, Early Artinskian.

Superfamily LINOPRODUCTACEA Stehli, 1954

Family LINOPRODUCTIDAE Stehli, 1954

Subfamily LINOPRODUCTINAE Stehli, 1954

Genus *Linoproductus* Chao, 1927a

Type species. (OD) *Productus cora* d'Orbigny, 1842.

Linoproductus dorotheevi (Frederiks, 1932)

Plate 15, figures 25–28; Plate 16, figures 1–9, 11; Figure 31

1902 *Productus cora* (d'Orbigny); Chernyshev, p. 621, Pl. 33, figs. 2, 3; Pl. 35, fig. 1; Pl. 54, figs. 1–5.

1902 *Productus lineatus* (Waagen); Chernyshev, p. 625, Pl. 48, fig. 4.

1914 *Productus lineatus* (Waagen); Wiman, p. 70, Pl. 13, figs. 14, 15.

1932 *Cora dorotheevi* Frederiks, p. 35 (footnote).

1957 *Linoproductus* cf. *L. lutkewitschi* (Stepanov); Cooper, p. 38, Pl. 6D, figs. 27–29.

1964 *Linoproductus dorotheevi* (Frederiks); Gobbett, p. 98, Pl. 10, figs. 8, 9; Pl. 11, figs. 1–5.

1969 *Linoproductus* cf. *L. neffedievi* (Verneuil); Czarniecki, p. 285, Pl. 9, fig. 7; Pl. 10, figs. 2, 3.

Holotype. The ventral valve figured by Chernyshev (1902, Pl. 48, figs. 14, 15), from the Sakmarian Stage of the Urals (no catalogue number was provided); kept at CNIGRI, St. Petersburg.

Diagnosis. Large, strongly concavo-convex *Linoproductus* with slightly transverse to slightly elongate outline; no sulcus; halteroid spines few; about 15 costellae in 10 mm at midlength of ventral valve.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53818	3		
GSC loc. 54001	1		
GSC loc. 56937	5, 5(im)		
JBW loc. 109	2		2
JBW loc. 110	1	1(im)	1
JBW loc. 537	1		

Description. External. Shell of large size, slightly transverse to slightly elongate in outline, strongly concavo-convex in profile without distinct geniculation; widest along hinge line.

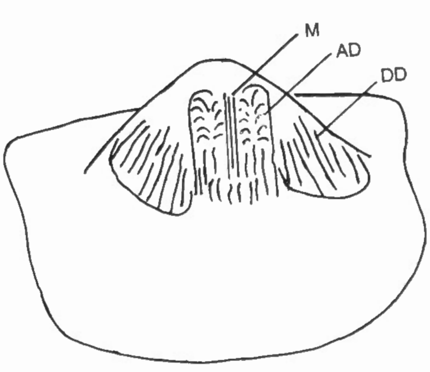


Figure 31. *Ventral internal mould of* ***Linoproductus dorotheevi*** *(Frederiks) (GSC 97067, x1). M, myophragm, other abbreviations as in Figure 27.*

Ventral valve strongly inflated, most convex over posterior third of shell length (Pl. 16, fig. 5); umbo low and massively swollen, not projecting beyond hinge line; umbonal angle broad, usually between 100° and 110°; umbonal slopes moderately high and steep, convex in outline; ears mostly damaged, bases well demarcated from strongly swollen umbonal region (Pl. 16, fig. 2), anteriorly tending to merge with lateral margins in some specimens; trail broadly curved from visceral disc without distinct geniculation (Pl. 16, fig. 5), strongly convex in profile, large and gently spreading to lateral margins; no sulcus. Costellae well rounded on crests, 22 in 10 mm at 10 mm from umbo, 15 in 10 mm at midlength, increasing anteriorly by frequent intercalation, separated by interspaces of equal or slightly narrower width; three or four broad rugae crossing ear bases and umbonal slopes, strongest near hinge margin, not crossing umbonal region. Fine spines lie in single row near hinge margin, about 0.5 mm in diameter; few large halteroid spines scattered over venter, about 2 mm in diameter (Pl. 15, fig. 25), suberect to erect, rising from two or three costellae, bases not swollen or elongated; costellae continuing in front of spine bases or curving around them.

Dorsal valve moderately to deeply concave (Pl. 16, fig. 4), delimiting narrow visceral cavity of about 5 to 8 mm deep, without abrupt geniculation. Dorsal ornament similar to that on ventral valve, but with more (5–8), stronger rugae and lack of spines.

Internal. Ventral adductor platform slightly raised, long and broad, 14 mm wide and 20 mm long, in one specimen weakly dendritic posteriorly and striated anteriorly (Pl. 16, fig. 2; Fig. 31), divided by low, median myophragm; large diductor imprints flabellate, strongly grooved and ridged longitudinally.

Comparison. The described material and the specimens from the Urals and Timan identified by Chernyshev (1902) with *Productus cora* d'Orbigny, 1842 and *P. lineatus* Waagen, 1884 appear to be conspecific and are all characterized by large size, absence of sulcus, fine costellae, broad umbo, strongly convex ventral valve without geniculation, and few large scattered halteroid spines on the venter. The first characteristic recalls that of types of *Linoproductus cora* (d'Orbigny) from the Lower Permian of Bolivia and *L. lineatus* (Waagen) from the Wargal Formation of Salt Range. The Bolivian species, as redescribed and figured by Kozlowski (1914, p. 48, Pl. 4, fig. 19; Pl. 5, fig. 5; Pl. 6, figs. 1–10), appears to be generally smaller and less elongate than *L. dorotheevi*, and contains more numerous halteroid spines. Types of *L. lineatus* figured by Waagen (1884, p. 673, Pl. 66, figs. 1, 2; Pl. 67, fig. 3) are more elongate and possess coarser costellae, 11 in 10 mm at midlength, compared with 15 in 10 mm at midlength of the present species. Moreover, the Salt Range species is strongly attenuated posteriorly with very high and steep lateral slopes. Frederiks (1932) noted the differences between the Salt Range species and *L. lineatus* (Chernyshev) (not Waagen) from the Urals and renamed the latter *Cora dorotheevi*. The genus *Cora* Frederiks, 1928, has been referred to synonymy of *Linoproductus* by Muir-Wood and Cooper (1960, p. 296).

Linoproductus neffedievi (Verneuil, 1845) from the Upper Carboniferous of the Russian Platform (Sarytcheva and Sokolskaya, 1952) was compared by Czarniecki (1969) to large Spitsbergen specimens, but these are here considered to be conspecific with the Yukon material. The Russian species is much smaller and has a less convex ventral valve as compared to *L. dorotheevi*. The same is also probably true of the single ventral specimen figured as *Productus* (*Cora*) *neffedievi* by Likharev and Einor (1939) from the Lower Permian Sedov Series of Novaya Zemlya.

Linoproductus rhiphaeus Stepanov (Ifanova, 1972, p. 107, Pl. 4, figs. 2–4; Kalashnikov, 1986, Pl. 115, fig. 2), from the Tastubian fauna of the Urals, is externally very close to the present species, especially in shell size and costation, but it appears to be more quadrate in outline and less inflated in lateral profile.

Cooper (1957) compared his large Oregon specimens with *L. lutkewitschi* (Stepanov, 1936), a species that was originally described from the Kungurian to Kazanian upper Kapp Starostin Formation of Spitsbergen and has been indicated to be possibly related to *Globiella* or allies (Grigor'yeva, 1962; Waterhouse, 1970a). The type specimen of *Linoproductus lutkewitschi* (Stepanov, 1936, Pl. 1, fig. 5) is only half the size or smaller of *L. dorotheevi*, and has a less convex ventral valve. *Linoproductus semisulcatus* Cooper and Grant (1975, p. 1148, Pl. 431, figs. 7–12) from the Neal Ranch and Lenox Hills formations, western Texas, is close in overall appearance but is more strongly curved in lateral profile and has a larger trail and a weak sulcus over the middle part of the ventral valve.

Occurrence. *Linoproductus dorotheevi* is found in the Ey and Ej zones in northern Yukon Territory. Elsewhere, this species was originally described from the Cora Limestone and the "Schwagerina Limestone" of the Urals and northern Timan (Chernyshev, 1902), of Asselian to Sakmarian age. The same species is also known from the Cyathophyllum Limestone, upper Wordiekammen Limestone, upper Gypsiferous Beds, and the Treskelloden Beds in Spitsbergen (Gobbett, 1964), of Asselian to Sakmarian age. Cooper (1957) described this species from the Sakmarian to Kungurian Coyote Butte Formation of central Oregon.

Genus *Schrenkiella* Barchatova, 1970

Type species. (OD) *Productus schrenki* Stuckenberg, 1875.

Diagnosis. Shell medium to large, gently to moderately and evenly concavo-convex in profile without geniculation; wide hinge and broadly converging lateral margins; ears large and extensive, but not well differentiated from venter; ventral valve with narrow tubiform extension in front; dorsal valve with tubiform sulcus; concentric rugae usually confined to inner ears and at times on umbonal slopes; spines confined to ventral valve, in a row along hinge margin and a few scattered on venter. Ventral adductor lobate, nondendritic. Dorsal interior with low cardinal process and thin and long median septum.

Discussion. The name *Schrenkiella* was proposed by Barchatova (1970, p. 67) in a footnote with a bibliographic reference to *Productus schrenki* Stuckenberg (1875, Pl. 2, fig. 1A), a poorly known species originally described from the Lower Permian of Timan. A diagnosis was later provided by Barchatova (1973, p. 98), and a photograph of a ventral internal mould of *Schrenkiella schrenki* from the Urals was kindly provided by Dr. N.V. Kalashnikov.

Although internal structures of *Schrenkiella* are still poorly known, its generic status is justified by its distinctive external morphology. The low, even ventral inflation of *Schrenkiella schrenki* approaches *Cancrinelloides* Ustritskiy, 1963, *Bandoproductus* Jin and Sun, 1981, and *Lyonia* Archbold, 1983b, but these three are usually subrounded in outline, lack a tubiform extension at the front, and have more numerous ventral spines and normally well defined concentric rugae. Moreover, the ears of *Schrenkiella* are more extensive than in any of these three genera.

Schrenkiella is similar to *Linoproductus* in ornament, and is distinguished in being only gently to moderately, and evenly, concavo-convex in profile without geniculation; it has a large triangular outline and nondendritic ventral adductor scars.

Schrenkiella sp.

Plate 16, figures 10, 12

1971 *Linoproductus schrenki* (Stuckenberg); Waterhouse *in* Bamber and Waterhouse, Pl. 12, fig. 6.

1971 *Linoproductus* cf. *L. schrenki* (Stuckenberg); Waterhouse *in* Bamber and Waterhouse, Pl. 14, fig. 1.

Material. One dorsal fragment from GSC loc. 54000; one poorly preserved dorsal fragment from GSC loc. 57; one dorsal external mould from JBW loc. 9; one dorsal external mould from JBW loc. 113.

Description. Dorsal valve large, more than 65 mm wide, 60 mm long, and about 8 mm high; gently and evenly concave without geniculation; umbonal region massive; hinge wide, probably representing maximum width of shell; ears extensive, flattened, or gently concave (Pl. 16, fig. 12), triangular in shape, gradually merging with gently spreading umbonal slopes; cardinal extremities approximately between 60° and 70°; tubiform extension well defined in GSC 97073 (Pl. 16, fig. 12), narrow and concave; no fold. Costellae fine and uniform, 16 to 18 in 10 mm at midlength, low, rounded, separated by narrower interspaces, increasing anteriorly by intercalation; concentric rugae ill defined (Pl. 16, fig. 10).

Comparisons. No ventral valves of the Yukon species were available for the present study, but they were figured by Waterhouse (*in* Bamber and Waterhouse, 1971). The dorsal valves examined here are very close in outline and size to the dorsal valve illustrated by Chernyshev (1902, Pl. 27, fig. 1) as *Productus schrenki* Stuckenberg from the Sakmarian beds of Timan, north Russia; but the Russian species appears to be more concave and more coarsely costellate. Ustritskiy and Chernyak (1963, p. 82, Pl. 12, figs. 4-7) figured as *Linoproductus schrenki* (Stuckenberg) one dorsal valve and three large ventral valves from the lower Turuzov Horizon of possibly Late Carboniferous or Early Permian age. Their dorsal valve is more deeply concave than the present dorsal material, and their ventral valves are more transverse and convex than the Yukon ventral valve figured in Bamber and Waterhouse (1971).

Occurrence. Ey, Eog, and Ej zones, Sakmarian to Early Artinskian.

?Subfamily AURICULISPININAE Waterhouse, 1986

Genus *Cancrinella* Frederiks, 1928

Type species. (OD) *Productus cancrini* Verneuil, 1845.

Discussion. Grigor'yeva et al. (1977) recognized two species groups of *Cancrinella*, potentially as subgenera, chiefly on the basis of shell ornament. The two groups are typified by *Cancrinella cancrini* (Verneuil) and *C. cancriniformis* (Chernyshev). The first group is characterized by inconspicuous rugae and long, swollen spine bases; whereas the other is distinguished by strong rugae, less elongate and more regularly spaced spine bases. The two groups need not be mutually exclusive, as pointed out by Archbold (1983b).

Cancrinella is conventionally classed within the Linoproductinae (Cooper and Grant, 1975; Waterhouse *in* Waterhouse and Briggs, 1986). Yet, its external characteristics are very distinct from *Linoproductus* and allies in that it possesses numerous ventral spines arising from elongate spine ridges, and usually well defined concentric wrinkles. These characteristics are shared with several other genera, notably *Magniplicatina* Waterhouse, 1983a, *Auriculispina* Waterhouse, 1975, and *Costatumulus* Waterhouse, 1983b. The last two were placed by Waterhouse (*in* Waterhouse and Briggs, 1986) in the Auriculispininae. Waterhouse (*in* Waterhouse and Briggs, 1986) characterized the Auriculispininae as having "depressed striated ventral adductors" that may be distinct from the dendritic adductors in *Cancrinella* and *Magniplicatina*. But Waterhouse (*in* Waterhouse and Briggs, 1986) also noted that the dendritic aspects of ventral adductors may also be developed at late maturity in members of the Auriculispininae. Whether the ventral adductors are dendritic, smooth, or striate have been regarded as a significant characteristic in the classification of Productidina (Muir-Wood and Cooper, 1960; Archbold, 1983b; Waterhouse and Briggs, 1986), but it is not known how significantly those genera with dendritic, ventral adductor scars derived only at late ontogeny (e.g., *Globiella* Muir-Wood and Cooper and *Costatumulus*) are distinct from genera with dendritic scars throughout ontogeny (e.g., *Cancrinella*). Waterhouse (*in* Waterhouse and Briggs, 1986, p. 56) stressed that "the ontogenetic development of muscle pattern cannot be disregarded, and ultimate convergence from different muscle imprints does not warrant familial or subfamilial lumping." If this is accepted, *Cancrinella* and *Magniplicatina* should be separated from the Auriculispininae and placed in a new subfamily, perhaps Cancrinellinae, as briefly mentioned but not formally defined by Grigor'yeva et al. (1977, p. 127), which may be characterized as linoproductaceans possessing normally distinct concentric wrinkles, short spines ridges, and dendritic ventral adductors throughout ontogeny.

Cancrinella cancriniformis (Chernyshev, 1889)

Plate 17, figures 1-9

1889 *Productus cancriniformis* Chernyshev, p. 283, Pl. 7, figs. 32, 33.

1902 *Productus cancriniformis* Chernyshev; Chernyshev, p. 629, Pl. 52, figs. 5, 6.

1981 *Cancrinella cancriniformis* (Chernyshev); Waterhouse, p. 86, Pl. 17, figs. 10-12; Pl. 18, figs. 1-5 (with synonymy).

Lectotype (selected by Grigor'yeva et al., 1977). CNIGR Museum 97/322 figured by Chernyshev (1889, Pl. 7, fig. 32) from the ?Asselian Stage in the Bijas River region, southern Urals (refigured by Grigor'yeva et al., 1977, Pl. 20, fig. 1).

Material. One conjoined shell from GSC loc. 53710; two ventral valves and one dorsal external mould from GSC loc. 53714; one dorsal external mould from JBW loc. 508.

Description. Shell moderately large for genus, subquadrate to slightly elongate in outline, approximately 30 mm wide and long, and 15 mm high for ventral valve; maximum width possibly at hinge line.

Ventral valve strongly convex, most inflated at posterior third of shell length (Pl. 17, fig. 1); visceral disc small and short, strongly inflated with high, convex umbonal slopes; umbo moderately extended, moderately to strongly incurved, with beak extending beyond hinge line for about 1.5 mm; umbonal angle between 75° and 90°; ears small, well demarcated from visceral disc, strongly curved in profile; trail long and narrow, at least twice as long as visceral disc, moderately to strongly convex in profile. Costellae fine, 12 in 5 mm at midlength, anteriorly increasing by intercalation, crossed by distinct concentric wrinkles (Pl. 17, fig. 1); wrinkles strongest on ears and lateral slopes, lower and split over median portion of valve, 1 to 1.5 mm across and 2 mm apart, strongly raised near hinge line. Hinge spines poorly preserved; body spines moderately abundant, mostly arising from distinct elongate ridges that are formed of single, or more often, double costellae (Pl. 17, fig. 9), or arising from small elongate bases particularly over umbonal region; spine ridges 3 to 5 mm long, about 2 mm apart, arranged in roughly quincunxial pattern, anterior ends usually slightly swollen and projecting small spines that lie at moderately high angle (between 50° and 60°) to shell surface; costellae continuing in front of spine ridges; a few additional fine spine bases also seen on inner ears.

Dorsal valve deeply concave with large broad visceral disc and short trail, geniculation abrupt with angle close to 85°; ears flat. Costellae similar to those of ventral valve, but rugae more numerous and prominent (Pl. 17, fig. 6), strongest on ears and trail, lower over median portion. Dorsal valve pitted without spines, pits sometimes prolonged with expanded anterior portions (Pl. 17, fig. 2).

Comparisons. The lectotype of *Cancrinella cancriniformis* (Chernyshev, 1889, Pl. 7, fig. 32) is a slightly elongate, strongly convex ventral valve that has fine costellae, 10 to 12 in 5 mm over midlength, distinct and close-set wrinkles, and well defined spine ridges. These characteristics are well displayed in the Yukon material.

This species and its synonymous forms were discussed by Waterhouse (1981, p. 87). *Cancrinella irwinensis* Archbold (1983b, p. 240, Figs. 1C–P) from the Sterlitamakian fauna of the Callytharra Formation, or equivalents in Western Australia, is close in ornament and shape but appears to have slightly finer costellae and smaller ears.

Occurrence. Cancrinella cancriniformis is present in the Eta and Ey zones of the Jungle Creek Formation in northern Yukon Territory. This species was originally described from the ?Asselian Stage of the Kijas River, southern Urals (Chernyshev, 1889). Elsewhere, it has been recorded from the Sakmarian Trogkofel Limestone in Carnian Alps; the Sakmarian faunas of the Urals; the Sakmarian upper Kigiltas and Lower Artinskian lower Echii Suites in Verchoyan Mountains; the Upper Carboniferous Chakelime Complex and Upper Carboniferous to Lower Permian Kokpecten Complex of eastern Kazakhstan; the probably Asselian Paren and Sakmarian Irbichan horizons of the Kolyma-Omolon Massif; the Sakmarian Wangchiapa Limestone (equivalent to lower Qixia Formation) of southwestern China; the Sakmarian Shanmainjin Formation of northeastern China; and the Sterlitamakian Kao Yo Noi Formation of southern Thailand.

Cancrinella singletoni Gobbett, 1964

Plate 17, figures 10–20

?1934 *Productus* (*Linoproductus*) *villiersi* var. *koninckianus* (Verneuil); Stepanov, p. 36, figs. 18, 19.

1964 *Cancrinella singletoni* Gobbett, p. 102, Pl. 12, figs. 1–7.

1969 *Cancrinella singletoni* Gobbett; Czarniecki, p. 287, Pl. 6, figs. 1–3.

Holotype. SME 18232 figured by Gobbett (1964, Pl. 12, figs. 1, 7) from the Sakmarian upper Wordiekammen Limestone of Spitsbergen, kept at the Sedgewick Museum, London.

Diagnosis. Small, subrounded to slightly elongate; ventral valve strongly convex and wrinkled, most inflated at about the posterior third of shell curvature length; 10 to 11 costellae in 5 mm over midlength; spine ridges with strongly swollen anterior ends and arising usually from double costellae.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 56937	3		
JBW loc. 59	1		
JBW loc. 60	1(em)		
JBW loc. 63	1(em)		
JBW loc. 88	2	1(em)	1
JBW loc. 89	3	2(em)	

Description. Shell small, 11 to 16 mm wide and long, and 6 to 11 mm high; subquadrate to slightly elongate in outline.

Ventral valve strongly curved in lateral profile (Pl. 17, fig. 11), most inflated at posterior third of shell curvature length; geniculation area broad and well rounded, angle close to 90°; venter high, delimited by high and nearly vertical lateral slopes (Pl. 17, fig. 16); visceral disc strongly inflated with high and steep umbonal slopes; umbo moderately extended and incurved; umbonal angle between 70° and 85°, little protruding beyond hinge line; ears very small, but well segregated from venter (Pl. 17, fig. 14), triangular, gently convex; cardinal extremities rounded at about a right angle; hinge line equal to or slightly narrower than maximum width; lateral margins nearly parallel; trail moderately convex, approximately twice as long as visceral disc. Costellae fine, 10 or 11 in 5 mm at midlength, separated by narrower interspaces, increasing by intercalation; concentric wrinkles distinct, crossing entire valve (Pl. 17, fig. 18), fine and low over umbonal region, 10 in posterior 5 mm, five in 7 mm on trail, symmetrical in section or with steeper posterior slope, irregular (discontinuous or merged) over median portion, crests sharp. Ventral spines generally less than 0.3 mm in diameter, in single row along hinge line, four to six on ears, and quincunxially distributed over venter where they arise from either small, slightly elongate bases (mostly on anterior trail) (Pl. 17, figs. 16–18) or, more often, from well prolonged, tear-shaped ridges (Pl. 17, figs. 19, 20); spine bases formed from single or, more often, double costellae which continue in front of spine bases (Pl. 17, fig. 20).

Dorsal valve deeply concave with large, moderately concave visceral disc and abruptly geniculated trail, geniculation angle close to 90°; ears flat. Ornament similar to that on ventral valve, with finer costae, 11 to 13 in 5 mm on trail, and lower concentric wrinkles; no spines, pits distinct.

Comparisons. The specimens are poorly preserved, but agree well in shape and ornament with similar-sized *Cancrinella singletoni* Gobbett, 1964 from the upper Wordiekammen Limestone of Spitsbergen.

The two ventral valves from the Upper Permian of the Russian Platform and Spitsbergen, figured by Grigor'yeva et al. (1977, p. 133, Pl. 16, 17) as *C. singletoni*, are probably not conspecific. They are much larger, more elongate specimens, and have more numerous spines over the umbonal region.

Gobbett (1964) recognized four species from the "*C. cancrini–C. koninckiana*" group from Spitsbergen, including *C. singletoni*. *Cancrinella crassa* Gobbett (1964, p. 105, Pl. 12, figs. 13–15), from the upper Cyathophyllum Limestone, is very close in size and overall appearance but has coarser costellae (eight in 5 mm), and its spine ridges arise from a single costella. *Cancrinella spitsbergeniana* Gobbett (1964, Pl. 12, figs. 8–12), from the upper Gipshuken Formation and lower Kapp Starostin Formation, is moderately close in overall appearance but differs in its large size, narrower hinge line, low ventral convexity, and more numerous spines. *Cancrinella tenuissima* Gobbett (1964, p. 105, Pl. 12, figs. 13–15), from the upper Kapp Starostin Formation, is well distinguished by its very fine costellae, 18 in 5 mm, and by its spine ridges arising from four or five costellae.

Cancrinella koninckiana (Verneuil) described by Keyserling (1846, p. 203, Pl. 4, fig. 4a–c) from the Upper Permian in the Russian Platform is smaller than *C. singletoni* and has a deeply concave dorsal valve and less strongly wrinkled ventral valve. Spine bases in the Russian species arise mainly from single costella. Poorly preserved shells identified with *Linoproductus villiersi* var. *koninckianus* (Verneuil) by Stepanov (1934) from the Sakmarian fauna in Kolva River, northern Urals, seem to belong to *Cancrinella singletoni*, judging from strong wrinkles, shallowly concave dorsal valve, and a long trail.

Occurrence. Cancrinella singletoni is found in the Ey and Ej zones in northern Yukon Territory. Elsewhere, the species is known from the Sakmarian upper Wordiekammen Limestone in Spitsbergen and possibly from the Sakmarian Bryozoa Limestone in the Kolva River area, northern Urals.

Subfamily STEPANOVIELLINAE Waterhouse, 1975

Genus *Globiella* Muir-Wood and Cooper, 1960

Type species. (OD) *Productus hemisphaerium* Kutorga, 1844.

Diagnosis. See Archbold (1983b, p. 247).

Discussion. Globiella, as discussed by Grigor'yeva et al. (1977) and Archbold (1983b), is distinguished from *Stepanoviella* Zavodovskiy, 1960 by lacking dorsal spines and possessing more numerous ventral body spines and coarser costellae. *Globiella* differs from *Linoproductus* in being smaller in size and globular in shape, and in having normally finer costellae, smaller and less frequent ventral body spines, and largely smooth, lobate ventral adductors.

Grigor'yeva et al. (1977) adopted a narrow diagnosis and range for *Globiella* and included in it only one species, in addition to the type species: *G. tschernyschewi* (Nechaev, 1911). Archbold (1983b, p. 247) slightly extended the diagnosis of the genus and assigned to it "a large, widely distributed group of Gondwanan species . . . ." The Gondwanan occurrence of *Globiella*, as discussed by Waterhouse (1970a) and Archbold (1983b), appears to be confined to the Sakmarian strata, but the range of the genus extends from Early to Late Permian in the northern hemisphere. Grigor'yeva (1962) and Waterhouse (1970a) (both regarding *Globiella* as a junior synonym of *Stepanoviella*) indicated two Early Permian occurrences of *Globiella* in the Arctic region, including *Productus ufensis* Frederiks, 1915a and *Productus lutkewitschi* Stepanov, 1936. *Globiella costellata* n. sp., described below, is an additional record of an Early Permian occurrence of *Globiella* from the northern hemisphere.

Globiella costellata n. sp.

Plate 15, figures 9–24; Figure 32

1971 *Linoproductus simensis* (Chernyshev); Waterhouse *in* Bamber and Waterhouse, Pl. 16, figs. 8, 11.

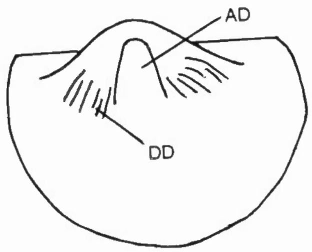


Figure 32. *Ventral internal mould of* ***Globiella costellata*** *n. sp. (GSC 97061, x1.5). M, myophragm, other abbreviations as in Figure 27.*

Etymology. Latin *costa*, rib; *-ellus,* fine, little.

Holotype. GSC 97060 from GSC loc. 53720, section 116H-1B; Ey zone, Jungle Creek Formation (Pl. 15, figs. 9-12, 15).

Diagnosis. Large and transverse with moderately convex ventral valve and deeply concave dorsal valve; costellae fine, seven to nine in 5 mm at midlength.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53703	4		2
GSC loc. 53704		1	
GSC loc. 53705	4		1
GSC loc. 53713	3		
GSC loc. 53714	1		
GSC loc. 53715	2		
GSC loc. 53720	2		1
GSC loc. 53774	1		
GSC loc. 53947	2		
GSC loc. 53951	1, 1(im)	1	
GSC loc. 57052	7		
GSC loc. 57266	5		5
GSC loc. 57275	1		
JBW loc. 24	1	1	
JBW loc. 88	3		
JBW loc. 113	5	1	

Description. External. Shell large for genus, transverse in outline with wide hinge (Pl. 15, figs. 9, 20); strongly concavo-convex in profile without geniculation (Pl. 15, fig. 10); visceral cavity narrow, up to 5 mm deep; widest along hinge line.

Ventral valve strongly, and nearly symmetrically, arched in longitudinal direction with highly swollen visceral disc; umbo low and massive, slightly extended, strongly incurved; beak small, little incurved beyond hinge line; umbonal slopes high and steep, gently convex in outline and section; umbonal angle broad at 110°; hinge line equal to or slightly wider than midwidth, well extended by ears; ears moderately large (Pl. 15, fig. 20), not well discriminated from venter, strongly curved in section; lateral and anterior slopes high and steeply sloping; no flattening or sulcus. Costellae fine, eight in 5 mm at midlength in holotype (Pl. 15, fig. 9), ranging from seven to nine in 5 mm at midlength, separated by equally wide or slightly wider interspaces, increasing anteriorly by intercalation; three to four low, broad rugae crossing umbonal slopes and inner ears in some specimens (Pl. 15, fig. 12), strongest towards hinge margin. Ventral spines in distinct row near hinge line (Pl. 15, fig. 10), about five each side of umbo, pointing posterolaterally, 0.5 mm in diameter, slightly diminishing in strength towards umbo, occasionally joined by second row of finer, and fewer, spines; halteroid spines rare on venter, one seen from GSC 97115 (Pl. 15, fig. 13), arising from two costellae, which continue in front of spine base; spine bases slightly swollen, about 1 mm in diameter.

Dorsal valve deeply and evenly concave without geniculation (Pl. 15, fig. 15), fitting well into the ventral valve profile; ears flattened. Dorsal ornament similar to that on ventral valve, but lacks spines and has more distinct rugae, which in places cross median part of visceral disc (Pl. 15, fig. 16).

Internal. Ventral adductor lobate, slightly raised, smooth (Pl. 15, fig. 17; Fig. 32); diductor scars larger and slightly impressed, marked by weak radial ridges. Dorsal interior poorly known, thin median septum extending to about midlength of visceral disc.

Dimensions (in mm).

Specimen	Valve	Length	Width	Height	Umbonal angle
GSC 97059	DOR	28	?40	17	—
GSC 97060	VEN	+23	34	?12	110°
GSC 97062	VEN	+28	44	16	112°
GSC 97063	VEN	20	22	9	?95°

Comparisons. The Yukon material appears to be closer to species from the southern hemisphere than to those from the Arctic region. *Globiella umariensis* (Reed, 1928, p. 371, Pl. 31, figs. 1-6) from the Tastubian Umaria beds of the Indian Peninsula, redescribed and figured by Archbold (1983b, p. 247, Figs. 4A-L), resembles the new species in size and density of costellae, but it differs in being subrounded to slightly elongate in outline, having a less concave dorsal valve, and possessing a lower and more massive ventral umbo and, anteriorly, weakly striated, ventral adductors as in

Costatumulus Waterhouse, 1983b. In addition, the Indian species appears to have more numerous ventral halteroid spines. The large size and transverse outline of the Yukon species recall *G. flexuosa* (Waterhouse, 1970a, p. 45; Pl. 14, figs. 1-8, 15, 16) from the Aktastinian Jimba Jimba Calcarenite, Western Australia, also recorded by Archbold (1983b). The Australian species is distinguished in having a less concave dorsal valve and conspicuously coarser costellae, five to six in 5 mm at midlength.

Globiella? ufensis (Frederiks, 1915a, p. 51, Pl. 4, figs. 3-6) from the Sakmarian fauna of the Ufa Plateau, south Urals, is generally smaller than the Yukon species and has a conspicuously higher, narrower umbo. *Globiella lutkewitschi* (Stepanov, 1936, p. 121, Pl. 1, fig. 5) from the Kungurian to Kazanian Kapp Starostin Formation of western Spitsbergen is larger and less convex than the Yukon species and possesses stronger rugae on the ventral valve.

Some specimens of *Linoproductus simensis* (Chernyshev, 1902, Pl. 55, figs. 2-5) from the Sakmarian Stage at Tastuba Village, southern Urals, are moderately close to the Yukon species in overall appearance, but differ in being most convex at the posterior third of shell curvature length or behind it, more elongate in outline, having a geniculated and less concave dorsal valve and having finer costellae (10 in 5 mm at midlength).

Occurrence. Ey, Eog, and Ej zones, Sakmarian to Early Artinskian.

Subfamily PAUCISPINAURIINAE Waterhouse, 1986

Genus *Terrakea* Hill, 1950

Type species. (SD by ICZN, 1957) *Productus brachythaerus* Morris, 1845.

Discussion. Allied genera are *Paucispinauria* Waterhouse, 1983a with type species *Terrakea convexa* Waterhouse, 1964, and *Saetosina* Waterhouse (*in* Waterhouse and Briggs, 1986) with type species *Terrakea multispinosa* Dear, 1971. Both genera are distinguished from *Terrakea* in lacking the brush of spines over the inner ventral ears. *Saetosina* differs further in having more numerous, finer, and undifferentiated spines on the dorsal valve.

The Yukon species described below is essentially based on dorsal details; its ventral aspects are almost unknown. The generic position of this species is therefore open to question.

Terrakea? sp.

Plate 17, figures 21, 22, 24

Material. One dorsal external mould with fragmentary ventral aspects attached, from JBW loc. 113; one dorsal external mould with anterior fragment of ventral valve, from JBW loc. 537.

Description. Shell large for genus, dorsal valve strongly subquadrate to slightly rectangular in outline (Pl. 17, fig. 21); ventral umbo prominent and strongly incurved, beak overhanging hinge line and projecting beyond it for 1.5 mm; umbonal angle at approximately 60°; dorsal valve strongly concave as a whole, visceral disc large and flatly concave, trail sharply geniculate at anterior third of curvature length with geniculation angle close to 90° (Pl. 17, fig. 24); dorsal ears small, well discriminated from umbonal slopes; hinge margin probably as wide as midwidth or slightly narrower; cardinal extremities rounded at about 90°. Costellae very fine (Pl. 17, fig. 24), 10 or 11 in 5 mm at midlength of dorsal visceral disc, increasing chiefly by intercalation; rugae inconspicuous, strongest on umbonal slopes and anterior disc, generally low and broad, 1 to 2 mm in diameter. Ventral spines known from fragments attached to dorsal valves (Pl. 17, figs. 21, 24), coarse on posterolateral slopes, about 1 mm in diameter, pointing laterally; finer erect spines on trail, approximately 0.5 mm in diameter. Dorsal spines differentiated, fine, and widely spaced in roughly quincunxial pattern over visceral disc, about 0.3 to 0.5 mm in diameter; coarser spines on trail and posterolateral slopes (Pl. 17, fig. 24), 1 mm in diameter on average, 2 mm apart, bases not elongated or swollen, erect.

Comparisons. The two dorsal specimens with fragmentary ventral aspects are very distinctive in their large size, strongly subquadrate outline, broad umbo, very fine costellae, and well differentiated dorsal spines.

Of *Terrakea* species so far described from the Arctic region (Waterhouse, 1970a; Grigor'yeva et al., 1977), none is particularly close to the Yukon species and all are younger.

Eastern Australian *Terrakea* species of moderately large to large size include the type species *T. brachythaera* (Morris), 1845, and *T. solida* (Etheridge and Dun), 1909. The first, figured by Waterhouse and

Jell (1983, Pl. 1, figs. 9, 11-18; Pl. 2, fig. 1) and Waterhouse (*in* Waterhouse and Briggs, 1986, Pl. 12, figs. 1-3), from the Kazanian Flat Top Formation of the Bowen Basin, is smaller and more transverse than the Yukon material and has finer costellae on the dorsal valve. *Terrakea solida*, as described and figured by Dear (1971, p. 19, Pl. 6, figs. 1-7) from the Upper Permian beds of the Bowen Basin, is about the size and shape of the Yukon species, but differs in having finer costellae, 25 in 10 mm on the dorsal trail, flatter dorsal visceral disc, and a longer trail.

Occurrence. Ey zone, Early Sakmarian.

Linoproductid gen. sp. indet.

Plate 17, figures 23, 25, 26

Remarks. One dorsal external mould from JBW loc. 113. The overall appearance of this specimen appears to suggest *Linoproductus*, except for the distinct dorsal spines. It is large, transversely subrounded in outline, moderately concave without distinct geniculation; concentric rugae poorly developed; costellae coarse, eight to nine in 5 mm, and increasing anteriorly by both intercalation and bifurcation (Pl. 17, fig. 23); spines scattered over entire valve, small, about 0.5 mm in diameter, arising from single costella without swollen or elongated bases, arranged in roughly quincunxial pattern.

The general appearance of the specimen and the presence of dorsal spines also suggest *Stepanoviella* Zavodovskiy, 1960, but the costellae are much finer in the type species *S. paracurvata* Zavodovskiy.

Occurrence. Ey zone, Early Sakmarian.

Family ANIDANTHIDAE Waterhouse, 1968

Genus *Protoanidanthus* Waterhouse, 1986

Type species. Protoanidanthus compactus Waterhouse, 1986.

Diagnosis. Anidanthid shells distinguished by having small dorsal ears, which do not extend forward as large wings; spines in a row along ventral hinge line and a few scattered over venter.

Discussion. This genus differs from *Anidanthus* Whitehouse, 1928, *Megousia* Muir-Wood and Cooper, 1960, and *Nothokuvelousia* Waterhouse, 1986 primarily in lacking pronounced dorsal alae.

Abramov and Grigor'yeva (1988, p. 135) recently created a new genus *Akatchania* for anidanthid shells also lacking alate dorsal ears, but the Russian genus may be distinguished from *Protoanidanthus* in lacking ventral body spines, and possessing a very narrow visceral cavity (about 2 mm deep in the type species) and numerous well defined small tubercles within the ventral valve.

Many species previously assigned to *Anidanthus* were not shown to have alate ears, and appear to be related to *Protoanidanthus* or *Akatchania*; without examination of the material it is almost impossible to establish which of these are true *Protoanidanthus* or *Akatchania*, and which are incompletely preserved *Anidanthus* or its allies, from which large ears are very readily broken.

The name *Protanidanthus* was proposed by Liao (1979, p. 536) in a different sense for an Asselian ?anidanthid species (*P. elegans* Liao) from southwestern China. Species of this genus lack concentric rugae on the dorsal valve, unlike *Anidanthus* and allied genera.

Protoanidanthus umbonatus. n. sp.

Plate 18, figures 1-16

Etymology. Latin *umbo*, knob; *-natus*, having the nature of.

Holotype. GSC 97128 from JBW loc. 89, Ettrain Creek; Ey zone, Jungle Creek Formation (Pl. 18, fig. 6).

Diagnosis. Small, usually less than 20 mm in width; ventral ears moderately large, well defined, triangular; costellae conspicuously increasing in strength towards anterior margin, nine to 11 costellae in 5 mm over umbonal region and six to seven in 5 mm near anterior margin; no sulcus or fold.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53703	1		
GSC loc. 53999	1		
JBW loc. 9		1(im)	
JBW loc. 57	2(im)		
JBW loc. 64	1(im)	1(im)	
JBW loc. 88	5, 10(em)	7(em)	3
JBW loc. 89	23(em), 19(im)	11(im)	7(im)

Description. External. Shell small, usually less than 20 mm wide and 14 mm long, strongly concavo-convex; widest along hinge line.

Ventral valve strongly and evenly inflated with high and steep lateral slopes (Pl. 18, fig. 11); umbonal region strongly swollen; umbo distinct, moderately incurved beyond hinge line; umbonal angle between 90° and 100°; umbonal slopes conspicuously convex both in outline and section; ears moderately large (Pl. 18, figs. 8, 13), well segregated from high venter, triangular in shape, not extending forwards, gently convex in section; cardinal extremities acute, angle between 45° and 50°; no sulcus. Ventral costellae very distinctive, coarse in general and rapidly increasing in strength anteriorly (Pl. 18, fig. 6), 10 costellae in 5 mm over umbonal region, six to seven in 5 mm near anterior margin, not extending to ears, anteriorly increasing by intercalation, crests well rounded, separated by interspaces as wide as costellae or slightly narrower; rugae high and narrow on inner ears and over posterolateral slopes in some specimens (Pl. 18, fig. 8), about 1 to 2 mm wide and 2 mm apart, very faint over median portion of valve. Spines in single row along hinge line (Pl. 18, fig. 6), three to four each side of umbo, 0.5-0.8 mm in diameter; ventral body spines occasional, arising from single costella, bases as wide as costellae or slightly swollen (Pl. 18, fig. 13), little elongated.

Dorsal valve gently concave in general (Pl. 18, fig. 17), either not geniculate or very broadly so; visceral disc large and subrounded, gently concave; complete specimen (Pl. 18, fig. 12) shows very small but clearly delineated ears, flat, triangular in shape, not extending forwards, no wing-like extensions. Costellae nearly uniform in size from umbo to anterior margin (Pl. 18, fig. 12), nine to 11 costellae in 5 mm over midlength; rugae distinct on entire dorsal valve, low and rounded, closely and evenly spaced on posterior portion, seven to eight rugae in 5 mm, slightly more close-set and overlapping near anterior margin (Pl. 18, fig. 12), evenly crossing costellae to form fine and regular reticulation (Pl. 18, figs. 4, 12); no fold or spines.

Internal. Ventral visceral cavity large and deep (Pl. 18, fig. 13); ear baffles prominent, low and slightly crenulate, clearly separating ears from visceral cavity; adductor platform depressed posteriorly and slightly raised anteriorly, triangular-oval in shape, smooth (Pl. 18, figs. 1, 2); diductor impressions depressed, each about as large as adductor platform, anterolateral to adductor scars, subrounded, with weak radial markings; anterior floor crossed by low but well defined marginal ridge separating visceral cavity from anterior trail (Pl. 18, fig. 8); rest of floor smooth.

Dorsal cardinal ridges distinct (Pl. 18, figs. 3, 16), broadly diverging from hinge line at 30°, crossing ears as prominent ear baffles, anteriorly extending as low and thin ridges (0.5 mm in diameter) to encircle visceral disc; median septum arising at 2 to 3 mm from cardinal process (Pl. 18, fig. 16), extending to midlength, ending with distinct terminal swelling or "pillar"; anterior marginal ridge low but well defined (Pl. 18, fig. 16); anterior floor marked by 2 to 3 rows of low, rounded, small tubercles, separated by small dimples.

Dimensions (in mm).

Specimen	Valve	Length	Width	Height
GSC 97123	DEM	8.5	16	3
GSC 97126	VIM	13	18	7
GSC 97127	VIM	12	20	8
GSC 97129	VIM	13	21	7
GSC 97132	VEN	10	18	4
GSC 97133	VIM	12	20	9

Comparisons. The overall appearance and, particularly, the coarse costellae of the new species suggest *Anidanthus victori* Abramov and Grigor'yeva (1988, p. 133, Pl. 9, figs. 12-15) from the Aktastinian Akatchan and lower Echii Suites of the Verchoyan Mountains. However, the poorly preserved dorsal material of the Russian species fails to show details of the ears and hence renders the Russian species of uncertain generic identification. Moreover, the Russian species appears slightly larger (more than 20 mm in width) and its ventral valve less convex. Its ventral ears appear to be smaller and less well discriminated.

Anidanthus hallinae Kotlyar (Grigor'yeva and Kotlyar, 1977, p. 58, Pl. 5, figs. 14-16) from the Sakmarian upper Kigiltas and Aktastinian lower Echii Suite of the Verchoyan Mountains is also small and seems to lack alate dorsal ears, suggesting *Protoanidanthus*. It differs from the Yukon species in having finer costellae, seven to nine in 5 mm near the anterior margin, a shallow sulcus, and stronger rugae on the dorsal valve. *Anidanthus sarytchevae* Zavodovskiy of Zavodovskiy and Stepanov (1970, p. 111, Pl. 27, figs. 1-4) from the probably Asselian Paren Horizon of the Kolyma-Omolon Massif, northeast Siberia, also appears to be related to *Protoanidanthus*, as indicated by Waterhouse (*in* Waterhouse and Briggs, 1986). The dorsal ears are poorly preserved in the Russian species. It is distinguishable from the new species in having a larger size and finer costellae, eight in 5 mm near the anterior margin of the ventral valve.

Anidanthus aagardi Zavodovskiy of Zavodovskiy and Stepanov (1970, p. 112, fig. 11; Pl. 28, figs. 2-5;

Pl. 36, figs. 1, 9; Pl. 37, fig. 13) (not Toula) from the Asselian Paren and Sakmarian Irbichan horizons in the Kolyma-Omolon Massif, northeastern Siberia, share many ventral attributes with the Yukon species, but it possesses finer costellae. No dorsal material was illustrated for the Soviet species.

Anidanthus minor Cooper (1957, p. 38, Pl. 6A, figs. 1-17) from the Sakmarian to Kungurian Coyote Butte Formation of central Oregon was also said to have small ears. It is about the size and shape of the Yukon material but is more finely costellate (10 to 13 in 5 mm at the frontal margin, 12 to 15 over the umbonal region).

The type species *Protoanidanthus compactus* Waterhouse (*in* Waterhouse and Briggs, 1986, p. 61, Pl. 13, figs. 19-22; Pl. 15, figs. 16-18) from the Late Carboniferous Fairyland and Dresden formations of southeastern Bowen Basin, eastern Australia, is comparable in overall appearance, but differs in its consistently larger size and finer, more uniform costellae (9 to 11 in 5 mm).

Occurrence. Ey and Eog zones, Sakmarian.

Genus *Anidanthus* Whitehouse, 1928

Type species. (by subsequent monotypy, see Melville, 1984) *Linoproductus springsurensis* Booker, 1932.

Discussion. Megousia Muir-Wood and Cooper, 1960 is possibly synonymous with *Anidanthus*, as pointed out by Waterhouse (*in* Waterhouse and Briggs, 1986). Both are identical in internal structures, according to Cooper and Grant (1975, p. 1190). Cooper and Grant (1975) considered that the major distinction between the two lies "in the development of the elaborate wings on the lateral extremities of the brachial valve of *Megousia*" (p. 1190). But this supposed distinction for *Megousia* is called into question, as moderately large alate ears are found also in *Anidanthus sprinsurensis* (e.g., a dorsal paratype, QMF 2543, at the Queensland Museum) and in other *Anidanthus* from eastern Australia (Briggs, 1987).

Kuvelousia Waterhouse, 1968b differs from *Anidanthus* by its strongly enrolled, narrowly and prominently sulcate, ventral valve; flattened, conspicuously thickened anteriorly ("wedged-shaped"), dorsal valve; and a denticulate hinge line. *Nothokuvelousia* Waterhouse (*in* Waterhouse and Briggs, 1986) was named for anidanthid shells with a similar wedge-shaped dorsal valve, but lacking denticles along the hinge margin.

Anidanthus cf. *A. boikowi* (Stepanov, 1946)

Plate 18, figures 17-24; Figure 33

cf. *Productus* (*Linoproductus*) *boikowi*
1946 Stepanov, p. 198, Pl. 1, figs. 13-16.
cf. *Anidanthus boikowi* (Stepanov); Abramov
1988 and Grigor'yeva, p. 130, Pl. 8, figs. 1-12.

Material.

Locality	Ventral	Dorsal
GSC loc. 53818	1, 1(im)	
JBW loc. 2	4	1(em)
JBW loc. 14	1(im)	
JBW loc. 526	1(im)	1
JBW loc. 545	1	

Description. External. Shell of medium size, over 35 mm wide and 25 mm long when completely preserved, transverse with large alate ears, widest at hinge line.

Ventral valve strongly inflated, most convex at posterior third to quarter of shell curvature length, broadly curving onto trail; visceral disc highly swollen (Pl. 18, fig. 17), delimited by high and steep umbonal slopes; umbo moderately extended, strongly incurved, beak not protruding beyond hinge line; umbonal angle between 90° and 100°; ears damaged, probably large and transverse; bases well demarcated from high visceral disc; shallow and broad median depression in some specimens (Pl. 18, fig. 22), poorly defined from flanks, best developed over midlength, disappearing towards anterior margin. Costellae, 13 in 5 mm on umbonal region, 7 to 10 in 5 mm near anterior margin, well rounded, anteriorly increasing by intercalation; concentric rugae only developed on ears (Pl. 18, fig. 18), generally low, 2 mm apart. Ventral spines in single row along hinge line, about four each side of umbo, bases rounded, 0.5 mm across; body spines few,

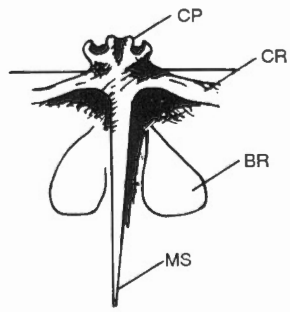


Figure 33. *Dorsal interior of* ***Anidanthus*** *cf.* ***A. boikowi*** *Abramov and Grigor'yeva (GSC 97143, x4). Abbreviations as in Figure 27.*

arising from single costella, bases not swollen or elongated.

Dorsal exterior poorly known apart from costellae, concentric rugae, and their collectively formed distinct reticulation; large alate dorsal ears clearly shown in well-preserved dorsal interior (Pl. 18, fig. 24), extending both laterally and anteriorly.

Internal. Ventral adductor scar small, elongate-oval in shape, slightly raised, smooth (Pl. 18, fig. 18); diductor impressions obscure. Cardinal process small and sessile (Fig. 33), quadrilobate in posterior view with median lobe divided by deep and long sulci; myophore of median lobe slightly curved dorsally; posterior platform thickened; median septum arising from base of cardinal process, posteriorly thick (0.5 mm across), tapering anteriorly, extending to midlength; adductor scars placed 3 mm in front of base of cardinal process, slightly raised, suboval in shape, smooth; brachial ridges obscure; cardinal ridges beginning from base of cardinal process, slightly diverging from hinge line, narrow, probably crossing inner ears; lateral and anterior ridges indistinct.

Comparisons. The Yukon species is poorly preserved, especially its dorsal exterior. It is of moderately large size and has a weak median sulcus in some ventral specimens, coarse costellae, and well defined moderately alate dorsal ears. These characteristics suggest *Anidanthus boikowi* (Stepanov, 1946, p. 198, Pl. 1, figs. 13–16) commonly found in the Aktastinian lower Echii Suite or equivalents in northern Siberia. The Russian species appears to be variable in shell size, extension of ears (with uncertainty over degree of damage), and development of ventral median depression, as described and figured by different authors. The holotype, a ventral valve, is slightly larger than the Yukon material and possesses slightly coarser costellae, six to eight in 5 mm at near anterior margin, and an ill defined sulcus. Specimens of the same species figured by Abramov and Grigor'yeva (1988, Pl. 8, figs. 1–12) also tend to be slightly larger than the Yukon specimens, but are similar in having a very shallow ventral median depression in some specimens, and in the density of costellae.

Anidanthus megensis Solomina (1981, p. 68, Pl. 6, figs. 4, 5) from the Sakmarian upper Megen Suite of the Verchoyan Mountains is much larger than the Yukon material and has more extensive ears and a less convex ventral valve, but is similar in outline and in density of costellae.

Occurrence. Anidanthus cf. *A. boikowi* is restricted to the Ej zone in northern Yukon Territory. *Anidanthus boikowi* was originally described (Stepanov, 1946) from the Lower Permian (probably Artinskian) strata in the Verchoyan Mountains, Siberia. Abramov and Grigor'yeva (1988) considered this species to be one of the characteristic forms for the Asselian–Sakmarian Osennin Horizon or equivalents in northeastern Siberia.

Family YAKOVLEVIIDAE Waterhouse, 1975

Genus *Yakovlevia* Frederiks, 1925

1947 *Muirwoodia* Likharev, p. 187.

Type species. (OD) *Yakovlevia kaluzinensis* Frederiks, 1925.

Diagnosis. Shell of medium to large size, subquadrate to transverse in outline, both valves strongly geniculated; widest at hinge line; sulcus and fold variably developed; surface capillate to costellate; strut spines few, confined to ventral valve, one pair from cardinal extremities, one or two pairs on trail on each side of sulcus, sometimes with additional pairs on lateral slopes; in addition, there are a few smaller spines in a row near the hinge line and scattered over the disc and trail. Ventral interior with wide, high, thickened hinge margin (ginglymus); narrow, strongly elevated adductor platform; and large flabellate diductor scars. Dorsal interior with corresponding ginglymus; cardinal process low and small, trilobate in posterior view; median septum extending to midlength and often with terminal swelling; muscle field sharply depressed, posteriorly located; marginal ridges variably developed.

Discussion. Yakovlevia was proposed first as a subgenus of *Chonetes* Fischer de Waldheim, 1829 by Frederiks (1925, p. 7) with the following description: "Shell concavo-convex, productid-like, with area (interarea) in ventral valve. Ventral interior, probably, with development of apical plates and usually filled by secondary shell substance; anterior end of the apical plates extend forwards as well developed ridges to enclose strongly depressed muscle field. Presence of a (ventral) median septum is not known." The type species, *Y. kaluzinensis*, is represented only by ventral internal moulds, in which a high linear band about 3 mm across, was well shown along the hinge line (Frederiks, 1925, Pl. 2, figs. 64–66).

Frederiks' diagnosis of *Yakovlevia*, particularly the presence of an interarea with "apical plates," was accepted by Likharev (1947), who subsequently proposed *Muirwoodia* for *Productus mammatus*

Keyserling, 1846, primarily because it has a thickened marginal area instead of an interarea with a median delthyrium, supposedly characteristic of *Yakovlevia*. *Muirwoodia* was recognized by Muir-Wood and Cooper (1960) and Abramov and Grigor'yeva (1983).

Kotlyar (1961) critically examined the alleged presence of an "interarea" and a "delthyrium" in *Yakovlevia*, based on more material, and concluded that the interarea was in reality "none more than a thickened hinge margin which B. K. Likharev called 'a marginal area'." This thickened hinge margin was described as a ginglymus by Cooper and Grant (1975, p. 1177).

In addition to the ginglymus, the hinge area of the ventral valve of *Yakovlevia* is usually marked by a well demarcated transverse band just below or anterior to the ginglymus (Fig. 34C). Unlike the ginglymus, which never reaches the cardinal extremities, the transverse band extends for the entire width of the hinge margin and, in some specimens, swings across the inner ears into lateral margins as low, flattened ridges that are often marked by striae (Fig. 34C). On separate internal moulds of *Yakovlevia* from the Yukon Territory, the transverse band is well preserved in many specimens of ventral valves and marked by small, irregularly spaced tubercles (pits on internal moulds) (Fig. 34C). An identical transverse band along the hinge area of the dorsal valves is also observed in the Canadian material and marked by tubercles (dimples on internal moulds) corresponding to pits on the ventral valves (Fig. 34D).

The function of the ginglymus, the transverse band, and the embedded pits and tubercles in *Yakovlevia* is not clear, but Cooper and Grant (1975) suggested that they may be related to helping with the articulation of these transverse shells.

The alleged presence of apical plates and a delthyrium in the ventral interior of *Yakovlevia* is clearly a misinterpretation, judging by observations on the Canadian material as well as examination of the illustrations of *Yakovlevia* from Texas by Cooper and Grant (1975). One of the most conspicuous features that characterize *Yakovlevia* is its large, broadly heart-shaped muscle field on the posterior floor of the ventral interior (Fig. 34C). The diductor scars are large, flabellate and deeply striate, separated anteriorly by a thick, narrow platform, which decrease in height posteriorly. The adductor scars are located between, but posterior to, the diductor scars and posteriorly separated from the latter by a layer of smooth callus that covers much of the posterior part of the diductors scars (Fig. 34C). The whole muscle field is posteriorly located, deeply depressed, and encircled by strongly developed shell thickening, which in many specimens is strongly elevated and extends posteriorly right into the beak, therefore making a false impression of a delthyrium and apical plates under the beak and the ginglymus (Fig. 34C).

Apart from the misinterpretation of the thickened hinge margin (and ginglymus) and the posterior extension of the deeply depressed ventral muscle field, other internal structures of both *Yakovlevia* and *Muirwoodia* have been considered to be essentially the same by many authors (Muir-Wood and Cooper, 1960; Kotlyar, 1961; Abramov and Grigor'yeva, 1983). Thus, in view of the above observations and interpretation, we suggest following Kotlyar (1961) and Cooper and Grant's (1975) conclusion that *Yakovlevia* and *Muirwoodia* are synonyms and consequently suppressing the latter.

Yakovlevia transversa (Cooper, 1957)

Plate 19, figures 1–32; Figures 34, 35

1957 *Muirwoodia transversa* Cooper, p. 39, Pl. 5A, figs. 1–13.
1971 *Yakovlevia* sp. Waterhouse *in* Bamber and Waterhouse, Pl. 14, figs. 2–5; Pl. 15, fig. 1; Pl. 16, fig. 7.
1985 *Yakovlevia transversa* (Cooper); Nelson and Nelson (partim.), Pl. 1, figs. 10, 11; not fig. 12.
1995 *Yakovlevia transversa* (Cooper), Shi, Fig. 6A-O.

Holotype. USNM 125339 figured in Cooper (1957, Pl. 5A, figs. 2, 3) from the Coyote Butte Formation, central Oregon, United States.

Diagnosis. Large, transverse *Yakovlevia* with flattened to gently convex ventral visceral disc and strongly geniculated trail; sulcus and fold well developed at maturity; five to seven costellae in 5 mm on ventral trail.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53703			8
GSC loc. 53705			11
GSC loc. 53710	1(im)		
GSC loc. 53720	1		1
GSC loc. 53721			6
GSC loc. 53857		1(em)	
GSC loc. 53858	4		
GSC loc. 53860	10	5(em)	
GSC loc. 53861	1	1(em)	

GSC loc. 53862	4	1(em)	
GSC loc. 53946	1		
GSC loc. 53952	3	1(im)	
GSC loc. 53999	2, 3(im)	2	
GSC loc. 56917	1		
GSC loc. 56922		1(em)	
GSC loc. 56972	5	3	
GSC loc. 56977		1(em)	
GSC loc. 57141	7		2
JBW loc. 2	4, 2(im)	1	
JBW loc. 24	1, 1(im)		
JBW loc. 58	1(em)		
JBW loc. 63	1, 2(im)		
JBW loc. 88	3, 11(im)	3(em), 4(im)	2
JBW loc. 109	1(em)		
JBW loc. 113	6, 4(em)	3(em)	
JBW loc. 512	2		
JBW loc. 537	2, 1(im)		

Description. External. Shell medium to moderately large, transverse in outline; hinge line at maximum width.

Ventral valve abruptly geniculated with geniculation angle between 60° and 80° (Pl. 19, fig. 16; Fig. 34B); visceral disc flattened to gently convex, subrectangular to trapezoidal in shape; umbo tiny, flattened; no prominent umbonal slopes; ears large, well extended (Pl. 19, fig. 3), but poorly differentiated from umbo, slightly to moderately rounded in section; hinge line usually slightly wider than midwidth; cardinal extremities acute at 80° on average; angle between hinge margin and lateral margin of visceral disc ranging between 55° and 65°; lateral margins nearly parallel; trail approximately one and one-half times as long as visceral disc when completely preserved (Pl. 19, fig. 18), subquadrate to slightly elongate; sulcus distinct in all ventral specimens, but varying in depth and distance from umbo in specimens even from the same locality, usually commencing 2 to 4 mm from umbo with sulcal angle between 40° and 50° (Pl. 19, fig. 4), deepening and widening forward, strongest over geniculation area with angular floor (Pl. 19, fig. 17), slightly shallower anteriorly and floor more broadly rounded; flanks bounding sulcus high and narrowly rounded in section, with nearly vertical lateral slopes. Costellae well defined, low and rounded, eight in 5 mm at 6 mm from umbo (Pl. 19, fig. 13), five to seven in 5 mm on trail (Pl. 19, fig. 16), anteriorly increasing by intercalation, separated by narrow interspaces, slightly converging in sulcus in some specimens (Pl. 19, fig. 15); rugae much weaker than costellae (Pl. 19, fig. 9), low and rounded, one or two rugae per mm, better defined on inner ears, slightly crossing costae; reticulation indistinct. Spines few, well differentiated (Fig. 34A); coarse strut spines usually measuring 1 to 1.5 mm in diameter, interrupting two or more costellae (Pl. 19, fig. 16) which continue forward in front of spine bases, slightly varying in number and position, but always with one pair of spines from cardinal extremities (Pl. 19,

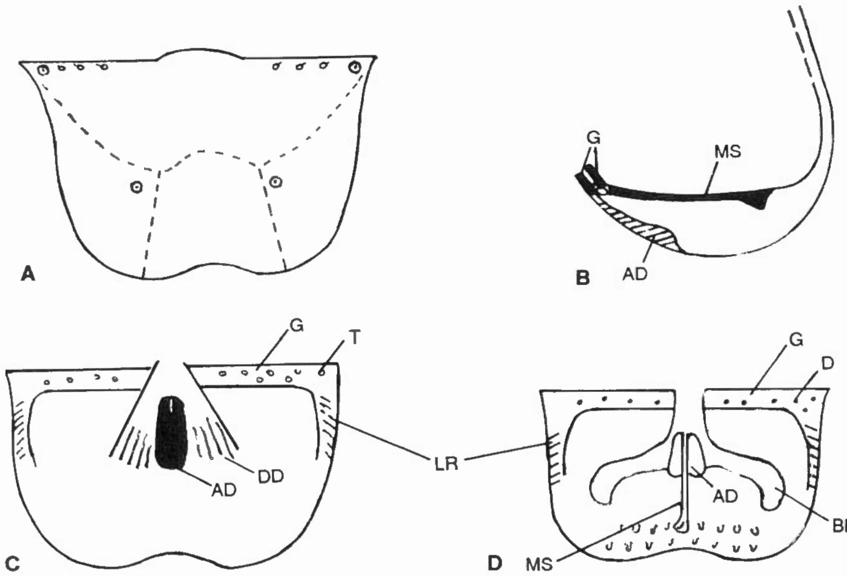


***Figure 34. Yakovlevia transversa** (Cooper). A, ventral spine pattern (GSC 97045); B, idealized reconstruction of shell articulation; C, ventral internal mould (GSC 97057); D, dorsal interior (GSC 97052). (All approx. x1.2). D, dimples; G, ginglymus; T, tubercles; other abbreviations as in Figure 27.*

fig. 13), one or rarely two pairs on flanks bounding sulcus (Pl. 19, fig. 16), rare on lateral slopes, and sometimes one strut spine in sulcus (Pl. 19, fig. 19); finer spines comparatively more numerous, in row along hinge line (Pl. 19, fig. 3; Fig. 34A) and rare over trail and visceral disc where they arise from a single costella, 0.5 mm in diameter.

Dorsal valve strongly concave on the whole (Pl. 19, fig. 31), visceral disc flat, trapezoidal in shape; geniculation abrupt and narrow with angle between 50° and 75°; trail approximately as long as disc; fold variable as ventral sulcus, normally beginning at 3 to 5 mm in front of dorsal umbo, strongest over geniculation area, crest well rounded. Costellae similar to those on ventral valve; but rugae slightly stronger and more regularly defined, confined to visceral disc, about five to seven in 5 mm, crossing costellae to form more prominent, at times well defined, reticulation in visceral disc (Pl. 19, fig. 10); no spines observed on dorsal valves. Shell pseudopunctate, punctae preserved as fine pits on worn surface (Pl. 19, fig. 17).

Internal. Ginglymus not preserved; transverse band along posterior margin of both valves distinct in many specimens, 3 to 4 mm in diameter, irregularly pitted on ventral side and matched by tubercles on dorsal side, extending laterally across ears to lateral margins, where

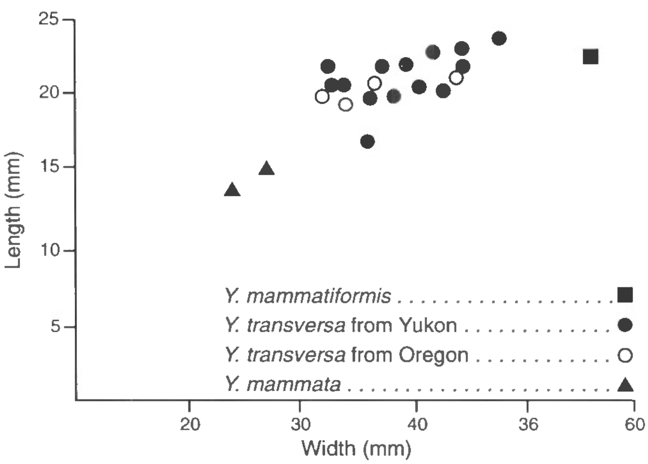


Figure 35. *Relation of length and width in three Arctic* ***Yakovlevia*** *species.* ***Yakovlevia transversa*** *from Yukon and central Oregon falls in a compact and continuous field and is larger than* ***Y. mammata*** *from the Urals but smaller and less transverse than* ***Y. mammatiformis*** *from the northern Urals. Measurements of* ***Y. mammata*** *were taken from specimens figured by Keyserling (1846) and Chernyshev (1902), and those of* ***Y. mammatiformis*** *from syntypes figured by Frederiks (1926).*

it is replaced by lateral ridges (Figs. 34C, D); lateral ridges striated and not reaching anterior margin.

Ventral muscle field deeply depressed just below ginglymus (Pl. 19, figs. 12, 26, 28), triangular in shape, posteriorly narrower and extending across ginglymus, leaving small, smooth, triangular opening simulating delthyrium (Fig. 34C), outlined by low ridges; adductor platform strongly raised, narrow and elongate, sometimes divided by very thin median groove, slightly striate on anterior portion, posteriorly smooth; large diductor scars to each side, deeply depressed below valve floor, flabellate, posteriorly smooth, anteriorly marked by distinct radial grooves and ridges; rest of valve floor densely granulate and pitted, stronger towards anterior margin.

Dorsal adductors small, weakly raised (Pl. 19, fig. 14; Fig. 34D), oval in shape, smooth; brachial ridges distinct with slightly recurved anterior portions, smooth inside loops; median septum weak between adductor scars, extending slightly beyond midlength and ending with high anterior swelling; floor irregularly granulate and pitted; two or three concentric rows of small endospines in front of brachial ridges and median septum (Pl. 19, fig. 4).

Dimensions (in mm).

Specimens (Ventral valves)	Length	Width	Height	Cardinal angle
GSC 97045	23	44	20	80°
GSC 97046	—	47	—	70°
GSC 97047	+18	36	18.5	81°
GSC 97050	22	40	18	75°
GSC 97058	—	30	15	—

Comparisons. The holotype of *Yakovlevia transversa* (Cooper, 1957) from the Coyote Butte Formation of central Oregon has a slightly deeper and longer sulcus than some of the Yukon specimens, but this feature is variable in the Yukon collections. Smaller specimens usually have a gentle sulcus (e.g., Pl. 19, fig. 17). Larger and more transverse specimens possess a slightly deeper and longer sulcus (e.g., Pl. 19, fig. 24) which can be fully compared with that of the Oregon types. The two specimens figured as *Y. transversa* by Nelson and Nelson (1985) seem to be conspecific, but the ventral internal mould identified in their figure 12 as the same species, seems to have been mislabeled; it is perhaps a ventral internal mould of *Purdonella* Reed or ally, because it has long subparallel adminicula and a well impressed, elongate muscle field; this is not like any of the ventral interiors of *Yakovlevia transversa* from northern Yukon.

Yakovlevia mammata (Keyserling, 1846, p. 206, Pl. 4, figs. 5a, b) and *Y. mammatiformis* (Frederiks, 1926, p. 87, Pl. 3; figs. 4-6) are the two species most similar to *Y. transversa*. The first was originally described from the possibly Sakmarian fauna of the Urals and has now been widely reported from primarily the Lower Permian (Asselian to Sakmarian) in Arctic Russia, Arctic Canada, and northeastern China. The type material of this species is similar to some small specimens of the present species, but this Russian species has a shallow sulcus. Types of *Y. transversa* and most Yukon hypotypes are much larger and more transverse than *Y. mammata* (Fig. 35) and have a deeper sulcus. *Yakovlevia mammatiformis* (Frederiks, 1926, p. 87, Pl. 3, figs. 4-6), from the Sakmarian beds in Kejim Terovey River of Timan, appears to be closer to *Y. transversa* in general appearance. The Russian types are poorly preserved but do have a large size (Fig. 35), a more transverse outline, and coarser, more widely spaced costellae (see Abramov and Grigor'yeva, 1983, Pl. 10, figs. 13, 14).

Occurrence. In northern Yukon Territory, *Y. transversa* occurs in the Ey, Eog, and Ej zones of the Jungle Creek Formation, but is most abundant in the Ey zone. Outside the Yukon Territory, and apart from its occurrence at the type locality from the Sakmarian to Kungurian Coyote Butte Formation in central Oregon, *Y. transversa* is known also from the possibly Sakmarian fauna in southeastern British Columbia (Nelson and Nelson, 1985).

Order RHYNCHONELLA Kuhn, 1949

Superfamily RHYNCHONELLACAEA Gray, 1848

Family PUGNACIDAE Rzhonsnitskaya, 1956

Genus *Rhynoleichus* Abramov and Grigor'yeva, 1983

Type species. (OD) *Rhynoleichus delenjaensis* Abramov and Grigor'yeva, 1983.

Diagnosis. Shell rounded-triangular to rounded-trapezoidal with strongly dorsally folded, triangular anterior commissure and steep flanks; sulcus and fold anteriorly developed, tongue prominent, deeply indenting dorsal valve; ventral valve flat or slightly convex over umbonal region, dorsal valve greatly inflated; costae few, only over fold and sulcus, commencing at some distance from umbo. Dental plates not reaching posterior third of shell length. Dental sockets not crenulate; dorsal median septum thin and low; septalium small and buried by umbonal callus; hinge plate triangular, thickened, and divided; crura not observed.

Discussion. The above diagnosis is translated and reworded from Abramov and Grigor'yeva (1983, p. 95). Species of *Rhynoleichus* have the so-called dorsal median septum often expressed as a rather fine median ridge, about 0.3 to 0.5 mm across, sometimes discontinuous. This thin and low ridge may alone serve to distinguish the genus from *Leiorhynchus* Hall, 1860 and *Leiorhynchoidea* Cloud, 1944, which both have a thick, high median septum. *Leiorhynchoidea* may be further distinguished by its entire hinge plate and lack of a small septalium. *Bryorhynchus* Cooper and Grant, 1969, 1976a resembles *Rhynoleichus* in possessing an "often obsolete" dorsal median ridge and a few coarse costae over the sulcus and fold, but it is distinguished by its strongly crenulate sockets and nearly entire hinge plate.

Rhynoleichus dorsoconvexa n. sp.

Plate 20, figures 1-13

Etymology. Latin *convexus*, arched outward.

Holotype. GSC 97157 from JBW loc. 15, Ettrain Creek; Ey zone, Jungle Creek Formation (Pl. 20, figs. 8-12).

Diagnosis. Moderately large, subpentagonal to subrounded *Rhynoleichus* with strongly convex dorsal valve; ventral valve gently inflated over umbonal region, deeply and broadly sulcate anteriorly; two costae over sulcus and fold.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53812	2, 1(im)	4, 1(im)	
GSC loc. 53952			1
GSC loc. 53999	1(im)		
JBW loc. 2			1(m)
JBW loc. 15			1
JBW loc. 24			1

Description. External. Shell medium to large in size, holotype measuring 32 mm wide, 25 mm long, and 25 mm high (Pl. 20, figs. 8-12); subpentagonal to subrounded in outline; strongly and unequally biconvex with flattened ventral valve and greatly inflated dorsal valve, semispherical in posterior view (Pl. 20, fig. 12); anterior commissure strongly folded dorsally; widest at midlength.

Ventral valve usually gently convex over umbonal region, anteriorly flat to concave, anterior half broadly and deeply sulcate (Pl. 20, fig. 10); umbo small and low, little extended, truncated by small circular foramen about 1 mm in diameter (Pl. 20, fig. 12); umbonal angle between 90° and 100°; umbonal slopes straight, broadly rounded in section; hinge margin concealed by incurved umboes (Pl. 20, fig. 9); cardinal extremities broadly rounded into lateral margins, anterolateral margins well rounded; sulcus beginning from midlength, widening and deepening anteriorly, delimited by high and steep sides (or slopes), floor flat, broadly U-shaped in section, occupying over two thirds of shell width at front; anterior tongue well pronounced, deeply indenting dorsal valve, extending for half of shell curvature length (Pl. 20, fig. 10); anterior commissure broad-triangular in outline (Pl. 20, fig. 11); flanks about half sulcus in width, strongly rounded in section; sulcus carrying two low and broad costae (Pl. 20, fig. 5), arising simultaneously with sulcus, crests sharp, interspaces low and well rounded.

Dorsal valve at least three times as convex as ventral valve (Pl. 20, fig. 12), narrowly and evenly arched in transverse section with high, nearly vertical lateral slopes; fold observable only over anterior half of valve length, crest well rounded onto lateral slopes, anteriorly sharply meeting sulcal tongue, carrying three high and sharp-crested costae, which are separated by narrow, deep, and angular interspaces. Concentric growth lamellae developed in some specimens (Pl. 20, figs. 6, 10), strongest towards anterior margin.

Internal. Thin dental plates (Pl. 20, figs. 1, 4) extend for posterior 5 mm of shell length, about 0.5 mm in diameter, slightly converging posteriorly, reaching posterior floor, but not united at apex; muscle field poorly impressed, adductor scars just in front of dental plates, narrow-elongate in shape, smooth; diductors slightly more conspicuous, anterolateral to adductor scars, weakly striated longitudinally.

Dental sockets not crenulate; hinge plate divided at median (Pl. 20, fig. 1); septalium very small and apically placed; median septum thin and low, about 0.3 mm in diameter, posteriorly supporting septalium, anteriorly discontinuous in some specimens, not reaching midlength; muscle scars obscure; radial pallial markings weakly impressed just in front of septalium and beside median septum.

Comparisons. In many aspects the new species approaches the type species *Rhynoleichus delenjaensis* Abramov and Grigor'yeva (1983, p. 96, Pl. 11, figs. 8, 9) from the Upper Carboniferous Sieder Suite of the Verchoyan Mountains, also recorded by Abramov and Grigor'yeva (1988) from the Aktastinian lower Echii Suite of the same region. The holotype of the Russian species is about the size and general appearance of the Yukon species, but it has one more pair of costae over the sulcus and fold. In addition, the Russian species is nearly equally biconvex and has a shorter ventral tongue. Specimens attributed to *R. delenjaensis* by Abramov and Grigor'yeva (1988) are small.

A single shell figured (not described) by Abramov and Grigor'yeva (1988) as *Rhynoleichus* sp. from the Upper Carboniferous lower Akatchan Suite of the Verchoyan Mountains is very similar to the Yukon species in having a high dorsal valve and a broad, deep sulcus carrying two coarse costae, but it appears to have a slightly longer ventral tongue and higher ventral costae separated by deeper interspaces.

Rhynoleichus triangulatus Abramov and Grigor'yeva (1983, p. 97, Pl. 11, figs. 10–14; Textfig. 24) from the "Middle Carboniferous" Darnin Suite of the southern Verchoyan Mountains differs from the Yukon species in having two more costae over the sulcus and fold and a much less convex dorsal valve. The same may be also said of the comparison with *R. etschensis* Abramov and Grigor'yeva (1988, p. 139, Pl. 15, figs. 1–6) from the Aktastinian lower Echii Suite of the western Verchoyan Mountains, which may be further distinguished by the presence of a few additional, broad anterior plicae on the flanks of the Russian species.

Specimens with a similar outline, size and an inflation have been referred to *R. subglobosa* Abramov and Grigor'yeva (1988, p. 143, Pl. 16, figs. 1, 2) from the Sakmarian Olichan and Baigendzinian to Kungurian Privolinin suites of the Verchoyan Mountains. The Russian species appears to include two essentially different morphotypes, one with as many as four costae in the sulcus and five on the fold, and the other lacking any costae. Neither is similar to the Yukon material.

Some species strongly resembling *Rhynoleichus* in external morphology have been previously referred to *Leiorhynchus*. *Leiorhynchus*? sp. (sp. nov. ?) of Likharev (1934b, Pl. 8, figs. 11, 12) from the Early Permian fauna of the Omolon River, northeastern Siberia, and *Leiorhynchus ripheicus* Stepanov of Zavodovskiy and Stepanov (1970, p. 125, Pl. 28, fig. 6; Pl. 29, figs. 1, 2; Pl. 31, fig. 4; Pl. 33, fig. 11) from the probably Asselian Paren Horizon of the Kolyma–Omolon Massif, northeastern Siberia, are rather like the new species in general external features. Unfortunately, none of them exhibit internal structures, except for one (Zavodovskiy and Stepanov, 1970, Pl. 31, fig. 4b), which displays a very low, fine, short dorsal median ridge. This median ridge is similar to that observed from the Yukon species. *Leiorhynchus ripheicus* has more costae than the Yukon species.

Occurrence. Ey and Eog zones, Sakmarian.

Family TETRACAMERIDAE Likharev *in* Rzhonsnitskaya, 1958

Genus *Septacamera* Stepanov, 1937

Type species. (OD) *Camarophoria kutorgae* Chernyshev, 1902.

Discussion. Though initially placed in Stenoscimatidae Oehlert by Grant (1965), *Septacamera* was subsequently transferred to the Tetracameridae of the Rhynchonellacea by the same author (Grant, 1971), in line with the Russian classification scheme (Rzhonsnitskaya et al., 1960).

As noted by Grant (1971), *Septacamera* is externally very close to *Rotaia* Rzhonsnitskaya, 1959, type species *Rhynchonella subtrigona* Meek and Hayden, 1866. Comparisons of thin sections of the type species of the two genera, illustrated by Rzhonsnitskaya et al. (1960, p. 250, Figs. 289, 290), revealed obvious internal differences. The spondylium is largely sessile in *R. subtrigona* but is elevated on a thick median septum in *Septacamera kutorgae*. Buttress plates are larger, thicker, and extend further forward in *Rhynchonella subtrigona* than in *Septacamera kutorgae*. Within the dorsal interior, *Rhynchonella subtrigona* has a more extensive septalium supported by a low but rather thick median septum, in contrast to the very small septalium, elevated on a high but generally thin median septum, in *Septacamera kutorgae*.

Septacamera triangulata n. sp.

Plate 20, figures 14–27; Figure 36

1971 *Septacamera* cf. *S. plicata* (Kutorga), Waterhouse *in* Bamber and Waterhouse, Pl. 16, fig. 9.

Etymology. Latin *triangulatus*, having three angles.

Holotype. GSC 97163 from GSC loc. 57275, section 116C-2 (Fig. 5); Ej zone, basal Tahkandit Formation (Pl. 20, fig. 27).

Diagnosis. Moderately large triangular shell with maximum width placed near anterior margin; ventral valve gently convex, dorsal valve much more inflated; costae low and well rounded in general, strongest over sulcus and fold.

Material.

Locality	Ventral	Dorsal
GSC loc. 56917	2	1(im)
GSC loc. 56922	3, 2(im)	3, 1(im)
GSC loc. 57052	2	2, 1(im)
GSC loc. 57275	1, 1(im)	

Description. External. Shell 28–32 mm long, 32–37 mm wide, 10–16 mm high; triangular in outline, very unequally biconvex, widest near anterior margin.

Ventral valve flattened or plano-convex in overall appearance (Pl. 20, fig. 27), moderately convex over umbonal region, deeply and broadly sulcate anteriorly; umbo small, slightly extended and incurved, angle between 90° and 100°; umbonal slopes straight or gently concave in outline, broadly rounded in section; foramen obscure; anterolateral margins acutely rounded; sulcus commencing at posterior third of shell length (Pl. 20, figs. 23, 27), deepening and widening forward, sulcal angle ranging between 45° and 60°, floor broadly rounded with gentle and moderately high slopes, occupying approximately half of shell width in front; anterior tongue short, moderately indenting dorsal valve; flanks well rounded on crests. Costae simple, all starting from umbo, though inconspicuous over umbonal region in some specimens (Pl. 20, fig. 27), generally very low and broadly rounded, especially on flanks, five over sulcus and five to seven on each flank; sulcal costae high and narrowly rounded, sometimes with sharp crests, increasing in size towards anterior margin, separated by interspaces as wide as costae; costae on flanks lower and more rounded, diminishing in strength towards lateral margins.

Dorsal valve strongly to globally convex with high and steep flanks (Pl. 20, fig. 21); fold recognizable over anterior half to third of valve length (Pl. 20, fig. 14), broadly rounded in section, not well discriminated from flanks; dorsal costation generally similar to that on ventral valve, with six costae on fold and five to seven on each lateral flank; costae on fold high and narrowly rounded (Pl. 20, fig. 25), at times sharp crest (Pl. 20, fig. 25), separated by narrow and deep interspaces; costae on flanks low and well rounded.

Internal. Spondylium large, (Pl. 20, fig. 22; Fig. 36A), each convergent plate braced posteriorly by small triangular horizontal buttress plate about 0.5 mm thick (Pl. 20, figs. 15, 19); median septum distinct, about 0.5 to 1 mm in diameter, supporting spondylium posteriorly, extending beyond midlength anteriorly; pallial markings prominent (Pl. 20, fig. 17; Fig. 36B), symmetrically disposed to median septum; muscle scars obscure within spondylium.

Dorsal interior (Pl. 20, figs. 20, 25; Figs. 36C, D) lacks cardinal process; septalium very small and shallow, normally 3 mm wide and 4 mm long, placed at apex of umbonal cavity, supported by thin and high median septum, which extends beyond midlength; adductor impressions obscure; pallial markings prominent in some specimens, well in front of septalium, represented by fine radial ridges oblique to median septum (Fig. 36B), three to four each side.

Dimensions (in mm).

Specimen	Valve	Length	Width	Height
GSC 97163	VEN	30	36	+10
GSC 97165	DOR	28	32	12
GSC 97167	VEN	28	35	10
GSC 97168	DOR	32	37	16
GSC 97169	DOR	32	37	16

Comparisons. Externally, the new species approaches *Septacamera plicata* (Kutorga, 1844, Pl. 9, fig. 3), a species originally described primarily from the Sakmarian faunas of the Urals. The holotype of the Russian species is typified by its large size (about 50 mm wide, 37 mm long and high), equally biconvex profile, subelliptical outline with maximum width placed at midlength, and high, equally strong costae over sulcus and flanks. These characteristics differ

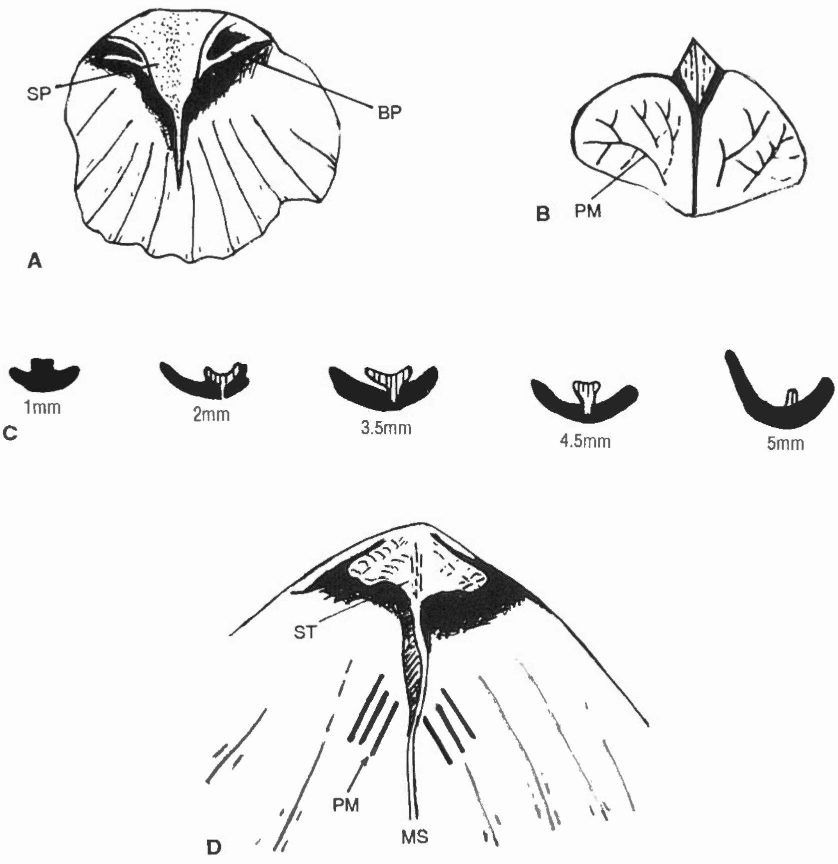


Figure 36. Septacamera triangulata *n. sp. A, ventral interior showing spondylium and buttress plates (GSC 97170, x2); B, ventral internal mould showing pallial markings (GSC 97164, x1); C, transverse serial sections of dorsal valve (x1); D, dorsal interior (GSC 97168, x3). BP, buttress plate; MS, median septum; PM, pallial markings; SP, spondylium; ST, septalium. Figures show distance from dorsal umbo.*

from those of the Yukon species, in which the shells are less than 37 mm wide and 32 mm long, are triangular in outline with maximum width placed near anterior margin, are unequally biconvex with more inflated dorsal valve, and have stronger costae over the sulcus and fold than on the flanks. Specimens from the Coyote Butte Formation of central Oregon, referred to as *Septacamera* cf. *S. plicata* by Cooper (1957, p. 54, Pl. 10E, figs. 32–35) are much the same as the new species in size, outline, and inflation, but they have higher and narrower costae.

The type species *S. kutorgae* (Chernyshev, 1902, p. 500, Pl. 22, figs. 16, 17) is similar in general attributes but it differs in being smaller in size and subrounded–subelliptical in outline, in having its maximum width usually at midlength, and in possessing higher and narrower costae.

Grant (1971) described three species of *Septacamera* from Alaska and the Canadian Arctic, of which *S. pybensis* Grant (1971, p. 320, Pl. 2, figs. 1–16) from the probably Baigendzinian Pybus Formation at Pybus Bay on Admiralty Island, and Saginaw Bay near Kuiu Island, southeastern Alaska, is probably closely allied. It resembles the Yukon species in size, shape, inflation, and internal structures. The holotype of the Alaskan species appears to be more rounded and has conspicuously higher and narrower costae.

Occurrence. Ej zone, Early Artinskian (Aktastinian).

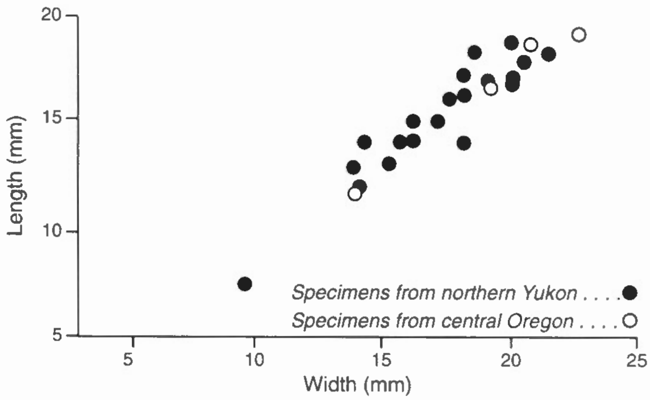


Figure 37. *Relation between length and width of **Rhynchopora magna** Cooper, illustrating the linear development of shell size. Specimens from central Oregon fit well within the size range field.*

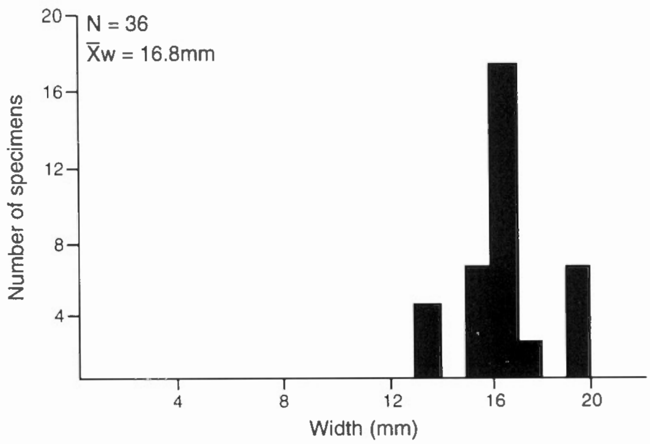


Figure 38. *Frequency distribution of shell width in **Rhynchopora magna** Cooper.*

Family RHYNCHOPORIDAE Muir-Wood, 1955

Genus *Rhynchopora* King, 1865

Type species. (OD) *Terebratula geinitziana* Verneuil, 1845.

Rhynchopora magna Cooper, 1957

Plate 20, figures 28–34; Plate 21, figures 1–3; Figures 37, 38

1957 *Rhynchopora magna* Cooper, p. 55, Pl. 9B, figs. 11–14; Pl. 10D, figs. 18–31.

1963 *Rhynchopora* cf. *R. magna* Cooper; Yole, Pl. 2, fig. 18.

1971 ?*Rhynchopora* cf. *R. magna* Cooper; Waterhouse *in* Bamber and Waterhouse, Pl. 15, figs. 5, 6.

Holotype. USNM 125392 figured by Cooper (1957, Pl. 10D, figs. 18–22) from the Coyote Butte Formation of central Oregon.

Diagnosis. Large, pentagonal *Rhynchopora* with broad umbo, deep sulcus, and high fold; seven costae over sulcus, nine or 10 on each flank, costae generally high and narrowly rounded over anterior shell.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53714			54
GSC loc. 53720			1
GSC loc. 53722			1
GSC loc. 56977			1
GSC loc. 57266			1

JBW loc. 2	2	2	
JBW loc. 56	1(im)		
JBW loc. 88			5
JBW loc. 89		1(im)	3
JBW loc. 113			1im
JBW loc. 545			1

Description. External. Shell large for genus at maturity (Figs. 37, 38); pentagonal in outline (Pl. 20, fig. 32), triangular in profile; widest at midlength or in front of it.

Ventral valve gently convex with greatest convexity slightly behind midlength; umbo well extended with angle of 105° at maturity; umbonal slopes gently concave in outline, narrowly rounded in section; beak truncated by epithyridid foramen (Pl. 20, fig. 29); palintrope prominent, narrow and concave; sulcus commencing from midlength, deepening anteriorly, delimited by high flanks, floor flat, U-shaped in section at front; anterior tongue broad, flanks narrower than sulcus, broadly rounded in section. Costae start from beak, posteriorly fine, low and rounded, generally seven over sulcus, nine or 10 on each flank, separated by rather narrow, angular interspaces, tending to be sharp on crests over anterior portion of sulcus, but becoming broadly rounded or flattened again on anterior surface, where sulcal costae are penetrated and anteriorly replaced by median grooves, giving appearance of interlocking spine system with opposite valve (Pl. 20, fig. 34); costae on flanks broadly rounded in posterior portion, sharp-crested at front, flattened on lateral slopes.

Dorsal valve apparently more convex than ventral valve; umbo slightly extended with broad angle; fold indistinct in juvenile specimens, moderately developed in immature material, and becoming distinct into maturity (Pl. 21, fig. 1), beginning at midlength, crest flat, abruptly curved ventrally at frontal margin to join recurved sulcal tongue, forming large, flat, and prominent anterior surface; flanks moderately sloping to lateral margins and interlocking with reflected anterolateral extremities of ventral valve. Dorsal costation similar to that of ventral valve, usually with eight costae on fold and nine or 10 on each flank.

Micro-ornament of very fine concentric growth lines, about eight in 1 mm; punctae marked on shell surface as fine dark circular pits, about five or six in 1 mm.

Internal. Dental plates distinct, diverging forward by about 30° (Pl. 20, fig. 28). Dorsal interior with very small septalium, about 1.5 mm across, very posteriorly located, supported by median septum that extends to midlength (Pl. 20, fig. 29).

Dimensions (in mm).

GSC	L	W	H	UA	SB	NCB	NCS	NCF	SB/W	H/W	L/W
97176	16	18	12	105°	15	26	7	7	0.83	0.67	0.89
97177	17	19	15	93°	15	25	8	9	0.79	0.78	0.89
97672	16.5	20	16	102°	13	25		9	0.65	0.80	0.83
97673	17	20	12	107°	13.5	28	0	9	0.68	0.60	0.85
97674	18	21.5	15	105°	13	20		8	0.60	0.70	0.84
97675	17	20	16	108°	15	28	8	9	0.75	0.80	0.85
97676	15	17	12.5	99°	12.5	25		8	0.74	0.74	0.88
97677	12	14	9	95°	9.5	20	6	7	0.68	0.64	0.86
97678	7.5	9	—	—	—	17	—	5	—	—	0.83
97679	13	15	10	95°	10	25	7	7	0.67	0.67	0.87
97680	13	13.5	11.5	94°	8	20		7	0.59	0.85	0.96
97681	17	20	15	105°	15	18	7	8	0.75	0.75	0.86
97682	18.5	20	14.5	103°	12	24		7	0.60	0.73	0.93
97683	15	16	13	105°	12	22	6	7	0.75	0.81	0.94
97684	14	14	10	97°	11	24	6	7	0.79	0.71	1.00
97685	16	17.5	13	97°	12	22	8	8	0.69	0.81	0.91
97686	17	20	15	100°	15	22	8	9	0.75	0.75	0.85
97178	17	18	14	93°	14	20	6		0.78	0.78	0.94
97687	14	16	10	102°	10	27	9	10	0.63	0.63	0.86
97688	18	18.5	12.5	95°	11	24		7	0.59	0.68	1.00
97689	12	14	11	93°	10	21	7	8	0.71	0.76	0.86
97690	14	16	12	93°	10	22	8		0.63	0.75	0.86
97691	14	15.5	13	93°	9	23	7	8	0.58	0.84	0.90
97174	14	18	11	105°	9	25	6	6	0.50	0.61	0.78
X	15.2	17.1	12.9	99	12	23	7	8	0.69	0.74	0.89
Q	2.6	2.98	2.06	5.3	2.2	3	1	1	0.08	0.07	0.05
N	23	22	22	22	22	23	22	23	22	22	23

X, mean of observed variables; Q, variance; N, total specimens measured; L, shell length; W, shell width; H, shell height; SB, sulcal breadth measured at anterior margin; NCB, total costae of shell; NCS, costae in sulcus; NCF, costae on fold.

Comparisons. The Yukon material appears to be identical to *Rhynchopora magna* Cooper, 1957 from the Coyote Butte Formation of central Oregon and the specimen figured by Yole (1963) from the probably Lower Sakmarian Formation B on Vancouver Island. Dimensions from Cooper's type material are plotted with the Yukon material in Figure 39 and are in agreement with the Yukon material in shell length/width relationships.

Rhynchopora nikitini Chernyshev, 1889 from the Sakmarian fauna of the Russian Platform and the Urals, revised by Nikolskaya (1979, p. 46, Pl. 2, figs. 2-4), is very similar in overall appearance to the present species, but may be distinguished by its smaller size, rounded outline, shallower sulcus and lower fold, and finer, less rounded costae.

Rhynchopora arctica Likharev and Einor (1939, Pl. 13, figs. 7-10) from the Lower Permian of Novaya Zemlya, also recorded by Ustritskiy and Chernyak (1963, Pl. 26, fig. 18-20) from the Aktastinian lower Birrang Horizon of eastern Taimyr, northern Russia, is similar in size, but it differs in having a rounded outline, a narrower and more pointed umbo, and fewer costae over the sulcus and flanks. *Rhynchopora angulatiplicata* Ustritskiy (*in* Ustritskiy and Chernyak, 1963, p. 99, Pl. 26, figs. 21-24), from the upper Even and lower Efremov Suites (of Sakmarian to Artinskian age) of west Taimyr, also reported from the Aktastinian lower Echii Suite of the Verchoyan Mountains (Abramov and Grigor'yeva, 1988, Pl. 16, figs. 10, 16-19), is about half the size of mature *R. magna* and has a rounded outline and fewer costae.

Rhynchopora culta Waterhouse (1982c, p. 345, Pl. 2, figs. 6-11) from the Upper Asselian or Lower Sakmarian fauna of the pebbly mudstone in southern Thailand, also recently recorded from an Upper Sakmarian (Sterlitamakian) fauna in western Malaysia (Shi and Waterhouse, 1991), is close in overall appearance, but it differs in having a shallower sulcus and lower fold, and one or two fewer pairs of costae.

Occurrence. In northern Yukon Territory, *R. magna* ranges from the Eta to Ej zones within the Jungle Creek Formation, of Asselian to Early Artinskian (Aktastinian) age. Outside the Yukon Territory, *R. magna* is known from the Sakmarian to Kungurian Coyote Butte Formation in central Oregon and the probably Early Sakmarian "Formation B" on Vancouver Island.

Suborder STENOSCISMATIDINA
Waterhouse, 1981

Superfamily STENOSCISMATACEA Oehlert, 1887

Family STENOSCISMATIDAE Oehlert, 1887

Genus *Stenoscisma* Conrad, 1839

Type species. (OD) *Terebratula schlotheimi* Buch, 1834.

Stenoscisma mutabilis (Chernyshev, 1902)

Plate 21, figures 4-14

1902 *Camarophoria mutabilis* Chernyshev, p. 491, Pl. 22, fig. 18; Pl. 23, fig. 10; Pl. 45, figs. 1-15; Pl. 46, fig. 14.

1937b *Stenoscisma mutabilis* (Chernyshev); Stepanov, p. 5, Pl. 8, fig. 12.

1967 *Stenoscisma mutabilis* (Chernyshev); Mironova, p. 38, Pl. 3, fig. 6.

1976 *Stenoscisma mutabilis* (Chernyshev); Li and Gu, p. 272, Pl. 159, figs. 14-17.

1980 *Stenoscisma mutabilis* (Chernyshev); Kalashnikov, p. 71, Pl. 20, figs. 9-11.

Lectotype (selected here). A specimen with valves conjoined, figured by Chernyshev (1902, Pl. 22, fig. 18a-d) from the Sakmarian Stage of the Urals, kept at the CNIGR Museum, St. Petersburg.

Diagnosis. Medium to large, subtrigonal *Stenoscisma* with maximum width usually placed at midlength; umbonal slopes conspicuously concave, delimiting narrow umbo; sulcus well defined, carrying two or three high, rounded costae that begin near the umbo; lateral costae usually low and placed anteriorly.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53714		2	2
GSC loc. 53722			1
GSC loc. 53999			1(im)
GSC loc. 57141	1(im)		
JBW loc. 57	1		
JBW loc. 508	1	1(em)	1
JBW loc. 537	1		

Description. External. Shell of medium size, well preserved specimen measuring 20 mm wide, 16 mm long, and 13 mm high; rounded-oval and globular in juvenile shell, subtrigonal into maturity; widest in front of midlength, usually at anterior third.

Ventral valve most inflated over posterior third of shell length, anteriorly flattened due to development of broad sulcus; beak moderately to strongly extended, moderately incurved, truncated by small circular foramen about 0.8 mm in diameter (Pl. 21, figs. 12, 13); umbonal slopes high and steep; umbonal angle between 70° and 80°; delthyrium open; hinge margin arched, posterolateral margins butting with those of dorsal valve; sulcus commencing from about midlength, deepening and widening forward, delimited by high flanks at front, occupying roughly half anterior margin in width, sulcal floor flat; anterior tongue prominent, moderately indenting dorsal valve; flanks relatively narrow, well rounded in section; sulcus carrying two or three median costae commencing near umbo, occasionally with one additional, slightly shorter pair arising later on sulcal slopes, moderately high and narrowly rounded, slightly increasing in size towards anterior margin, separated by equally wide to slightly narrower interspaces; flanks mostly smooth, some specimens carrying few short, low, well rounded costae anteriorly, two to four on each flank; very fine growth lines seen near front in some ventral specimens; stolidium not preserved, but its presence indicated by the broken edge of abutting sulcus and fold in front in GSC 97180 (Pl. 21, fig. 9).

Dorsal valve strongly and evenly inflated longitudinally and laterally (Pl. 21, fig. 12), conspicuously higher than ventral valve; flanks high and steeply sloping to lateral margins; umbonal region flattened and beak concealed by ventral umbo; fold begins at about midlength, conspicuously elevated above flanks in front, anteriorly indented by ventral tongue to form angular anterior crest; fold bears four or five costae beginning at 4 mm from umbo, usually slightly higher and narrower than ventral sulcal costae; lateral costae rather weak, two to four on each flank, very anteriorly placed.

Internal. Ventral interior with broad spondylium (Pl. 21, fig. 5), supported by short median septum; muscle marks obscure.

Dorsal interior with small camarophorium supported by strong, long median septum extending to midlength (Pl. 21, fig. 5); intercamarophorial plate probably low; relatively large swollen cardinal process located above hinge plate, posteriorly striated with prominent median ridge.

Comparisons. The Yukon material appears conspecific with *Stenoscisma mutabilis* (Chernyshev, 1902) from the Late Carboniferous (Kasimovian) to Early Permian (Artinskian) faunas of the Urals. Syntypes of *S. mutabilis* seem variable in size and costation. They range from 12 to 30 mm in width, nine to 23 mm in length, and eight to 18 mm in height (all measured from Chernyshev's original illustrations, excluding stolidium). The lectotype selected here is the largest of all. With the size increase, costae tend to be longer, higher, and more numerous towards maturity, whereas immature specimens are mostly smooth. The syntypes normally carry two median costae over the sulcus arising from near the umbo, three on the fold, occasionally with one, rarely two, additional pairs arising from the sulcal slopes at various stages of growth. The umbo, sulcus, and fold of type *S. mutabilis* also appear to be broader into maturity. The Yukon material is smaller and has slightly shorter and fewer costae than the lectotype, but agrees well with some other syntypes such as those figured by Chernyshev (1902, Pl. 45, figs. 5, 6, 10, 11, 13). This implies that the present material is not fully mature.

Stenoscisma mutabilis has been widely recorded from Russia and Asia, and some of the records seem doubtful. A single specimen, figured by Mironova (1967), from the Upper Carboniferous of the Urals is possibly conspecific though it is smaller and has fewer and shorter costae as compared with mature types of *S. mutabilis*. It is strikingly similar to the Yukon specimens and some smaller syntypes of *S. mutabilis*. In the synonymy of *S. mutablis*, Mironova included *Camarophoria biplicata* Chernyshev (1902, Pl. 50, figs. 8–10) (not Stuckenberg) from the Sakmarian fauna at Sterlitamak of the Urals. The Sterlitamak shells are about the size of the Yukon material and possess fewer costae, especially on the flanks, than in the type material of *S. mutabilis*. Specific differences between Chernyshev's *Camarophoria biplicata* and mature *Stenoscima mutabilis* are in *Camarophoria biplicata* the maximum width is usually placed at midlength and the umbonal slopes are more strongly concave, delimiting a narrower, more pointed umbo. Also included in Mironova's (1967) synonymy of *S. mutabilis* were *Camarophoria uralica* Stepanov (1937a, Pl. 7, figs. 11–13) and *C. olgae* Stepanov (1937a, Pl. 7, figs. 4, 5), both originally from the Sakmarian fauna of Kolva River, northern Urals. *Camarophoria uralica* is unlikely to be conspecific with *Stenoscisma mutabilis* as it has only one costa in the sulcus and two over the fold. *Camarophoria olgae* appears to be more similar to typical *Stenoscisma mutabilis* in general attributes, with two or three costae over the sulcus and fold, and a few others on the flanks.

A single specimen figured as *S. mutabilis* from the Permian of Laos (Mansuy, 1913, Pl. 9, fig. 14) is of similar size, but it lacks costae on the flanks. Another specimen from southeastern Asia, figured as the same species, was reported from the Upper Permian of Cambodia (Chi-Thuan, 1961, Pl. 2, fig. 14); it has more numerous costae on the whole shell, stronger on the flanks than over the sulcus and fold. Very small specimens from the Artinskian to Kungurian Zhesi Formation of Inner Mongolia, northeastern China were probably incorrectly identified as *S. mutabilis* by Grabau (1931, Pl. 4, fig. 7; Pl. 5, figs. 1, 2). His specimen in Plate 4 has coarser costae on the flanks than over the sulcus, and the specimen in Plate 5 seems to be too small to be compared to *S. mutabilis* and may be further distinguished by its very anteriorly placed costae. *Stenoscisma mutabilis oregonense* Cooper (1957, p. 50, Pl. 9C, figs. 15–28), from the Artinskian to Kungurian Coyote Butte Formation of central Oregon, differs from typical *S. mutabilis* in being smaller and possessing higher and narrower costae. The Oregon species is mature, as indicated by the presence of a large stolidium.

Occurrence. Stenoscisma mutabilis comes from the Ey, Eog, and Ej zones in northern Yukon Territory. In the Urals and Russian Platform, *Stenoscisma mutabilis* is known to range from the Upper Carboniferous (Kasimovian) to Lower Permian (Artinskian) Stages, but it is most abundant in the Sakmarian Stage (Kalashnikov, 1980). Elsewhere, the species is known from the lower part of the Lower Permian (probably Asselian to Sakmarian in age) of Inner Mongolia, northeastern China (Li and Gu, 1976).

Family ATRIBONIIDAE Grant, 1965

Genus *Camerisma* Grant, 1965

Subgenus *Camerisma* (*Callaiapsida*) Grant, 1971

Type species. (OD) *Camerisma* (*Callaiapsida*) *kekuensis* Grant, 1971.

Diagnosis. See Grant (1971, p. 322).

Discussion. Grant (1971) recognized two subgenera within *Camerisma*: *Camerisma* (*Camerisma*) Grant, 1965 and *Camerisma* (*Callaiapsida*). The latter was distinguished for "several large species that seem to be confined to the Late Pennsylvanian and the Permian . . ." and that have "the additional features of the deep peripheral grooves with their peculiar set of flaps and flanges, . . ." (Grant, 1971, p. 323). Grant interpreted the peculiar peripheral structure of *Camerisma* (*Callaiapsida*) as conducting current from the anterior margin into lateral portions of the inner cavity. Martinez-Chacon (1977) described two species of *Camerisma* (*Callaiapsida*) from the Bashkirian of northern Spain, which also exhibit distinct peripheral grooves near the anterior margin. However, Lazarev (1976a) argued that this marginal structure was developed through an "irregular growth rhythm" of the shell, gave it no taxonomic value, and accordingly abandoned *Camerisma* (*Callaiapsida*). As far as the Yukon material is concerned, no such structure is preserved; perhaps, doubtfully, it has been damaged or obscured by sediments. In the absence of good material, it is very difficult to decide which interpretation is correct; provisionally, Grant's model is followed here.

Camerisma pentameroides (Chernyschev) was placed in *Camerisma* (*Callaiapsida*) by Grant (1971) primarily because of its large size, an additional characteristic of the subgenus.

Camerisma (*Callaiapsida*) *pentameroides* (Chernyshev, 1902)

Plate 21, figures 15–22; Plate 32, figures 2–4; Figure 39

1902 *Camarophoria pentameroides* Chernyshev (partim.), p. 510, Pl. 22, fig. 1; Pl. 23, figs. 1, 3; not fig. 2.

1970 *Camerisma pentameroides* (Chernyshev); Zavodovskiy and Stepanov, p. 131, Pl. 29, figs. 4, 5.

1971 *Camerisma* cf. *C. pentameroides* (Chernyshev); Waterhouse *in* Bamber and Waterhouse, Pl. 16, fig. 10.

1980 *Camerisma pentameroides* (Chernyshev) (partim.); Kalashnikov, p. 73, Pl. 21, fig. 10; Pl. 37, fig. 5; not Pl. 22, figs. 10, 11.

Lectotype (selected here). A specimen with valves conjoined, Chernyshev (1902, Pl. 1, figs. 1a–c) from the Asselian Stage of the Urals, kept at the CNIGR Museum, St. Petersburg.

Diagnosis. Large shell with moderately convex ventral valve and strongly convex dorsal valve; no median groove in sulcus, or median crest on fold.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53713	1		
GSC loc. 57052	1		1
GSC loc. 57053			3
GSC loc. 57266		1	
GSC loc. 57275	1		
JBW loc. 88			1
JBW loc. 109	1, 1(im)		
JBW loc. 113			4

Description. External. Shell large at maturity, up to 40 mm wide, 50 mm long, and 40 mm high; subtriangular to subpentagonal in outline, strongly biconvex in profile; widest at midlength or in front of it.

Ventral valve strongly convex in umbonal region (Pl. 21, fig. 21), strongly and broadly sulcate anteriorly; umbonal slopes high and straight; umbo prominent, strongly extended and incurved, overhanging dorsal umbo; umbonal angle normally at 78° (range between 75° and 90°); beak not truncated by foramen; posterolateral margins strongly overlapped by opposite margins (Pl. 21, fig. 21); sulcus originating at midlength, shallow and nearly flat-bottomed posteriorly, deepening and widening anteriorly with

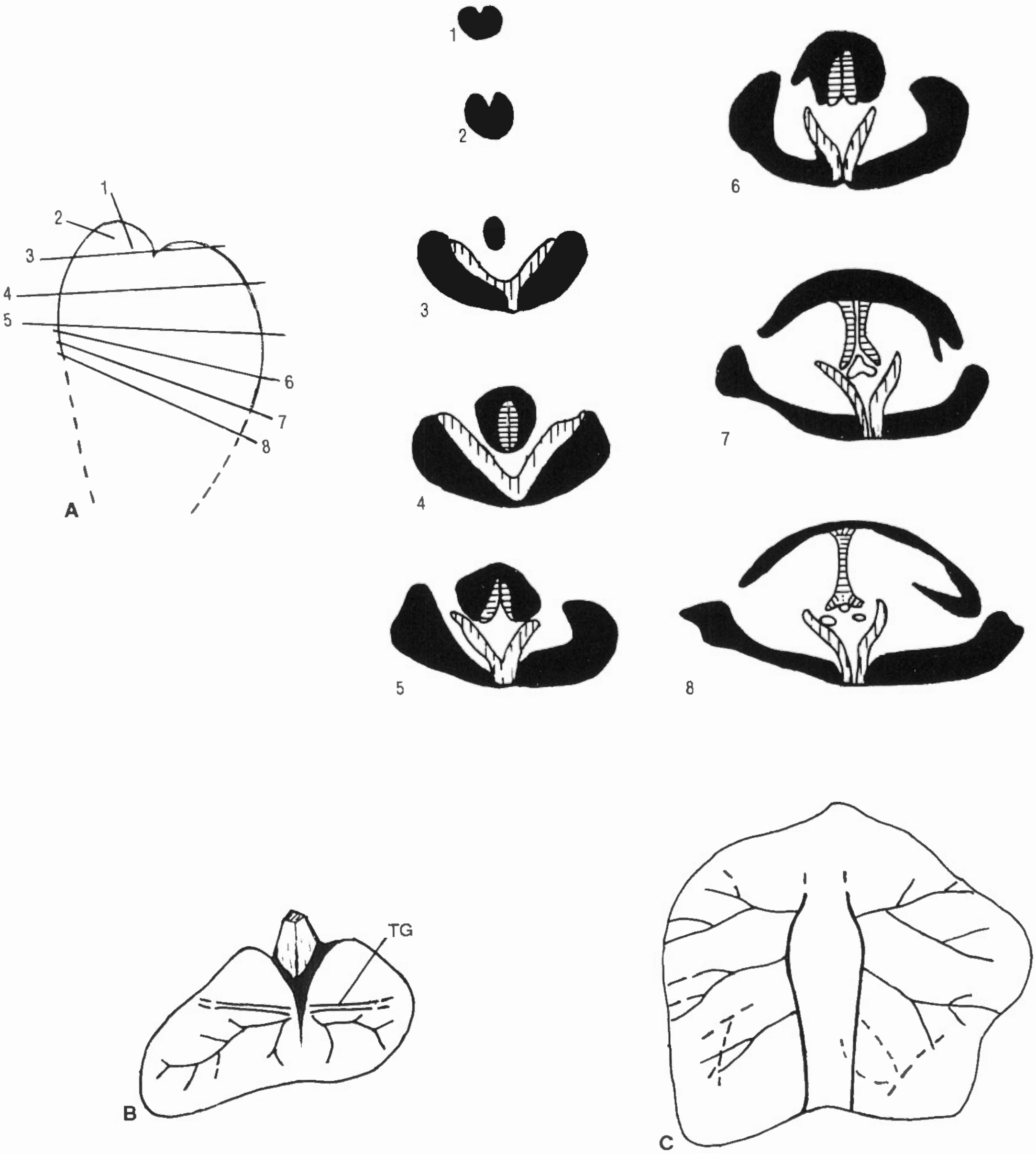


Figure 39. Camerisma (Callaiapsida) pentameroides *(Chernyshev). A, transverse serial sections; B–C, patterns of ventral pallial markings (GSC 97189, GSC 97190, respectively). (All x1). TG, transverse groove.*

well rounded floor, no median groove (Pl. 21, fig. 18); anterior tongue moderately long, broadly V-shaped in section (Pl. 21, fig. 19), strongly indenting dorsal valve; flanks approximately half sulcus in width, broadly rounded in section.

Dorsal valve more pronounced in convexity, especially at front where high fold is formed, strongly arched in section with high and steeply flared flanks, straight along crest; umbo entirely concealed by ventral beak; fold beginning from midlength, high and well demarcated from flanks at front, abruptly meeting sulcal tongue at anterior margin; fold crest well rounded without median ridge or groove.

Shell smooth except for fine concentric growth lines.

Internal. Ventral interior has wide, long, sessile spondylium (Pl. 21, figs. 16, 22; Fig. 39A), deep, posteriorly inserting into shell wall, smooth inside or marked by rather fine horizontal lines, anteriorly isolated from posterior wall and supported by thick median septum (Pl. 32, fig. 3), which tapers anteriorly and extends for approximately posterior two thirds of shell length; transverse groove low but prominent (Fig. 39B), about 1.5 to 2 mm across; pallial markings well developed in front of transverse groove, symmetrically distributed about median septum, frequently branching but not joining (Figs. 39B, C); peripheral grooves not observed.

Dorsal interior has small but distinct camarophorium, intercamarophorial plate, divided hinge plate, and median septum (Pl. 32, fig. 2; Fig. 39A); camarophorium posteriorly buried by umbonal thickening, elevated anteriorly on high and massive median septum (Pl. 32, fig. 2; Fig. 39A); intercamarophorial plate often surrounded by shell thickening in camarophorial cavity; hinge plate nearly horizontal, resting directly on top of intercamarophorial plate; muscle scars within camarophorium obscure.

Comparisons. Camerisma (*Callaiapsida*) *pentameroides*, as revised by Grant (1971) and Lazarev (1975), is now restricted to shells lacking a ventral median groove and a dorsal median crest. This revision excludes from typical *Camerisma* (*Callaiapsida*) *pentameroides* the specimens figured by Chernyshev (1902, Pl. 23, fig. 2) and by Kalashnikov (1980, Pl. 22, figs. 10, 11). Those shells with a prominent median groove and a crest that were previously identified as *C. pentameroides* have been referred to either *Camerisma* (*Callaiapsida*) *arctica* (Holtedahl, 1924) by Grant (1971) or *Camerisma pyramidata* Lazarev, 1975. The former, as redescribed and figured by Grant (1971), is similar to the present material in size and outline, but has a prominent ventral median groove and a sharp dorsal median crest running through the shell length. It is less convex with the dorsal valve being only slightly inflated. *Camerisma pyramidata* Lazarev (1975, p. 216, Pl. 8, figs. 5–9), from the Upper Carboniferous of the Moscow Basin and the Verchoyan Mountains, may be distinguished by its more inflated dorsal valve and less convex ventral valve, and its characteristic ventral median groove and dorsal median crest.

Camerisma (*Callaiapsida*) *kekuensis* Grant (1971, p. 330, Pl. 3, figs. 11–17, 22; Fig. 10) from the probably Upper Artinskian Halleck Formation of the Keku Islets, southeastern Alaska, is distinguished by having a prominent ventral median groove and a dorsal median crest.

Occurrence. Camerisma (*Callaiapsida*) *pentameroides* comes from the Ey, Eog, and Ej zones in northern Yukon Territory. Outside the Yukon Territory, the species has been described from the Asselian to Sakmarian stages in the Urals (Kalashnikov, 1980) and the Late Carboniferous Burgalii and probably Asselian Paren horizons in the Kolyma-Omolon Massif, northeastern Siberia (Zavodovskiy and Stepanov, 1970).

Order RETZIIDA Waterhouse, 1981

Suborder RETZIIDINA Boucot, Johnson and Staton, 1964

Superfamily RETZIACEA Waagen, 1883

Family RETZIIDAE Waagen, 1883

Genus *Hustedia* Hall and Clarke, 1893

Type species. (OD) *Terebratula mormoni* Marcou, 1859.

Hustedia cf. *H. remota* (Eichwald, 1860)

Plate 21, figure 23

cf. 1902 *Hustedia remota* (Eichwald); Chernyshev, p. 512, Pl. 47, figs. 8–11.

Remarks. Two crushed ventral fragments from GSC loc. 53947; one ventral external mould from JBW 89; one ventral valve from JBW loc. 109; one ventral valve and one ventral external mould from JBW loc. 559. These specimens are poorly preserved, small, subequally biconvex with a long subtrigonal ventral valve, and shorter, subcircular dorsal valve; ventral umbo narrow and pointed posteriorly, with angle close to 65°. Dorsal valve possibly less convex than opposite valve. Costae simple and coarse, crests flatly rounded, conspicuously increasing in size toward anterior margin, approximately 10 costae on ventral valve, usually with two median costae, and nine or more on dorsal valve with one median costa, separated by flat-bottomed interspaces obviously wider than costae.

The poorly preserved material resembles *Hustedia remota* (Eichwald) as figured by Chernyshev (1902) from the Sakmarian beds of the Urals, but it has a slightly higher convexity and lower costae.

Order ATHYRIDA Dagys, 1974

Suborder ATHYRIDIDINA Boucot, Johnson, and Staton, 1964

Superfamily ATHRIDACEA M'Coy, 1844

Family ATHYRIDIDAE M'Coy, 1844

Subfamily COMPOSITINAE Grunt, 1980

Genus *Composita* Brown, 1849

Type species. (OD) *Spirifer ambiguus* Sowerby, 1823.

Composita bamberi n. sp.

Plate 21, figures 24–29

Etymology. For Dr. E.W. Bamber, Geological Survey of Canada.

Holotype. GSC 97195 from GSC loc. 53703, section 116H-1A; Ey zone, Jungle Creek Formation (Pl. 21, figs. 26–29).

Diagnosis. Suboval shell with strongly convex dorsal valve and lacking distinct sulcus and fold at maturity; anterior commissure slightly folded dorsally.

Material. Two conjoined specimens including one juvenile from GSC loc. 53703 and four poorly preserved shells from GSC loc. 56972.

Description. External. Shell of medium size at maturity, holotype measuring 25 mm wide, 23 mm long, and 16 mm high (Pl. 21, figs. 26–28); strongly and unequally biconvex in profile, suboval in shape with length approximately equal to width, widest at midlength; anterior commissure gently uniplicate at maturity, no costae (Pl. 21, fig. 26).

Ventral valve most convex at posterior third of shell length; umbo prominent with moderately incurved beak, umbonal angle between 108° and 112°, truncated by small circular epithyrid foramen overhanging dorsal umbo (Pl. 21, fig. 28); umbonal slopes slightly concave in profile and gently convex in section; delthyrium fully covered by dorsal umbo; hinge line rather narrow and arched, about one third of shell width; cardinal extremities well rounded, merging with lateral margins.

Dorsal valve more convex than ventral valve (Pl. 21, fig. 26), most inflated over midlength; umbo massive; no distinct fold at maturity.

Concentric growth lines conspicuous at maturity (Pl. 21, fig. 24), more closely spaced towards anterior margin, but not developed into overlapping laminae.

Internal. Dental plates short and diverging forward by about 90°. Hinge plate strong and square in shape; cardinal process highly raised above hinge plate (Pl. 21, fig. 24).

Comparisons. The new species resembles *Composita tareica* Chernyak (*in* Ustritsky and Chernyak, 1963, p. 120, Pl. 45, figs. 10, 11), from the Late Carboniferous Makarov Horizon of western Taimyr, in overall appearance and the unequal biconvexity, but is distinguished by lacking a well defined anterior sulcus. In addition, the Taimyr species is more strongly expanded at midlength.

Several species from the Permian of western Texas, United States, are also similar to the new species. *Composita apheles* Cooper and Grant (1976a, p. 2143, Pl. 652, figs. 45–88) from the Skinner Ranch Formation is similar in size and outline, but it differs in having a well defined square-shaped sulcus at maturity and a less convex dorsal valve. The new species resembles some young adults of *C. strongyle* Cooper and Grant (1976a, p. 2167, Pl. 649, figs. 38–43; Pl. 654, figs. 69–88) from the Gaptank, Neal Ranch, Lenox Hills, and Hess formations in overall characteristics, but mature specimens of *C. strongyle* are distinguished by their larger size, a wider and more rounded outline, and prominent overlapping concentric laminae anteriorly.

Occurrence. Ey zone, Tastubian.

Composita sp.

Plate 21, figures 30, 31

Remarks. One small specimen (10.5 mm wide and long) from GSC loc. 53703 is similar to the new species, particularly in shape and convexity, but the specimen is readily distinguished by its shallow but distinctive, square-shaped sulcus bearing three weak costae near the anterior margin. No species from the Arctic region is particularly similar.

Occurrence. Ey zone, Tastubian.

Order SPIRIFERIDA Waagen, 1883

Suborder SPIRIFERIDINA Waagen, 1883

Superfamily CYRTIACEA Frederiks, 1924

Family AMBOCOELIIDAE George, 1931

Genus *Ogilviecoelia* n. gen.

Etymology. Ogilvie, Ogilvie Mountains, Yukon Territory; Latin *coelio*, belly.

Type species. *Ogilviecoelia inflata* n. gen. et sp.

Diagnosis. Small suboval ambocoeliid with massive, short, moderately incurved ventral umbo; ventral valve strongly convex, dorsal valve gently swollen in umbonal region, then flattened to gently concave anteriorly; ventral umbonal slopes usually less than one third of shell length; maximum width at midlength; sulcus narrow and deep. Micro-ornament of sparse, fine, and elongate grooves, no spines or tubercles. Ventral interior has strong median septum; muscle field large, well depressed as a whole at apex of umbonal cavity, narrow-elongate in shape, clearly differentiated with narrow adductor scars on broad, slightly elevated median ridge, smooth or faintly striated, anteriorly passing to massive median septum; diductor scars depressed to each side, broader, weakly to moderately striated. Crural plates distinct; brachidia unknown; dorsal adductors well impressed, poorly differentiated, narrow and elongate.

Discussion. The new genus is very close both to *Attenuatella* Stehli, 1954 (Cooper and Grant, 1976a), with type species *A. texana* Stehli, and to *Biconvexiella* Waterhouse, 1983b, 1987a, with type species *Attenuatella convexa* Armstrong, 1968. It differs from both, primarily, in possessing fine elongate grooves, rather than spinose ornament, and a large, depressed, and well differentiated ventral muscle field (Fig. 40). *Biconvexiella* and *Ogilviecoelia* both have a broad and massive ventral umbo coupled with short umbonal slopes, in contrast to the narrow, long, and strongly attenuated umbo in *Attenuatella* (Fig. 40). However, the umbo is not incurved more than about 80° in *Biconvexiella convexa* and does not conceal the apical part of the delthyrium; whereas it curves for about 90° in *Ogilviecoelia inflata* n. gen. et sp., and up to 180° in *Attenuatella texana*, concealing the apical part of the delthyrium (Fig. 40).

Convexity of the dorsal valve also differs among the three genera: the dorsal valve is gently but entirely convex in *Biconvexiella*, nearly flat in *Attenuatella*, and slightly swollen in the umbonal region, then flattened or very gently concave anteriorly in *Ogilviecoelia*.

Internal differences between the new genus and the other two mainly lie in the ventral musculature. The ventral adductor platform is said to be "very weak, barely discernible" in *Attenuatella texana* (Cooper and Grant, 1976a, p. 2133); whereas its diductor scars are distinct, on a highly raised median ridge, bisected by a prominent median groove (Fig. 40A). *Biconvexiella convexa* is similar to the Yukon species in having a well defined, narrow, long median adductor ridge and depressed lateral diductor scars, but the diductors are much narrower, longer, less regularly defined, and less depressed in the Australian species (Fig. 40C). The dorsal interior of the three genera appears to be very similar, although the adductors are clearly differentiated in *Biconvexiella convexa* (Fig. 40C), but undifferentiated or poorly so in *Attenuatella texana* and *Ogilviecoelia inflata*.

Some species previously assigned to *Attenuatella* appear to belong here, but the assignment can only be provisional as no mention was made, by authors, of the surface micro-ornament of any of these species; also, detailed aspects of the ventral musculature, though generally similar to the pattern in *Ogilviecoelia inflata* n. gen. et sp., were poorly preserved in these specimens or were not adequately figured in the literature, making it difficult to accurately compare them. These species include *Attenuatella taimyrica* Chernyak (*in* Ustritskiy and Chernyak, 1963), *Attenuatella omolonensis* Zavodovskiy, 1968, and *Attenuatella* aff. *A. frechi* (Schellwien, 1892) of Winkler Prins (*in* Wagner and Winkler Prins, 1970).

Ogilviecoelia inflata n. gen. et sp.

Plate 21, figures 32–44; Plate 32, figures 8–13

1971 *Attenuatella* aff. *A. omolonensis* Zavodovskiy; Waterhouse *in* Bamber and Waterhouse, Pl. 15, figs. 8, 9.

Etymology. Latin *inflatus*, swollen.

Holotype. GSC 97201 from GSC loc. 53715, section 116H-1A; Eog zone, Jungle Creek Formation (Pl. 21, figs. 35, 37, 40; Pl. 32, fig. 9).

Diagnosis. Shell very small, subrounded with width usually equal to length; ventral valve strongly inflated, umbo moderately incurved; dorsal valve gently swollen in umbonal region and anteriorly flattened or very gently concave; sulcus narrow and deep.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53715	11	3	35
GSC loc. 53716	17	1	23
GSC loc. 53952			6
GSC loc. 53999	23, 11(im)		13
GSC loc. 57266	1		
JBW loc. 57	2(im), 3(em)		1(em)

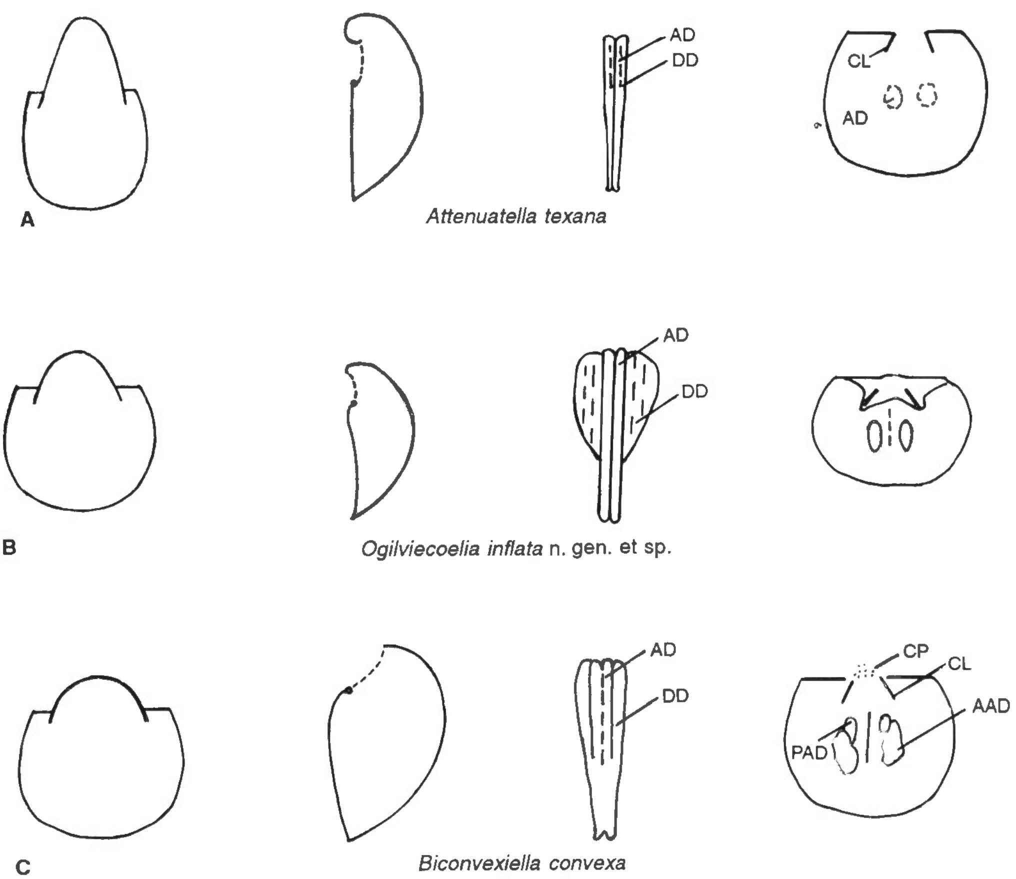


Figure 40. Comparison of external and internal characteristics between ***Attenuatella texana*** *Stehli,* ***Ogilviecoelia inflata*** *n. gen. et sp., and* ***Biconvexiella convexa*** *(Armstrong) (all approx. x3). CL, crural plate; CP, cardinal process; other abbreviations as in Figure 27.*

Description. External. Shell small, subrounded to slightly elongate in outline with length usually equal to width (Pl. 21, fig. 37); widest at midlength; anterior commissure emarginate (Pl. 21, fig. 40).

Ventral valve strongly inflated (Pl. 21, fig. 42), most convex at midlength or slightly behind it; umbo broad, short, and massive (Pl. 32, figs. 8, 9), moderately to strongly incurved with incurvature angle between 90° and 95°, slightly concealing apical part of delthyrium in some specimens (Pl. 21, fig. 37); umbonal angle between 45° and 60°; umbonal slopes usually less than one third of shell length (Pl. 21, figs. 32, 40, 41), high and steep, straight or very gently concave in outline, well rounded in section; hinge line approximately two thirds of shell width; cardinal extremities well rounded and broadly merging with lateral margins, anterior margin well rounded; interarea well defined, triangular in shape, apsacline to nearly orthocline, gently to moderately concave (Pl. 32, fig. 8), about one third as high as shell length or slightly less (Pl. 21, fig. 37), smooth; delthyrium narrow with delthyrial angle close to 25°, open except at apex a small delthyrial plate or umbonal callosity is observed in some specimens (Pl. 21, fig. 43); deltidial plates seemingly present (Pl. 32, figs. 8, 10); sulcus prominent, narrow and deep, extending from umbo to anterior margin without widening or deepening (Pl. 21, fig. 40). Some decorticated specimens show fine radial fibers (Pl. 21, fig. 34).

Dorsal valve approximately two thirds as long as ventral valve (Pl. 21, fig. 37), subrounded to subelliptical in outline, very gently swollen in umbonal region over posterior third to half of valve length (Pl. 21, fig. 37; Pl. 32, figs. 8, 10), flattened to very gently concave anteriorly; no fold.

Shell micro-ornament consists of sparse, short, elongate grooves only, irregularly arranged, seven to 10 per mm, usually with expanded posterior ends (Pl. 32, figs. 11-13); no spines.

Internal. Teeth robust, triangular, projecting out from anterolateral edges of delthyrium, slightly converging inward, not supported by plates (Pl. 21, fig. 39); muscle field large, prominently depressed under umbo (Pl. 21, figs. 33, 34), elongate-oval in shape, extending for about posterior third of shell length, well differentiated; adductor on broad, slightly raised median ridge, smooth or weakly striated in some specimens, myophragm indistinct; broader diductor scars depressed to each side, more prominently striated; median adductor ridge anteriorly passing to massive median septum that corresponds to external sulcus and extends almost as far as anterior margin (Pl. 21, figs. 43, 44).

Cardinal process not observed; crural plates sessile (Pl. 21, fig. 38), diverging forward by about 55°; crura and brachidia not observed; adductor scars weakly impressed just in front of crural plates and half way to anterior margin (Pl. 32, fig. 9), narrow-elongate in shape.

Dimensions (in mm).

Specimens	Valve	Length	Width	Height	Dorsal length
GSC 97198	VEN	12	6	—	
GSC 97200	CON	8	9	4	5.5
GSC 97201	CON	10	9.5	5.5	6.5
GSC 97202	VIM	6	6	+2	—
GSC 97203	VIM	9	9.5	3.5	—
GSC 97204	VEN	9	9	?4.5	—
GSC 97205	VIM	8	10	4	—

Comparisons. Two species from the Arctic region are comparable both in external and internal features. *Attenuatella omolonensis* Zavodovskiy (1968, p. 169, Pl. 48, figs. 2, 3; Zavodovskiy and Stepanov, 1970, p. 169, Pl. 33, figs. 1–4; Abramov and Grigor'yeva, 1983, p. 118, Pl. 17, figs. 10–13, Textfigs. 42, 43), from the probably Asselian Paren Horizon of the Kolyma-Omolon Massif, northeastern Siberia, and the Upper Carboniferous lower Kigiltas Suite of the Verchoyan Mountains, is similar to the Yukon material in shape, size, and internal aspects, especially in the large, well depressed ventral muscle field at the apex of the umbonal cavity (see Zavodovskiy and Stepanov, 1970, Pl. 33, fig. 3). The ventral valve differs by being less inflated and having a poorly defined sulcus (see Abramov and Grigor'yeva, 1983, Pl. 17, fig. 10) and a shorter ventral median septum, which does not appear to extend into the anterior third of the shell length (see Abramov and Grigor'yeva, 1983, Textfig. 42). *Attenuatella taimyrica* Chernyak (*in* Ustritskiy and Chernyak, 1963, p. 115, Pl. 42, figs. 5–9) from the Artinskian Birrang Horizon of eastern Taimyr, northern Russia, also has a subrounded outline and a broad massive ventral umbo, like the Yukon species. The figured ventral interior of the Taimyr species (ibid., Pl. 42, fig. 7b) looks very similar to one of the ventral interiors found in the Yukon species (Pl. 21, fig. 39). However, the Taimyr species may be distinguished by its large size (20 mm wide and 18 mm long) and less prominent ventral sulcus. No mention was made of the micro-ornament of *A. taimyrica*, nor of *A. omolonensis*.

Attenuatella aff. *A. frechei* (Schellwien) of Winkler Prins (*in* Wagner and Winkler Prins, 1970, p. 538, Pl. 36, figs. 1–5), from the Upper Carboniferous (Kasimovian) Branosera Formation of northwestern Spain, appears to be similar to the present species in its short, massive ventral umbo and a large depressed ventral muscle field, but it differs in having a very faint ventral sulcus and possessing a well defined ventral myophragm. *Attenuatella*? aff. *A. elgae* Beznosova (Beznosova et al., 1968, p. 186, Pl. 29, figs. 1–3), from the Upper Carboniferous (Gshelian) to Lower Permian (Asselian) Kokpekten Complex of eastern Kazakhstan, is perhaps more similar to *Biconvexiella* than to *Ogilviecoelia*, as it possesses a very short, massive, only slightly incurved ventral umbo as in *Biconvexiella convexa* Armstrong. The Kazakhstan species also lacks a ventral sulcus, and its dorsal valve is nearly flat. Micro-ornament was not mentioned for the Kazakhstan species.

Attenuatella spp. from the lower Jungle Creek Formation (*Kochiproductus-Attenuatella* Zone and *Tomiopsis-Attenuatella* Zone) in northern Yukon Territory, as figured by Waterhouse (*in* Bamber and Waterhouse, 1971, Pl. 12, figs. 8, 9), are very close to the new species in overall external appearance and may well prove to be congeneric. However, no ventral interiors were available for examination and no micro-ornament was observed, hindering further detailed comparisons.

Occurrence. Ogilviecoelia inflata n. gen. et sp. is confined to the Eog zone in northern Yukon Territory.

Superfamily SPIRIFERACEA King, 1846

?Family SYRINGOTHYRIDIDAE Frederiks, 1924

Genus *Yukonospirifer* n. gen.

Etymology. Yukon, Yukon Territory; Latin *spira*, coil; *fero*, to bear.

Type species. Yukonospirifer yukonensis n. gen. et sp.

Diagnosis. Pyramid-shaped shells with very high, triangular, almost catacline interarea, fine equidimensional and weakly fasciculate costae on entire shell, shallow sulcus, and low, well rounded fold. Ventral interior with distinct delthyrial plate and high, long adminicula, no syrinx or median septum, umbonal callosity weak. Dorsal interior unknown. Shell impunctate; micro-ornament not known except for fine concentric growth lines.

Discussion. The distinctive Yukon species described below is represented by three specimens, and is very characteristic in both external and internal features. It has the pyramidal shape, high interarea, and distinct delthyrial plate and adminicula of *Syringothyris* Winchell, 1863 and allies, but is impunctate, lacks the syrinx, and possesses numerous fine, bifurcating (or weakly fasciculate) costae over the entire shell, unlike any other members of the Syringothyrididae. The finely costate Yukon species with indistinct fasciculation resembles members of the Spiriferidae King, especially the Spiriferinae as diagnosed and discussed by Archbold and Thomas (1984b), but is distinguished from the latter by its extremely high and triangular interarea and distinct (long and high) adminicula. The new genus is provisionally assigned to the Syringothyrididae. It is possible that it may prove to be more related to the Spiriferidae, but this seems unlikely in view of overall shell morphology.

The new genus appears to be of essentially northern (Boreal) distribution. It is possibly present in the Lower Permian of Novaya Zemlya, northern Russia. Dr. N. W. Archbold (pers. comm., 1990) has kindly drawn our attention to *Spirifer petrenki* Einor (*in* Likharev and Einor, 1939, p. 81, Pl. 15, fig. 6) from the Lower Permian of Cape Krasnyi, Novaya Zemlya. This species is very similar to *Yukonospirifer yukonensis* n. gen. et sp. in external and internal characteristics, except for a short but prominent ventral median ridge (?myophragm or syrinx) in the Russian species. No such structure was revealed in the sectioned specimen of the Yukon species. It is not known whether this short median ridge is variable or consistent with ontogenic development.

Yukonospirifer yukonensis n. gen. et sp.

Plate 23, figures 8, 9, 11-16; Figure 41

Etymology. For the Yukon Territory, Canada.

Holotype. GSC 97225 from GSC loc. 53713, section 116H-1A; Ey zone, Jungle Creek Formation (Pl. 23, figs. 8, 9, 11-13).

Diagnosis. As for genus.

Material. One specimen with valves conjoined from GSC loc. 53713; one ventral valve and fragment of its external mould from JBW loc. 113.

Description. External. Shell moderately large, subelliptical in ventral view (Pl. 23, fig. 15), pyramid-shaped in lateral profile (Pl. 23, fig. 8), widest along hinge line; anterior commissure prominently uniplicate (Pl. 23, fig. 9).

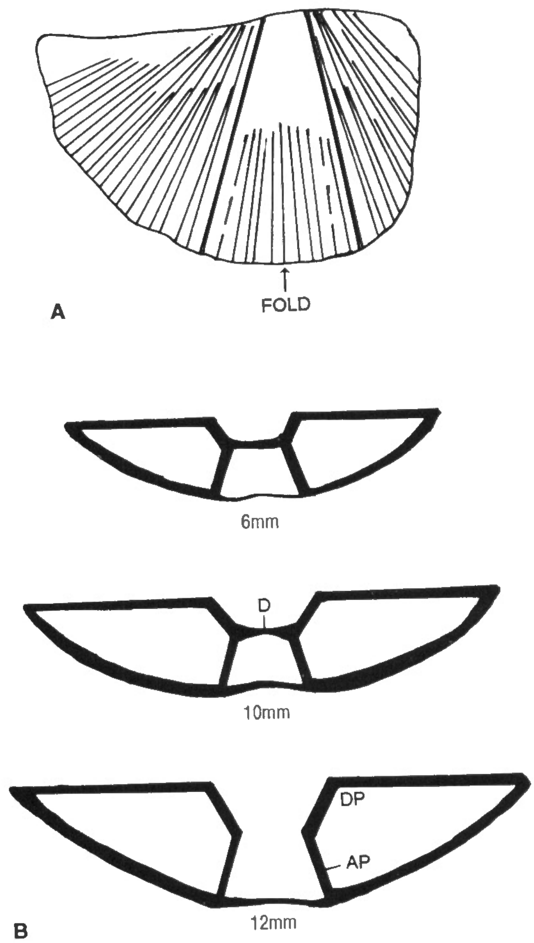


Figure 41. Yukonospirifer yukonensis *n. gen. et sp. A, costation pattern on dorsal valve (GSC 97225, x1); B, transverse serial sections of ventral valve (GSC 97226, x1). AP, adminicula, D, delthyrial plate; DP, dental plate. Measurements refer to distance from ventral umbo.*

Ventral valve moderately convex; umbo indistinct, beak small and erect; umbonal slopes straight or gently convex in outline, very broadly diverging to lateral margins, with umbonal angle about 140°; interarea nearly catacline (Pl. 23, fig. 8), flat or very gently concave, triangular, 60 mm wide and 20 mm high in holotype, marked by distinct vertical striae and less conspicuous horizontal striae (Pl. 23, fig. 16); hinge margin weakly denticulate; delthyrium moderately large, delthyrial angle 43°, no deltidial or peridelthyrial plates observed; cardinal extremities rounded at between 70° and 75°; lateral and anterior margins broadly and well rounded; sulcus prominent, shallow to moderately deep, not well demarcated from flanks (Pl. 23, figs. 11, 15), commencing from beak at sulcal angle between 25° and 30°; flanks flatly convex; anterior tongue short, broadly U-shaped in outline (Pl. 23, fig. 9), protruding beyond anterior commissure by 4 mm. Ventral costae fine (Pl. 23, fig. 15), equidimensional, crests well rounded, not grouped into clear bundles, separated by narrow shallow interspaces, each individual costa anteriorly bifurcating once or twice at varying distances from umbo, no distinct fasciculation, about 10 to 12 costae in 10 mm at midlength.

Dorsal valve moderately and evenly convex; interarea about one fifth as high as ventral interarea (Pl. 23, fig. 8); fold well formed, slightly more prominent than sulcus, well differentiated from flanks by deep lateral grooves, low and very well rounded on crest (Pl. 23, figs. 9, 12). Costae distinct on flanks, fine as on ventral valve, equidimensional, separated by narrow grooves; two to three costae grouped into plicae, which are separated by interspaces slightly wider than intercostal grooves (Pl. 23, figs. 9, 12; Fig. 41A); costae on fold poorly preserved, apparently as fine as lateral costae and seemingly not grouped into plicae (Pl. 23, fig. 12).

Micro-ornament not known except for rather fine concentric growth lines (Pl. 23, fig. 14), approximately five to seven lines in 1 mm. No punctae seen in thin sections of GSC 97226.

Internal. GSC 57266 (Pl. 23, figs. 13, 15, 16) was posteriorly sectioned and revealed deep and distinct delthyrial plate, almost unthickened dental plates, and adminicula (Fig. 41B), no median septum, ridge, or syrinx.

Dimensions (in mm).

Specimen	Valve	Length	Width	Height
GSC 97225	CON	47	70	35
GSC 97226	VEN	43	72	23

Comparisons. Spirifer petrenki Einor (*in* Likharev and Einor, 1939) is distinguished from the Yukon species by its more transverse outline, slightly higher costae, and the presence of a short median ridge in the ventral interior.

Occurrence. Yukonospirifer yukonensis n. gen. et sp. is confined to the Ey zone in northern Yukon Territory, of Early Sakmarian (Tastubian) age.

Family LICHAREWIIDAE Slusareva, 1958

Subfamily LICHAREWIINAE Slusareva, 1958

Genus *Tumarinia* Grigor'yeva and Solomina, 1973

Type species. (OD) *Tumarinia orientalis* Grigor'yeva, 1973.

Diagnosis. Transverse Licharewiinae with well developed delthyrial plate and long adminicula extending usually beyond midlength; micro-ornament of fine close-set papillae and grooves, arranged in quincunxial order. Ventral muscle field well impressed, posteriorly outlined by anterior portions of adminicula in some species; adductor ridge narrow, smooth or slightly striated, posteriorly bearing short and fine median ridge in some species; diductor imprints large, weakly striated.

Discussion. The above diagnosis is based on Grigor'yeva and Solomina (1973), elaborated from Yukon material. Micro-ornament is poorly known for the type species and has not been described in detail from other species of the genus.

Slusareva (1960), Grigor'yeva and Kotlyar (1966), and Grigor'yeva (1977) discussed licharewiinid genera and noted that their mutual distinction depended largely on ventral internal structures and shell micro-ornament. Comparison of ventral internal structures among several licharewiinid genera is shown in Figure 42. Genera closely allied to *Tumarinia* are *Licharewia* Einor, 1939, *Orulgania* Solomina and Chernyak, 1961, and *Yukonella* n. gen. described below. *Licharewia* is distinguished by its poorly defined initial dental plates and short adminicula, which never extend beyond shell midlength (Grigor'yeva and Kotlyar, 1966), and by its lack of a delthyrial plate. *Orulgania* is characterized by possessing a prominent median calcite rod within the umbonal cavity (Grigor'yeva and Kotlyar, 1966). Both *Olgerdia* Grigor'yeva, 1977 and *Pezhinella* Solomina, 1985 have a very high and triangular interarea and

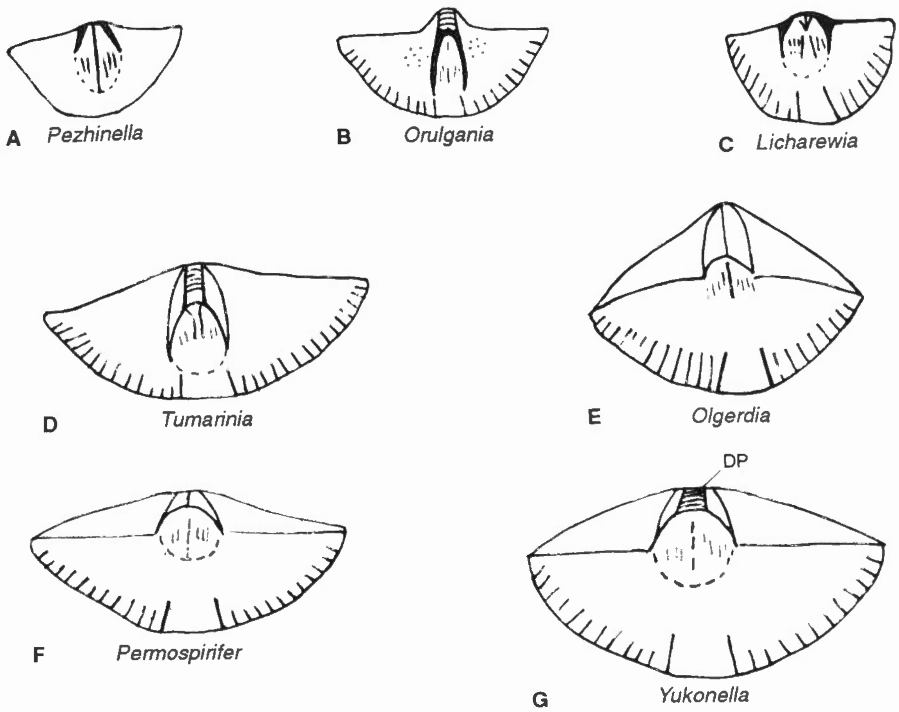


Figure 42. *Comparison of ventral interior between several allied licharewiinid genera (A–E after Solomina, 1985, Fig. 2; all approx. x1). For explanations see text. DP, delthyrial plate.*

much shorter adminicula, and lack a delthyrial plate (Fig. 42). *Permospirifer* Kulikov, 1950 is distinguished by its reduced adminicula, small and slightly extended umbo, lack of delthyrial plate, and sparse papillae without grooves. Comparison between *Tumarinia* and *Yukonella* will be discussed below under the latter genus.

Tumarinia yukonica n. sp.

Plate 22, figures 1–20; Plate 32, figures 5, 6; Figure 43

1971 Licharewinid or Syringothyridinid, Waterhouse *in* Bamber and Waterhouse, Pl. 15, fig. 15.

Etymology. For the Yukon Territory, Canada.

Holotype. GSC 97206 from GSC loc. 53714, section 116H-1A; Ey zone, Jungle Creek Formation (Pl. 22, figs. 9–11).

Diagnosis. Moderately large transverse shell with moderately deep sulcus and prominent, well rounded costae.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53712		1	
GSC loc. 53713		1	
GSC loc. 53714		2	6
GSC loc. 53951	1		
GSC loc. 53954	1, 1(em)		
GSC loc. 57053	1		
JBW loc. 88		1	
JBW loc. 113	1		

Description. External. Shell small to medium size for genus, transverse, width/length ratio generally at 1.7 to 2; widest along hinge.

Ventral valve moderately convex (Pl. 22, fig. 11), most inflated at midlength or slightly behind it; umbo prominent, well extended beyond posterior margin, slightly incurved above interarea; umbonal angle close to 110°; umbonal slopes apparently concave in outline (Pl. 22, fig. 8), broadly rounded in section, separated from interarea by sharp posterior margins; cardinal extremities pointed at between 35° and 40°; interarea wide and low (Pl. 22, fig. 1), apsacline, slightly concave under beak, horizontally striated; delthyrium triangular, apical angle close to 40°, posterior third

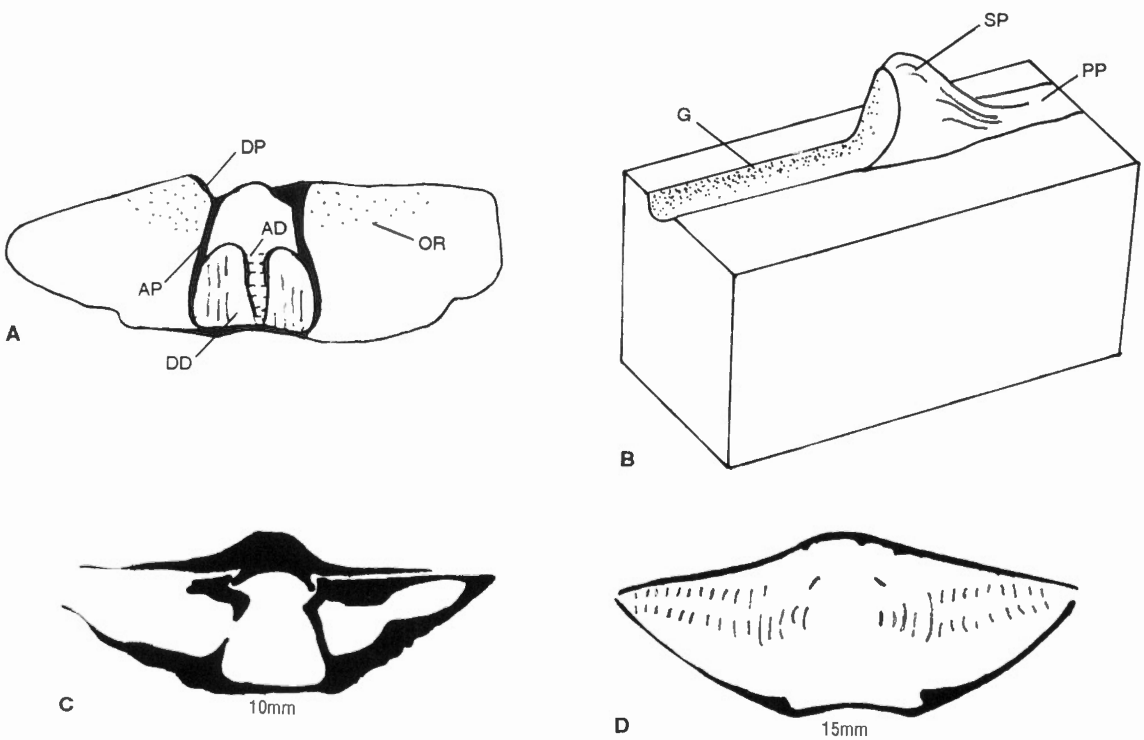


***Figure 43. Tumarinia yukonica** n. sp. A, ventral internal mould showing ventral plates and muscle impressions (GSC 97212, x1); B, micro-ornament (papillae and grooves) (approx. x20); C, D, transverse serial sections of a conjoined specimen (GSC 97669, x1.2). AP, adminicula plate; DP, dental plate; G, groove; OR, ornament; PP, papilla; SP, spine. The measurements refer to distance from the ventral beak.*

covered by well developed delthyrial plate (Pl. 22, figs. 13, 18); sulcus commencing from umbo with sulcal angle between 25° and 35° measured from umbo, gently widening and deepening over posterior half of shell length and then more rapidly on anterior portion (Pl. 22, fig. 15), approximately 11 mm wide and 5 mm deep measured at frontal margin of holotype, floor well rounded and smooth; anterior tongue short, well rounded in anterior outline (Pl. 22, fig. 7), usually protruding beyond anterior margin by 2 to 4 mm; flanks flatly convex, well spreading laterally, each bearing 13 to 15 prominent, simple, and well rounded costae, all commencing from umbonal tip or very close to it, diminishing in size towards cardinal extremities, separated by shallow and apparently narrow interspaces.

Dorsal valve equally or slightly less convex than ventral valve; interarea 2 to 3 mm high, marked by few horizontal lines; notothyrium wide, open; fold well defined above flanks (Pl. 22, fig. 6), gently increasing in height anteriorly, broadly and well rounded on crest, smooth; costation similar to that on ventral valve.

Micro-ornament consists of fine concentric lirae and radial papillae (Pl. 22, fig. 19); five to six concentric lirae in 1 mm; papillae poorly preserved on shell surface but well impressed on one external mould (Pl. 22, figs. 5, 19), thin and long, close-set, extending anteriorly and projecting small spines at anterior ends, then replaced anteriorly by equidimensional grooves (Fig. 43B), each groove located between a pair of papillae (Pl. 22, fig. 19), approximately seven to 10 papillae or grooves in 1 mm.

Internal. One ventral valve (Pl. 22, figs. 17, 18) was dissolved and serial sections were made from another specimen (Pl. 32, figs. 5, 6; Fig. 43C, D) to reveal internal structures. Teeth sturdy, triangular, not conspicuously projecting beyond hinge line, slightly converging inward, supported by elongate dental plates along edges of delthyrium, which are in turn elevated on thick adminicula; dental plates apically converging and connected at apex by slightly concave delthyrial plate; posterior portions of dental plates and adminicula buried by shell thickening; adminicula moderately diverging forward and away from dental plates, at least twice as high as dental plates (Pl. 22, fig. 18), extending well beyond midlength, apparently diminishing in size forward, anterior ends slightly curving inward to outline muscle field (Fig. 43A); muscle field large, elongate-oval in shape, well impressed; adductor ridge at median, narrow and elongate, slightly striated, delimited on posterior portion by two low ridges (Pl. 22, fig. 20; Fig. 43A); myophragm indistinct; diductor scars to each side, large, weakly striated; ovarian impressions distinct over posterolateral floor.

Dental sockets narrow and elongate (Pl. 22, fig. 14), posterior part roofed by interarea, bordered at inner sides by high inner socket ridges; cardinal process low and rounded, deeply grooved posteriorly; crural plates indistinct; muscle field obscure; spiralia consisting of at least 14 turns each side (Fig. 43D).

Dimensions (in mm).

Specimen	Valve	Length	Width	Height	Length of adminicula
GSC 97206	CON	28	46	18.5	—
GSC 97207	CON	22	39	13	—
GSC 97208	CON	24	40	17	—
GSC 97211	DOR	19	+40	6	—
GSC 97214	VEN	34	65	—	18

Comparisons. In addition to the type species from the Ufimian Omolon Horizon of the Kolyma-Omolon Massif, northeastern Siberia, Grigor'yeva and Solomina (1973) included in *Tumarinia* the following species: *Spirifer kolymaensis* Tolmachev, 1912 from the Omolon Horizon of the Kolyma-Omolon Massif, *Licharewia tumida* Zavodovskiy (*in* Zavodovskiy and Stepanov, 1970) from the same horizon, *L. ochotnikovi* Zavodovskiy, 1958 from the Kazanian Gijig Horizon of the Kolyma-Omolon Massif, *L. neosibirica* Einor, 1959 from the Omolon Horizon and its equivalents in the Verchoyan Mountains, *L. latiareata* (Nechaev, 1900) from the Kazanian Stage of the Russian Platform, and *Tumarinia barajaensis* Solomina (Grigor'yeva and Solomina, 1973) from the Upper Artinskian to Kungurian upper Echii and Tumarian Suites of the Verchoyan Mountains. These species can be arranged into two groups according to shell outline and shape of the interarea. One group, with a transverse outline and a wide and low interarea, includes the type species *Tumarinia orientalis* and *T. barajaensis*. This group resembles the new species in overall appearance, but differs in details. *Turmarinia orientalis* (Grigor'eva and Solomina, 1973, p. 474, Pl. 6, figs. 1-4) is less transverse and has a higher interarea and a deeper sulcus. *Tumarinia barajaensis* (Grigor'yeva and Solomina, 1973, p. 476, Pl. 6, figs. 5-8) is larger than the Yukon material and possesses a deeper sulcus and a higher fold.

The second group, incorporating the other species mentioned above, is distinguished from the new species by having a longer shell, a less transverse outline, and a higher, more triangular interarea.

Occurrence. Ey and Ej zones, Sakmarian to Early Artinskian (Aktastinian).

Genus *Yukonella* n. gen.

Etymology. For the Yukon Territory, Canada.

Type species. Yukonella plana n. gen. et sp.

Diagnosis. Licharewiinid shells with gently to moderately convex ventral valve and small, poorly defined ventral umbo; interarea low and wide, nearly orthocline. Micro-ornament of fine, sparse, elongate tubercles without grooves. Delthyrial plate large, covering posterior half or more of delthyrium. Adminicula reduced, not extending beyond interarea, buried by strong umbonal thickening; ovarian impressions poorly developed or absent. Crural plates indistinct.

Discussion. The low convexity, small and poorly defined beak, small tubercular micro-ornament without grooves, the strongly thickened umbonal cavity, and the reduced adminicula of the new genus are characteristics shared by *Permospirifer* Kulikov (1950, p. 5), type species *Spirifer keyserlingi* Nechaev, 1911 from the Kazanian Stage of the Russian Platform. On the other hand, there exist two major distinctions between the Russian genus and the present material. In their revision of licharewiinid genera, Grigor'yeva and Kotlyar (1966) stressed that the apex of the delthyrium in *Permospirifer* was not covered by a true delthyrial plate but by a "pseudodelthyrial plate," which results from the convergence and ultimate conjunction of thickened lateral parts of dental ridges, which we suggest equal to the pleromal plates of Campbell (1960) in "*Ingelarella*" and *Tomiopsis*. Grigor'yeva and Kotlyar believed that this structure was only present at the "very tip of the umbo." The pseudodelthyrial plate is apparently different from the large, well formed, slightly concave, and horizontally weakly striated transverse plate in the Yukon material (Pl. 22, fig. 24; Pl. 23, figs. 1, 4, 6; Fig. 44A), a structure that is commonly called a delthyrial plate in spiriferids, allegedly a homologue of the pedicle collar of living terebratulaceans, according to Williams and Rowell (1965, p. 87). This transverse plate deepens slightly anteriorly and has a concave frontal margin. It is flanked on each side by a dental ridge (rather than a plate), which is rather low and is normally strongly thickened (Fig. 44A). On the external surface of the interarea, the dental ridges are marked by very narrow and shallow, sometimes obscure, elongate grooves separating the delthyrial plate from the interarea (Pl. 23, figs. 1, 6; Fig. 44A). These grooves occasionally can be rather deep (Pl. 23, fig. 6).

The second distinction lies in the ovarian impressions. These are well developed on the posterolateral portions of the ventral floor and around the ventral muscle field in *Permospirifer keyserlingi* (Nechaev) (Slusareva, 1960, Pl. 9, fig. 2) and *P. kulikovi* Slusareva (1960, Pl. 8, fig. 6). By contrast, ventral interiors of the Yukon species show no sign of such impressions (Pl. 22, fig. 24; Pl. 23, fig. 3).

Olgerdia Grigor'yeva, 1977 is distinguished by its transverse-elliptical outline, high interarea, greater inflation, more strongly developed umbonal thickening, and the lack of a delthyrial plate. *Licharewia* Einor, 1939 differs in having longer, better defined adminicula, a normally well defined ventral umbo, and the lack of a delthyrial plate (Fig. 42). *Penzhinella* Solomina, 1985 is subelliptical in outline with a very high, triangular interarea; and its delthyrial plate is rather weak or absent. *Tumarinia*, discussed above, has a well developed delthyrial plate, as in the present genus, but is distinguished by its long, well defined adminicula, a more prominent and isolated ventral umbo, greater inflation, and a micro-ornament with both regular papillae and grooves.

Yukonella plana n. gen. et sp.

Plate 22, figures 21–25; Plate 23, figures 1–7; Figures 44, 45

Etymology. Latin *planus*, flat.

Holotype. GSC 97217 from GSC loc. 53774, section 116G-5, Nahoni Range East, northern Ogilvie Mountains; Ej zone, Jungle Creek Formation (Pl. 23, fig. 2).

Diagnosis. Ventral valve gently to moderately convex with a small, poorly defined ventral umbo; dorsal valve more convex; interarea low and wide, nearly orthocline. Delthyrial plate large, covering posterior half or more of delthyrium. Adminicula reduced, not extending beyond interarea, buried by strong umbonal thickening; ovarian impressions poorly developed or absent. Crural plates indistinct.

Material. Fifteen ventral valves, four ventral internal moulds, five ventral external moulds, four dorsal valves, one dorsal external mould, and five dorsal external moulds from GSC loc. 53774.

Description. External. Shell moderately large, transverse, width/length ratio usually at 1.5 to 1.8; gently to moderately biconvex (Fig. 44B); widest at hinge line.

Ventral valve most inflated near midlength; umbo small, indistinct, flattened; beak erect (Pl. 23, fig. 2), little extended; umbonal angle close to 150°; umbonal slopes not well defined, flattened or gently concave, wide; interarea low and wide (Pl. 22, fig. 24), nearly orthocline, very finely striated in transverse direction; delthyrium comparatively narrow, delthyrial angle close to 35°, posterior half to two thirds sealed off by slightly concave delthyrial plate (Pl. 22, fig. 24; Pl. 23, fig. 1); delthyrial plate gently deepening forward, marked by weak, anteriorly concave striae, laterally separated from interarea by narrow longitudinal grooves (Fig. 44A); cardinal extremities pointed to moderately alate, angle about 65°; sulcus commencing

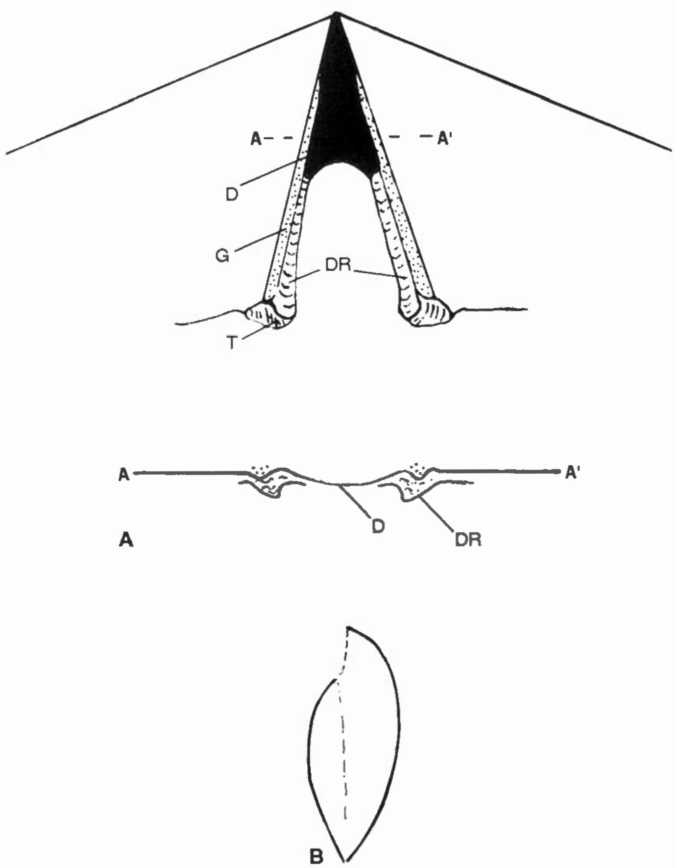


Figure 44. ***Yukonella plana*** *n. gen. et sp. A, interarea and transverse section of GSC 97219 (approx. x3), showing delthyrium, delthyrial plate, and low dental ridges; B, lateral profile of shell showing low inflation. D, delthyrial plate; DR, dental ridges; G, groove, T, tooth.*

from umbo, well segregated from flatly spreading flanks, sulcal angle measured from umbo between 20° and 30°, generally 9 to 11 mm wide and 3 to 5 mm deep at front, floor narrowly rounded posteriorly, more broadly rounded anteriorly, smooth; flanks flatly convex and spreading well to lateral margins, each carrying 15 to 18 simple costae; costae low, well rounded, separated by narrow interspaces, diminishing in strength towards cardinal extremities.

Dorsal valve equally or slightly less convex than ventral valve, interarea rather low; notothyrium wide, open, apical angle about 45°; fold distinct, generally low and well rounded, smooth; costation on flanks similar to that of ventral valve.

Micro-ornament poorly preserved, consisting of fine growth increments and rounded to slightly elongate tubercles, no grooves (Pl. 22, fig. 25), irregularly arranged. No punctae observed from exfoliated exteriors.

Internal. Teeth robust, rounded (Pl. 23, fig. 24); dental ridges low, strongly thickened, extending from teeth to umbo, posteriorly flanking delthyrial plate, initial dental ridges poorly defined (Fig. 45A); adminicula reduced, confined to posterior third of interarea length, posteriorly buried by strong umbonal thickening, anteriorly slightly isolated; umbonal cavity mostly filled by umbonal thickening; delthyrial plate almost entirely sessile on strongly thickened umbonal floor (Fig. 45A); ventral muscle field well impressed, elongate-oval in shape; adductor ridge at median (Pl. 23, fig. 3), low, poorly discriminated from surrounding diductors, smooth; myophragm short; diductor scars laterally depressed, well formed with raised marginal ridges in some specimens, weakly striated; ovarian impressions poorly or not developed.

Cardinal process small, posteriorly marked by 13 vertical ridges (Pl. 22, fig. 22); dental sockets deep, elongate, widening forward, bordered at inner sides by high inner socket ridges (Fig. 45B); crural plates

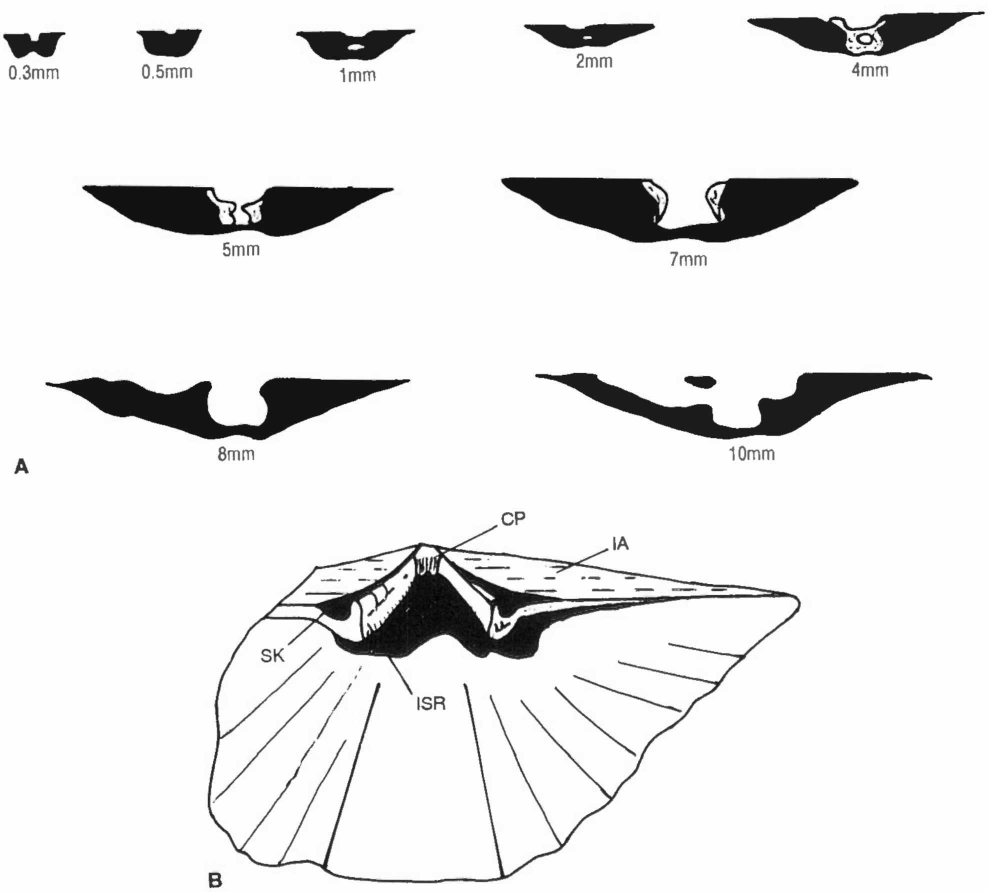


Figure 45. Yukonella plana *n. gen. et sp. A, transverse serial section of ventral valve (x1); B, dorsal interior showing cardinalia (GSC 97220, approx. x2.5). CP, cardinal process; IA, dorsal interarea; ISR, inner socket ridge; SK, socket. The measurements refer to distance from the ventral beak.*

slender; fine median ridge in some specimens (Pl. 23, fig. 7), not corresponding to any external groove along dorsal fold (see Pl. 22, fig. 21); muscle field obscure.

Dimensions (in mm).

Specimen	Valve	Length	Width	Height	Height/Width
GSC 97215	VIM	35	50	?4	?0.08
GSC 97217	VEN	26	46	5	0.11
GSC 97220	DIM	18	46	3	0.06

Comparisons. The Yukon material resembles species of *Permospirifer* in many respects, especially the type species *P. keyserlingi* (Nechaev) as redescribed by Slusareva (1960, p. 76, Pl. 9, figs. 1–6; Pl. 12, figs. 1–5, 7), but it is clearly distinguished by possessing a large, well developed delthyrial plate and lacking distinct ovarian impressions in the ventral interior. *Permospirifer kulikovi* Slusareva (1960, p. 77, Pl. 8, figs. 1–6; Pl. 12, fig. 6) from the Ufimian to Kazanian stages of the Russian Platform and northeastern Siberia differs further in being smaller, less transverse, and more strongly convex.

Permospirifer? *wardakensis* Legrand-Blain (1968, p. 205, Pl. 1, fig. 5; Pl. 4, figs. 1, 2a–c; Figs. 5, 6) from the Sakmarian beds at Wardak, central Afghanistan, is close to the Yukon species in its small and poorly isolated ventral umbo, reduced adminicula, and well defined delthyrial plate, but differs in being large, with a more transverse outline and a broader, deeper sulcus. Micro-ornament is not known from the heavily exfoliated Afghan specimens. Termier et al. (1974) considered *Permospirifer*? *wardakensis* synonymous with *Punctocyrtella spinosa* Plodowski, 1968, 1970 from the same area (not the same locality), and placed it in *Licharewia*, which they considered synonymous with *Permospirifer*. However, some of Plodowski's specimens show a well defined median groove along the dorsal fold (Plodowski, 1970, Pl. 7, fig. 3a), which appears to be absent from the material figured by Legrand-Blain (1968) and Termier et al. (1974). *Punctocyrtella spinosa* was originally characterized as having punctae and a dorsal median groove, therefore approaching *Cyrtella* Frederiks, 1924. But Termier et al. (1974) asserted that *Punctocyrtella spinosa* was not punctate. Apart from the presence of a distinct median groove along the dorsal fold and the controversial punctation in *P. spinosa*, there seems no other significant distinction between the Afghan species and the Yukon species, either in external morphology or internal structures. If *Punctocyrtella* has punctae and a dorsal median groove, as recognized by its author, it appears to be a junior subjective synonym of *Cyrtella*, as pointed out by Thomas (1971); if, on the other hand, it is not punctate, as argued by Termier et al. (1974), it seems congeneric with the Yukon species. However, it may also be possible that at least some of Plodowski's original material of *Punctocyrtella spinosa* did show punctae and a grooved dorsal fold, and these shells should be assigned to *Cyrtella*. Other Afghan specimens which are neither punctate nor have a grooved dorsal fold, such as those specimens figured by Termier et al. (1974) and possibly those figured by Legrand-Blain (1968) as *Permospirifer*? *wardakensis*, may be assigned to the present genus, *Yukonella*. The above controversy can only be solved by further collecting and studying well preserved material from the type localities of both *Punctocyrtella spinosa* and *Permospirifer*? *wardakensis*. Until then, it is not possible to make a decision about the generic assignment of the Afghan species.

Occurrence. Yukonella plana n. gen. et sp. is confined to the Ej zone in northern Yukon Territory, of Early Artinskian (Aktastinian) age.

Family SPIRIFERELLIDAE Waterhouse, 1968
(nom. transl. herein ex. Spiriferellinae
Waterhouse, 1968)

Genus *Spiriferella* Chernyshev, 1902

Type species. (OD) *Spirifer saranae* Verneuil, 1845.

Discussion. The familial position of *Spiriferella* and allies is difficult to resolve. It was placed by Pitrat (1965) with the Brachythyridae Frederiks, a placement followed Cooper and Grant (1976a). Carter (1974), then Archbold and Thomas (1985), referred the Spiriferellinae to the Spiriferidae King on the basis of costation and plication pattern. However, Waterhouse et al. (1978) and Waterhouse and Waddington (1982) stressed that the micro-ornament and ventral internal plates of *Spiriferella* were probably more closely related to the Licharewiinae, and transferred the Spiriferellinae to the Licharewiidae. This has been accepted by Abramov and Grigor'yeva (1988).

Members of the Spiriferellinae appear to bridge the Licharewiidae and the Spiriferidae in plication, micro-ornament, and ventral plates. *Spiriferella* and its allies possess a thickened ventral umbo, prominent dental plates and adminicula, and a distinct micro-ornament of radial capillae and concentric lamellae, as in the Licharewiidae. However, they also have a costate sulcus, fold, and lateral slopes, recalling the Spiriferidae. As the origin of the Spiriferellinae remains obscure (Waterhouse et al., 1978; Archbold and Thomas, 1985), we tentatively upgrade this subfamily to family rank.

Waterhouse et al. (1978) recognized five possible lineages of *Spiriferella*, two of which were subsequently nominated (Waterhouse and Waddington, 1982) as two new genera: *Alispiriferella* for *Spiriferella ordinaria* lineage and *Plicatospiriferella* for *S. gieliensis* lineage. *Spiriferella* is distinguished from *Alispiriferella*, *Plicatospiriferella*, and *Timaniella* Barchatova, 1968 by its normally elongate outline, narrow hinge line, and non- or weakly costate lateral plicae. It may be further distinguished from *Alispiriferella* by possessing a low, narrow median groove along the dorsal fold rather than a wide median cleft, and from *Plicatospiriferella* by its stronger, more conspicuous costae.

Waterhouse and Waddington (1982, p. 14, 17) described and discussed in detail *Spiriferella pseudodraschei* and *S. saranae* referred to below. Their descriptions are supplemented here.

Spiriferella pseudodraschei Einor *in* Likharev and Einor, 1939

Plate 24, figures 1–20

1939 *Spirifer* (*Spiriferella*) *keihavii* var. *pseudodraschei* Einor in Likharev and Einor, p. 219, Pl. 24, figs. 6–9.

1982 *Spiriferella pseudodraschei* Einor; Waterhouse and Waddington, p. 14, Pl. 2, figs. 14–19; Pl. 3, figs. 1–13; Fig. 13 (with synonymy).

Holotype. The specimen figured by Likharev and Einor (1939, Pl. 24, fig. 9), from the Lower Permian strata of Novaya Zemlya, northern Russia, and kept at CNIGR Museum, St. Petersburg.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 57053	2, 1(im)	2	
JBW loc. 2	1, 2(em)		
JBW loc. 14	1(im)		
JBW loc. 24	6(im), 5(em)	2(em)	
JBW loc. 54	4		
JBW loc. 57	1		
JBW loc. 58	1		
JBW loc. 59	1		
JBW loc. 63	2		1(im)
JBW loc. 88	6, 2(im), 2(em)	1(im), 2(em)	2
JBW loc. 89	3, 4(im), 5(em)		1(im)
JBW loc. 109	8, 1(im), 3(em)	1, 1(em)	
JBW loc. 110	1(im)	1(im)	1(im)
JBW loc. 506	9, 1(im)		
JBW loc. 507	10	2	
JBW loc. 545	8, 2(im)		1(im)
JBW loc. 546	1, 2(em)		

Description. External. Shell small, widest at midlength or slightly behind, rarely at hinge line.

Ventral valve strongly inflated; beak short, not protruding beyond hinge line; umbonal angle normally over 100°; umbonal slopes high, steep, gently concave; delthyrial angle about 40°; sulcal angle between 10° and 20°, narrowly but not angularly rounded on floor, broadly U-shaped in section, generally carrying two to five costae, median costa usually present; flanks bearing five pairs of plicae, low and broad, well rounded, separated by shallow, narrow interspaces, inner pairs normally asymmetrically subdivided into two to three costae over anterior half of valve, rarely into four, distal pair or pairs normally simple; plicae not costate in immature (small) specimens.

Dorsal fold normally narrow and well demarcated from flanks by deep lateral grooves (Pl. 24, fig. 8), crest divided by thin median groove beginning from umbo or, more often, at about 2 to 5 mm from it, each lateral portion then bifurcated at about posterior third to half of valve length; flanks normally covered with four pairs of sharp-crested plicae, with first inner pair subdivided into three costae in mature specimens, other pairs into two over anterior third of valve. Approximately eight capillae in 1 mm and five or six lamellae in 1 mm (Pl. 24, fig. 16), small pustules arising from intersections.

Internal. Adminicula short, supporting posterior portions of dental plates, thickened and buried within umbonal thickening in most specimens; muscle field posteriorly sessile and deeply depressed (Pl. 24, figs. 17, 18), anteriorly elevated on massive, well extended median ridge; adductors narrow and elongate, located at median; diductors longitudinally striated.

Cardinal process small and vertically laminated; helicophores poorly preserved; median ridge occasionally present.

Dimensions (in mm).

Specimen (Ventral valves)	Length	Width	Height	Umbonal angle
GSC 97233	18	20	7	?90°
GSC 97236	26	24	13	+95°
GSC 97239	25	26	10	102°
GSC 97550	22	22	?7	?100°
GSC 97553	24	25	13	107°
GSC 97660	20	20	8.5	84°

Remarks. Waterhouse and Waddington (1982, p. 15, 17) compared at length this species with other representatives. Additional comparisons with *Spiriferella saranae* (Verneuil) are discussed below under that species.

Occurrence. In northern Yukon Territory *S. pseudodraschei* is particularly abundant in the Ey zone and occurs sporadically in the overlying Eog and Ej zones. Outside the Yukon Territory, this species is known from the Lower Permian (possibly Sakmarian) in Novaya Zemlya and from the Sakmarian to Kungurian fauna of the Coyote Butte Formation in central Oregon.

Spiriferella saranae (Verneuil, 1845)

Plate 24, figures 21-32; Plate 25, figures 1-5

1845 *Spirifer saranae* Verneuil, p. 169, Pl. 6, fig. 15.

1960 *Spiriferella saranae* (Verneuil); Harker and Thorsteinsson (partim.), p. 71, Pl. 22, figs. 1-3; not figs. 4-8.

1982 *Spiriferella saranae* (Verneuil); Waterhouse and Waddington, p. 17, Pl. 4, figs. 1-11; Figs. 14, 16a, c (with synonymy).

Holotype. A ventral valve figured by Verneuil (1845, Pl. 6, fig. 15a, b) from the Sakmarian beds in Sarana River, south of Krasnoufimsk, the Urals, kept at CNIGR Museum, St. Petersburg.

Diagnosis. See Waterhouse and Waddington (1982, p. 17).

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53715	7		
GSC loc. 53720	2		
GSC loc. 53818	1	2	
GSC loc. 54000	3		
GSC loc. 53860	1		
GSC loc. 56972	2		
GSC loc. 56977	4		
GSC loc. 57141	11, 2(im)		
JBW loc. 113	6, 3(im), 3(em)	2(im)	
JBW loc. 508	4	1	
JBW loc. 558	3, 1(im), 1(em)		2(im)

Description. External. Shell of medium size, elongate at maturity, widest at midlength.

Ventral valve strongly inflated (Pl. 24, fig. 22); umbo highly inflated, moderately extended for immature specimens, massive and strongly incurved at maturity with beak sometimes protruding beyond hinge line, tip blunt, umbonal angle usually less than 90° at maturity, though may be slightly broader in immature specimens; interarea height/width ratio ranging from 0.55 in immature specimens to 0.38 at maturity; sulcus well defined by two high, sharply defined plicae, sulcal angle at 25°, broad and deep over anterior half, typically V-shaped in section, moderately to strongly costate; sulcal costae of immature specimens rather weak or entirely absent, mature specimens usually carry five to seven rounded sulcal costae, median costa prominent; flanks bear four or five pairs of plicae, moderately high and broadly to narrowly rounded, innermost pair conspicuously higher than all other pairs and angular-crested; costae differentiated with primary costae normally one and a half times wider than other costae.

Fold bears thin distinct median groove running through its entire length (Pl. 24, fig. 31), each lateral portion bifurcated at about midlength or slightly behind it; flanks have four pairs of plicae. Four to six radial capillae in 1 mm, sometimes discontinuous (Pl. 24, fig. 32); concentric lamellae less prominent, four or five in 1 mm, with small pustules arising from intersections.

Internal. Dental plates isolated over anterior half of their length, strongly thickened posteriorly and united below apex of delthyrium; adminicula short, often fused within umbonal callosity; muscle field with prominent bordering ridges in some specimens, spoon-shaped, posteriorly well depressed, anteriorly elevated on massive median ridge, which apparently extends beyond midlength; adductor ridge narrow and slightly raised, divided by fine myophragm; diductor scars relatively large, vertically striated.

Helicophores moderately developed at inner sides of socket ridges (Pl. 25, fig. 1); median ridge distinctly present in some specimens, arising some 6 mm in front of cardinal process.

Dimensions (in mm).

Specimen (Ventral valves)	Length	Width	Height	Umbonal angle
GSC 97553	41	?30	18	?93°
GSC 97555	33	25	15	75°
GSC 97557	+25	20	13	105°
GSC 97662	+23	?26	13	97°
GSC 97663	25	22	12	88°

Comparisons. As discussed by Waterhouse and Waddington (1982), *Spiriferella saranae* is usually larger than *S. pseudodraschei* and has a narrower umbonal angle. In addition, the ventral sulcus and plicae also appear to vary from each other in that *S. saranae* usually has a deeper and more angular-floored sulcus, bordered by conspicuously higher plicae, and its ventral plicae are generally higher and less rounded.

A small ventral valve from the Aktastinian lower Echii Suite of the Verchoyan Mountains, figured as *Spiriferella* sp. by Abramov and Grigor'yeva (1988, Pl. 25, fig. 3), is close to some of the smaller specimens of the present material, with few and simple costae, but it seems to differ in having a narrower and deeper sulcus.

Comparisons of *S. saranae* with other species were discussed by Waterhouse and Waddington (1982).

Occurrence. Spiriferella saranae appears to have a long range in the Permian strata of northern Yukon Territory, occurring in Eta through Ey, Eog, and Ej zones to F and G faunas, ranging in age from Asselian to probably Kungurian. However, this species is more commonly found in the Ej zone. Elsewhere, the species has been found in the Sakmarian to Artinskian faunas of the Urals; the Lower Permian (possibly Sakmarian) faunas of Novaya Zemlya; and the Sakmarian Yasachnin Horizon in the Kolyma-Omolon Massif.

Spiriferella sp.

Plate 25, figures 6–10

Material. Three ventral valves from JBW loc. 57.

Description. Shell of medium size at maturity, 34 mm wide, 29 mm long, and 14 mm high for large specimen; subquadrate in outline; cardinal extremities moderately alate, widest at hinge line; ventral valve strongly arched both transversely and longitudinally (Pl. 25, fig. 9), most inflated near posterior third; umbo prominent, strongly extended and incurved over delthyrium, angle close to 85°; umbonal slopes gently convex, high and steep; interarea high, horizontally striated; delthyrium open, delthyrial angle about 50°; cardinal extremities alate, ears prominent, cardinal angle 70°; sulcus well defined by highly elevated lateral plicae (Pl. 25, figs. 6, 7), commencing at umbo with sulcal angle about 22°, markedly deepening and widening in front, floor angular, typically V-shaped in section, bearing three pairs of faint costae, median costa present in some specimens; flanks narrow and steeply sloping to lateral margins, with four pairs of high sharp-crested plicae, innermost two pairs weakly bifurcated over anterior two thirds of shell length, primary costae high and well defined; distal pairs moderately high, rounded, and simple; interspaces approximately as wide as plicae.

Comparisons. The Yukon material appears to be similar to *Spiriferella digna* Barchatova (1968, p. 161, Pl. 46, fig. 3; 1970, p. 175, Pl. 20, figs. 5, 6), from the Late Sakmarian (Sterlitamakian) Digna Horizon of northern Timan, in its wide hinge and deep sulcus, but the latter has broader and well rounded plicae and a very weakly costate sulcus.

Occurrence. Eog zone, Sterlitamakian.

Genus *Alispiriferella* Waterhouse and Waddington, 1982

Type species. (OD) *Spirifer* (*Spiriferella*) *keilhavii* Buch var. *ordinaria* Einor *in* Likharev and Einor (1939).

Diagnosis. Spiriferellinae distinguished by its transverse-subrounded outline with moderately alate cardinal extremities and broadly sulcate dorsal valve.

Alispiriferella ordinaria (Einor, 1939)

Plate 25, figures 11–15; Figure 46

1939 *Spirifer* (*Spiriferella*) *keihavii* var. *ordinaria* Einor *in* Likharev and Einor, p. 140, Pl. 23, figs. 6, 7; Pl. 24, fig. 1.

1982 *Alispiriferella ordinaria* (Einor); Waterhouse and Waddington, p. 30, Pl. 2, figs. 7–13; Figs. 11i, j, 20 (with synonymy).

1988 *Alispiriferella ordinaria* (Einor); Abramov and Grigor'yeva, p. 158, Pl. 22, fig. 7.

Diagnosis. Shell slightly wider than long with moderately alate cardinal extremities and low, well rounded costae; sulcus moderately deep, broadly V-shaped in section, with two prominent sulcal costae; fold low, divided by single, broad median cleft.

Holotype. The shell figured by Likharev and Einor (1939, Pl. 24, fig. 1) from the Lower Permian strata on the western coast of the south island, Novaya Zemlya, northern U.S.S.R., kept at CNIGR Museum, St. Petersburg.

Material. Two conjoined specimens and one fragment of a ventral external mould from GSC loc. 53714.

Description. External. Shell moderately large, generally about 38 mm wide and long, 32 mm high; subpentagonal in outline, slightly wider than long; moderately biconvex; widest at hinge line; anterolateral margins distinctly convex; anterior commissure strongly uniplicate.

Ventral valve moderately to strongly convex, most inflated at posterior third of shell length; transverse profile evenly and broadly arched (Pl. 25, fig. 13); umbo broad, convex, well incurved over delthyrium, well demarcated from umbonal slopes; umbonal angle close to 90°; umbonal slopes gently concave; interarea moderately high, close to triangular in shape, slightly concave, with sharp shoulders; cardinal extremities slightly to moderately alate with cardinal angle close to 90°; sulcus distinct (Pl. 25, fig. 14), commencing from umbo with sulcal angle measured from umbo at about 25°, well defined by high lateral plicae, moderately deep, floor broadly angular, anteriorly extended as short tongue indenting dorsal valve, bearing one pair of weak costae on sulcal slopes, no median costa; flanks bounding sulcus moderately convex and sloping to lateral margins, with four or five pairs of moderately high, broad, and well rounded plicae, separated by narrow interspaces, innermost two pairs (bounding sulcus) weakly costate on anterior half.

Dorsal valve equally convex as ventral valve (Pl. 25, fig. 12); fold low, not well differentiated from well spreading flanks, medianly divided by well defined, broad groove one third as wide as fold; plication similar to that on ventral valve.

Micro-ornament of fine radial capillae and concentric lamellae with a few minute pustules at intersections.

Internal. Dental plates high, diverging forward, supported by short but prominent adminicula (Fig. 46).

Comparisons. Nelson and Nelson (1985, Pl. 1, fig. 20) figured a ventral valve as *Spiriferella ordinaria* from the possibly Sakmarian Harper Ranch Group near Kamloops, southern British Columbia. This single valve is close in shape, with moderately alate cardinal extremities, but appears to differ in its simple, higher, sharp-crested plicae separated by broad, deep interspaces. Its sulcus also looks deeper than in the Yukon material, but this may have been caused by lateral crushing.

Spiriferella sp. of Liu and Waterhouse (1984, p. 34, Pl. 8, figs. 13–15), from the Sakmarian Houtoumiao Formation of Inner Mongolia, northeast China, is similar to the present species in having moderately alate cardinal extremities and a broad median cleft on the dorsal fold; it differs in its small size and lower convexity.

Occurrence. Eta, Ey, and Eog zones in northern Yukon Territory, of Asselian to Sakmarian age. The species was originally collected from the possibly Sakmarian strata on the southern island of Novaya Zemlya, northern Russia. It is also known from the Artinskian Echii Suite of the western Verchoyan Mountains, northeastern Russia.

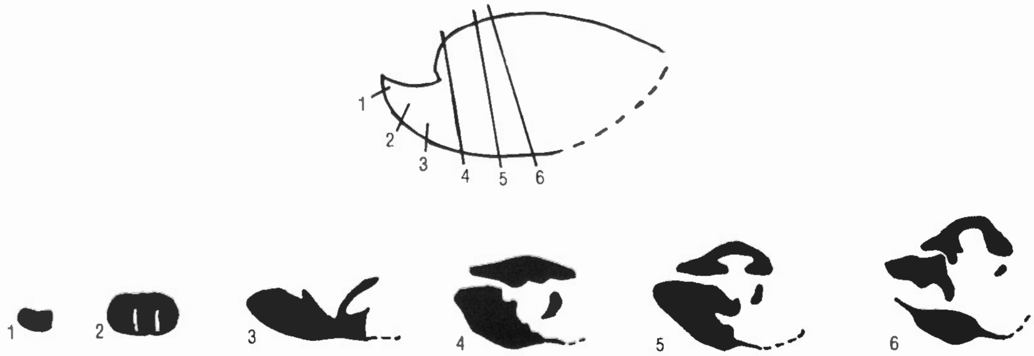


Figure 46. *Transverse serial sections of* ***Alispiriferella ordinaria*** *(Einor) (x1).*

Genus *Timaniella* Barchatova, 1968

Type species. (OD) *Timaniella festa* Barchatova, 1968.

Diagnosis. Transverse to strongly alate shells, moderately to strongly convex; plicae few, distinct, weakly to strongly costate; sulcus weakly to strongly costate, fold with broad median groove; micro-ornament of fine network of radial and concentric lines with minute pustules. Ventral interior with well defined dental plates supported by short adminicula; umbonal thickening strong; muscle field well depressed with low bounding ridges.

Discussion. Rhombospirifer Duan and Li (*in* Ding et al., 1985, p. 135), from the Artinskian to Kazanian Zhesi and overlying Yihewusu formations of Inner Mongolia, northeastern China, strongly resembles *Timaniella* in having a very transverse outline, strong, costate plicae, strongly grooved fold, and strong umbonal thickening, but it is distinguished by its smooth sulcus and micro- ornament restricted to fine concentric lamellae.

Timaniella convexa n. sp.

Plate 25, figures 16–28; Figure 47

Etymology. Latin *convexus*, arched outward.

Holotype. GSC 97568 from JBW loc. 526, Ettrain Creek; Ej zone, Jungle Creek Formation (Pl. 25, figs. 18, 21).

Diagnosis. Alate shell with strongly convex ventral valve and gently convex dorsal valve; sulcus weakly costate; ventral plicae narrow and moderately high, inner two or three pairs weakly bifurcated; dorsal median groove narrow, lateral plicae broad and low, innermost pair usually trifurcated; lateral margins near cardinal extremities not plicate or costate.

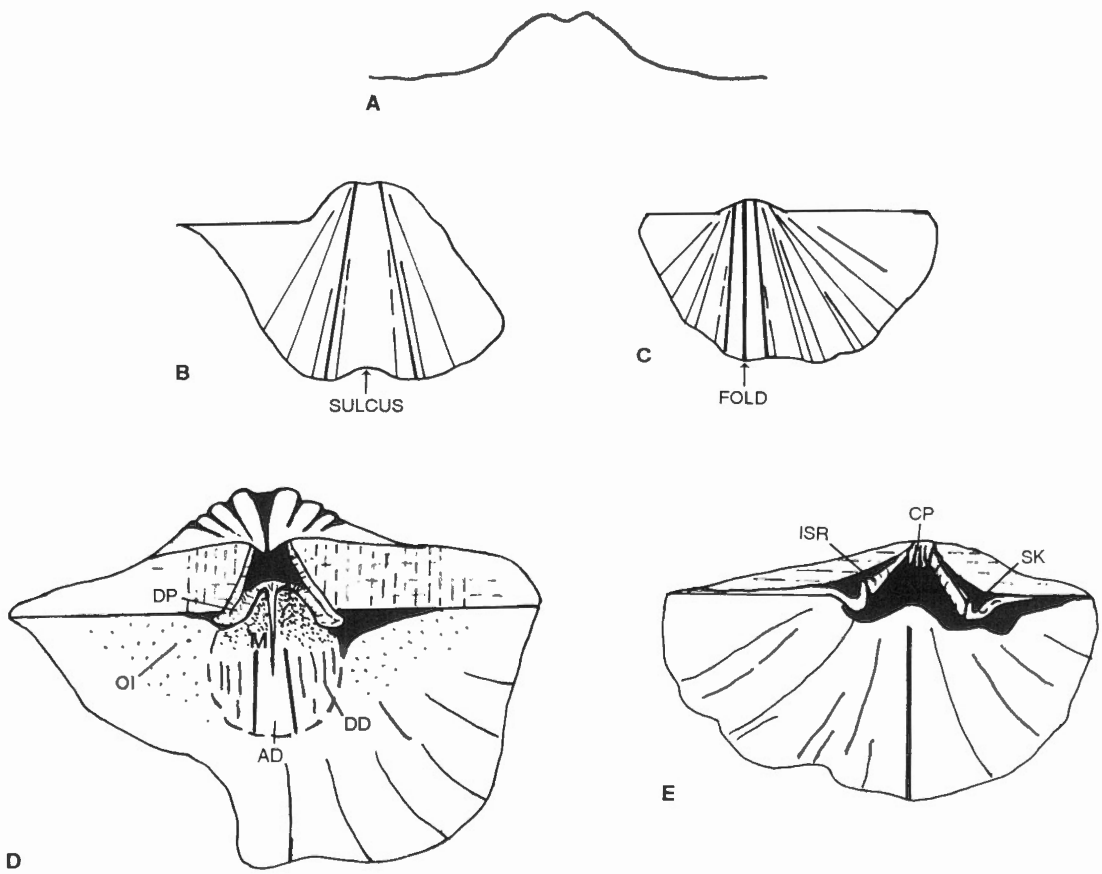


Figure 47. Timaniella convexa *n. sp. A, transverse profile of a ventral valve showing high venter and alate cardinal extremities (GSC 97658, x1); B, C, ventral and dorsal costation patterns (GSC 97655, GSC 97576, both x1); D, E, ventral and dorsal interiors (GSC 97572, GSC 97569, both approx. x3). M, myophragm; OI, ovarian impressions; other abbreviations as in Figures 27, 45.*

Material. Three ventral valves, three ventral external moulds, six ventral internal moulds, two dorsal external moulds, and three dorsal internal moulds from JBW loc. 526.

Description. External. Shell moderately large, strongly transverse with large ear-like lateral extensions and alate cardinal extremities (Pl. 25, figs. 17, 18; Fig. 47A); strongly unequally biconvex.

Ventral valve strongly inflated (Pl. 25, fig. 21), most convex over posterior third to half of shell length, with high and steep lateral slopes and flattened ear-like extensions and alate cardinal extremities (Fig. 47A); umbo prominent, well extended and strongly incurved over apex of delthyrium, umbonal angle close to 60°; umbonal slopes high and steep, moderately concave in outline, gently convex in section; interarea wide and low (Pl. 25, fig. 16), slightly concave, marked by distinct vertical striae which are occasionally intersected by horizontal lines (Fig. 47D); hinge margin weakly denticulate; delthyrium relatively narrow, open, delthyrial angle about 35°; cardinal extremities acute, angle between 30° and 45°; sulcus distinct, commencing from umbo with sulcal angle between 15° and 25°, gently widening and deepening forward, bounded on each side by high, narrowly rounded plica, generally shallow, 5 mm wide and 4 mm deep at frontal margin, floor broadly concave in section, very weakly costate (Pl. 25, fig. 23), with median costa in some specimens (Pl. 25, fig. 18) and one pair of lateral costae (Fig. 47B), sulcal costation obscure on worn specimens; flanks narrow, well rounded to lateral slopes, bearing three to five pairs of discernable plicae; plicae narrow and moderately high, rounded on crests, separated by shallow, narrow interspaces, diminishing in strength laterally and gradually disappearing before reaching ear-like lateral extensions where ornament is dominated by fine concentric lamellae (Pl. 25, figs. 18, 21, 23), inner one or two pairs occasionally bifurcated, lateral pairs remaining simple.

Dorsal valve flatly convex (Pl. 25, fig. 28); umbo flattened; interarea low, notothyrium prominent, relatively wide; fold slightly raised above flanks, delimited to each side by deep broad lateral groove, bisected by narrow median groove running its full length (Pl. 25, fig. 28), groove about a quarter as wide as fold, each lateral part of fold weakly bifurcated in some specimens over anterior half of valve length (Pl. 25, fig. 28; Fig. 47C); flanks slightly inflated, with four or five pairs of low, broad, and well rounded plicae, innermost pair usually trifurcated (Pl. 25, fig. 28; Fig. 47C) with nearly equidimensional costae, other plicae simple, ear-like lateral portions and cardinal extremities not plicate or costate.

Micro-ornament of very well defined concentric lamellae, strongest over ear-like lateral extensions on both valves (Pl. 25, fig. 23), four to five in 1 mm; radial capillae poorly preserved.

Internal. Teeth elongate (Pl. 25, fig. 20), supported by distinct dental plates which are about 3 to 4 mm high and united under apex of delthyrium through strongly developed umbonal thickening (Fig. 47D); adminicula very short and entirely buried by umbonal thickening in some specimens, anteriorly isolated in others; muscle field deeply depressed under umbo, slightly raised anteriorly, ovate in shape (Fig. 47D), not outlined by prominent bounding ridges, posteriorly bisected by short median ridge or myophragm? in some specimens (Pl. 25, fig. 20; Fig. 47D); adductor poorly discriminated from diductors, in median location, narrow, elongate, smooth or feebly striated; diductors to each side comparatively large, posteriorly smooth, anteriorly striated; ovarian impressions well developed on posterolateral floors (Fig. 47D).

Cardinal process small, situated slightly below notothyrium (Pl. 25, fig. 27; Fig. 47E); sockets narrow and deep, elongate in shape, bordered by high inner socket ridges; no prominent crural plates; muscle field obscure.

Dimensions (in mm).

Specimen	Valve	Length	Width	Height
GSC 97567	VEN	+18	44	+8
GSC 97570	VIM	+21	40	—
GSC 97575	VEN	23	50	+8
GSC 97576	DOR	?18	38	2.5

Comparisons. Timaniella harkeri Waterhouse (*in* Bamber and Waterhouse, 1971, p. 218, Pl. 26, figs. 10–21; Waterhouse and Waddington, 1982, p. 32, Pl. 8, figs. 9–18; Fig. 21), from the Kungurian Assistance Formation of Devon Island, Arctic Canada, is similar in having a weakly costate sulcus and mostly simple plicae. Topotypes of *T. harkeri* from the type locality GSC loc. 26406 on Devon Island are distinguished by possessing higher, more frequently costate plicae on the dorsal valve, a conspicuously broader dorsal median groove, and a much less inflated ventral valve. Specimens with simple but much higher plicae from the upper Echii Suite of the western Verchoyan, of Late Artinskian to Kungurian age, have been referred to *T. magniplicata* Abramov and Grigor'yeva (1988, p. 159, Pl. 29, figs. 1–3) and differ further in having a deeper sulcus. Specimens figured as *Timaniella*? sp. (Abramov and Grigor'yeva, 1988, Pl. 24, fig. 12) from the Aktastinian lower Echii Suite appear to be very similar to the Yukon material in overall features, but differ in having a more prominently costate sulcus.

The type species *T. festa* Barchatova (1968, Pl. 46, figs. 4, 5) has an identical ventral interior but is well distinguished by its high, strongly and frequently costate plicae, and strongly costate sulcus.

Occurrence. Timaniella convexa n. sp. is confined to the Ej zone in northern Yukon Territory, of Aktastinian age.

Family SPIRIFERIDAE King, 1846

Subfamily NEOSPIRIFERINAE Waterhouse, 1968

Genus *Neospirifer* Frederiks, 1924

Type species. (OD) *Spirifer fasciger* Keyserling, 1846.

Neospirifer sp.

Plate 26, figures 3-9

1963 *Neospirifer*? sp. Yole, Pl. 2, figs. 15, 16.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 57154	1		
JBW loc. 2	1	2	
JBW loc. 54	1		1(im)
JBW loc. 109	2	1	
JBW loc. 113	1		
JBW loc. 508	1		

Description. External. Shell of average size for genus, moderately transverse, width/length ratio 1.69 in well preserved specimen (Pl. 26, fig. 8); moderately biconvex, widest along hinge line.

Ventral valve gently to moderately convex, most inflated in posterior 10 to 12 mm of shell length, flatly convex in transverse direction; umbo small but prominent, moderately extended and incurved, well isolated from rest of valve; umbonal slopes concave, umbonal angle between 80° and 100°; interarea broad-triangular in shape, moderately concave, vertical striae prominent (Pl. 26, fig. 6), two to three in 1 mm; delthyrium open, no delthyrial plate seen in poorly preserved exteriors, delthyrial angle about 35°; sulcus arising from umbo with sulcal angle of 25°, gently widening and deepening anteriorly, bordered posteriorly by proportionally high and narrowly rounded costae, anteriorly less well defined from lateral flanks due to fasciculation, shallow, floor posteriorly narrowly rounded, anteriorly broadly rounded; anterior tongue indistinct or not developed; flanks bounding sulcus flatly convex, spreading well anterolaterally. Approximately 25 to 30 pairs of fine, equidimensional costae present on ventral valve, separated by slightly narrower interspaces, median sulcal costa present, crests low and well rounded; costae near sulcus grouped into bundles of four to seven, first branching occurring within 5 mm from umbo, again at about midlength, and occasionally with final branching at about 10 mm to anterior margin, interspaces separating bundles of costae almost as wide as intercostal grooves, so that plication very weakly differentiated (Pl. 26, fig. 8), perceptible only within posterior 10 to 15 mm from umbo, fading anteriorly.

Dorsal valve equally convex or slightly less than opposite valve; fold well defined above flatly convex flanks. Costation similar to that of ventral valve.

Micro-ornament of fine concentric lamellae and radial capillae, approximately 10 capillae in 1 mm; no minute pustules.

Internal. Ventral interior with well developed dental plates and adminicula, no median septum or ridge.

Cardinal process rounded, strongly laminated in vertical direction (Pl. 26, fig. 9).

Comparisons. A single, poorly preserved ventral valve from the Sakmarian Formation B of Vancouver Island, figured as *Neospirifer*? n. sp. by Yole (1963), appears conspecific with the Yukon material. It is strongly transverse with sharp cardinal extremities.

Abramov and Grigor'yeva (1988, p. 164, Pl. 23, figs. 5-7; Pl. 24, figs. 5, 6; Pl. 25, figs. 6, 7; not Pl. 23, fig. 1; Pl. 28, figs. 5, 6) figured several specimens as *Neospirifer* aff. *N. subfasciger* (Likharev, 1934b) from the Aktastinian lower Echii Suite of the Verchoyan Mountains. These specimens are similar in general aspect and especially in their fine equidimensional costae, but appear to differ in having longer and better differentiated plicae and a narrower and deeper sulcus. Other Verchoyan specimens assigned to the same species are either very large and transverse or less convex with coarse costae. Typical *N. subfasciger* Likharev (1934b, p. 58, Pl. 1, fig. 11; Pl. 4, figs. 1-5) from a Lower Permian exposure in the Kolyma-Omolon Massif differs in its higher convexity, extended umbo, conspicuous plicae, and deeper, more narrowly rounded sulcus.

Occurrence. Ey and Ej zones in northern Yukon Territory. Elsewhere, the species is possibly present in the Sakmarian Formation B of Vancouver Island.

Genus *Lepidospirifer* Cooper and Grant, 1969

Type species. (OD) *Lepidospirifer angulatus* Cooper and Grant, 1969.

Diagnosis. See Cooper and Grant (1976a, p. 2204).

Discussion. The validity of *Lepidospirifer* has been questioned. When creating the genus, Cooper and Grant (1969, 1976a) drew attention to the tegulate micro-ornament. However, Waterhouse (1978b) and Archbold and Thomas (1984a) regarded this ornament as of no generic significance, as it is also known to be variably present in *Neospirifer* and *Aperispirifer* Waterhouse, 1968a; Waterhouse considered the tegulate ornament probably related to climate and substrate and an ecotypic parameter. Apart from the tegulate ornament of arguable generic significance, *Lepidospirifer* appears to be distinguished from *Neospirifer* by its very small, low delthyrial plate, finer costae, weakly differentiated plicae, and straighter umbo.

Two small dorsal valves from the Yukon are provisionally, and questionably, assigned to *Lepidospirifer* primarily because of their very strongly developed tegulate ornament.

Lepidospirifer? sp.

Plate 26, figures 10, 11

Remarks. Two dorsal external moulds from JBW loc. 24. The specimens are rather small for the genus, approximately 22 mm wide and 15 mm long, slightly transverse or suboval in outline; umbo blunt; fold narrow and high, well above flanks that spread laterally, carrying five to eight costae; flanks bearing three or more well defined plicae, each consisting of three to five slightly unequal or subequal costae, moderately high and fading away near anterior margin; primary costae normally coarser than costae arising later; plicae separated by deep interspaces over posterior third of shell length. Concentric lamellae distinct, highly raised over costae and interspaces, closely spaced, tiled-roof in appearance, four or five in 1 mm on average; radial ornament poorly developed.

Family CHORISTITIDAE Waterhouse, 1968

Subfamily PURDONELLINAE Poletayev, 1986

Genus *Purdonella* Reed, 1944

Type species. (OD) *Spirifer nikitini* Chernyshev, 1902.

Diagnosis. Elongate to transversely suboval Choristitidae with rounded margins, short denticulate hinge margin, small and triangular interarea; sulcus moderately to well developed, fold rather low and usually not elevated above flanks; costae low, narrow and well rounded, bifurcated and rarely trifurcated. Dental plates low, converging toward apex where they may be connected by umbonal thickening; adminicula thin, initially inserting into shell wall where they may be fused by secondary prismatic layers, anteriorly well separated and diverging, usually one and one half to two times longer (higher) than dental plates; ovarian impressions well developed on posterolateral portions of ventral floor.

Discussion. The above diagnosis is based on the emended concept of "*Munella*" Frederiks (now *Purdonella*, see discussion below) by Chao (1929) and the revision of *Spirifer nikitini* by Poletayev (1984, 1986).

Frederiks (1924) originally distinguished his *Munella* from *Choristites* Fischer de Waldheim, 1853 by the absence of an eseptoid, a wedge-shaped ridge between adminicula. Chao (1929) argued that the so-called eseptoid was formed solely by secondary shell thickening and consequently gave it no taxonomic weight. He restricted *Munella* to those choristitids with a short hinge line and a small triangular interarea. Reed (1944) proposed *Purdonella* to replace *Munella* that was pre-occupied, but he gave no diagnosis or discussion, though several workers had referred *Munella* to synonymy of *Choristites* (Likharev, 1934a; Semichatova, 1934; Miloradovich, 1936b). *Purdonella* was subsequently considered to be a junior subjective synonym of *Choristites* by workers such as Dunbar (1955), Gobbett (1964), Yanagida (1967), and Cooper and Grant (1976a). More recent Russian studies have recognized the genus (Prokofiev, 1975; Aleksandrov and Einor *in* Einor, 1979; Kalashnikov, 1980; Poletayev, 1984, 1986). Poletayev (1984) restudied syntypes and possible topotypes of *Purdonella nikitini* and concluded that *Purdonella* was distinguished from *Choristites* by its narrower hinge line coupled with a small triangular interarea, anteriorly well separated and diverging adminicula, weakly developed umbonal thickening, and widely spread ovarian impressions. Later, in 1986, Poletayev upgraded these distinctions and proposed the new subfamily Purdonellinae. According to Poletayev, degree of secondary shell thickening and the relative ratio of length of dental plates against adminicula are of primary taxonomic significance. For example, Poletayev (1984) described the adminicula of the lectotype of *Purdonella nikitini* as unfused, and not thickened, or very weakly thickened, by prismatic layers. He then extended these characteristics to *Purdonella*. However, a topotype of *P. nikitini*, examined by Likharev (1934a) exhibited strongly thickened and basally fused initial adminicula, and this is also evident in *P. nikitini* from the Yukon material described below. Therefore, we are in accordance with Chao (1929) in placing little generic value in secondary shell thickening; it is more related to surplus $CaCO_3$ generated under favorable conditions at late maturity. However, we agree with Poletayev (1984, 1986) in regarding the primary shape, extension of dental plates, and adminicula as consistent and rigorous evidence in taxonomy. As demonstrated by Poletayev (1986), *Choristites* has close-set adminicula, which extend forward parallel or subparallel and are approximately four to five times longer than the dental plates (Fig. 48A).

When proposing *Purdonella*, Reed (1944) also assigned several species from the Salt Range to this genus. As noted by Dunbar (1955, p. 159) and Cooper and Grant (1976a, p. 2191), these Salt Range species are quite different from *Purdonella nikitini*. Cooper and Grant (1976a) referred these species to their new genus *Cartorhium*, characterized by transversely ellipitical outline, narrow but prominent costae, conspicuous fasciculation, and much shorter and very broadly divergent adminicula.

Purdonella nikitini (Chernyshev, 1902)

Plate 26, figures 12–14

1902 *Spirifer nikitini* Chernyshev (partim.), p. 542, Pl. 10, figs. 1, 2; not Pl. 13, fig. 2.

?1913 *Spirifer nikitini* Chernyshev; Mansuy, p. 66, Pl. 6, fig. 4.

1968 *Spirifer nikitini* Chernyshev; Logan and McGugan, p. 1136, Pl. 144, figs. 14–16.

1971 *Purdonella* cf. *P. nikitini* (Chernyshev); Waterhouse *in* Bamber and Waterhouse, Pl. 14, fig. 10.

1975 *Spirifer nikitini* Chernyshev; Gorveatt and Nelson, p. 703, Pl. 2, figs. 1-3, 6; Fig. 3 (2–5); Fig. 6.

1980 *Purdonella nikitini* (Cheynyshev); Kalashnikov, p. 95, Pl. 28, fig. 4; not fig. 3; Pl. 33, figs. 6–9.

1984 *Purdonella nikitini* (Chernyshev); Poletayev, Fig. 1a.

Lectotype (selected by Poletayev, 1984). CNPM 1628/303 figured by Chernyshev (1902, Pl. 10, fig. 2) from the Sakmarian Stage at Tastuba, Ural Mountains.

Diagnosis. Moderately large, transverse-suboval in shape, maximum width at midlength; umbonal slopes concave; sulcus broad and moderately deep, poorly segregated from flanks, fold low and poorly defined; costae fine, six or seven in 10 mm at midlength of ventral valve.

Material. One ventral valve from GSC loc. 53705; two conjoined shells from GSC loc. 53720.

Description. External. Shell moderately large, suboval in shape, widest along midlength; anterior commissure strongly uniplicate.

Ventral valve strongly convex, most inflated over midlength or slightly behind it; umbo prominent, strongly extended and incurved, overhanging apex of interarea, with umbonal angle close to 45°; umbonal slopes moderately concave (Pl. 26, fig. 13), high and broadly rounded in section; anterior and lateral margins well rounded; interarea extends for about half of shell width or a little more, triangular in shape, apically strongly enrolled under umbo (Pl. 26, fig. 14); cardinal extremities obtusely rounded; sulcus commencing from umbo, narrow over posterior third of valve length, rapidly widening and deepening in front, V-shaped in section with narrowly rounded floor; anterior tongue short or not developed; flanks gently convex. Costae fine, numerous, narrow, well rounded, equidimensional, approximately five pairs plus one median costa over sulcus, 15 or more pairs on flanks, approximately seven in 10 mm at midlength, more prominent and often weakly bifurcated (rarely trifurcated) over anterior half of shell. Dorsal valve slightly less inflated than opposite valve, broadly swollen medianly as low and well rounded fold, poorly differentiated from laterally, gently spreading flanks. Micro-ornament of fine concentric lamellae, approximately four in 1 mm.

Internal. Adminicula long, strongly thickened posteriorly and fused by prismatic layers, extending anteriorly subparallel; muscle field well depressed, elongate-oval in shape, adductor scars weakly marked, myophragm poorly developed; diductors horizontally striated at least on posterior portions, otherwise obscure; ovarian impression widespread over posterior portions of valve floor.

Comparisons. Externally, the Yukon material is strikingly similar to the lectotype of *Purdonella nikitini* Chernyshev except for the slightly broader costae in the Russian specimen. This variation may be of little specific significance, as another syntype of *P. nikitini* figured by Chernyshev (1902, Pl. 10, fig. 1) has finer costae identical to those of the Yukon material. The specimen figured by Chernyshev (Pl. 13, fig. 2), as the same species from the Sim River of the southern Urals varies from the lectotype in that it is smaller, more rounded, its sulcus is represented by a narrow median noncostate groove, and its costae are consistently broader and less branched. Ozaki (1931) recognized these distinctions and regarded this specimen as a variety of "*Munella*" *nikitini* and named it "*Munella*" *nikitini tschernyshewi*.

Spirifer nikitini Chernyshev of Mansuy (1913) is poorly preserved on its surface, but its shape, size, and interarea are like typical *Purdonella nikitini*. The specimens figured as *P. nikitini* by Hayasaka (1922, Pl. 6, figs. 10-13) from northeastern China, and by Ozaki (1931, Pl. 4, figs. 8-11; Pl. 5, figs. 1-10; Pl. 6, figs. 1, 3a-c) from northern China are much smaller and more rounded than typical *P. nikitini*. Stepanov (1937a, Pl. 1, fig. 13) ascribed to *P. nikitini* a ventral valve from the Sakmarian beds of Kolva River, the northern Urals. This specimen has conspicuously broader and simple costae separated by deep interspaces, unlike typical *P. nikitini* from the southern Urals. The specimens named *P. nikitini* by Zavodovskiy (*in* Zavodovskiy and Stepanov, 1970) from the Upper Carboniferous Burgalii Horizon of the Kolyma-Omolon Massif seem to differ from types of Chernyshev's species in their more triangular outline and maximum width in the anterior third of the shell length, though their costation pattern is similar.

Occurrence. Waterhouse (*in* Bamber and Waterhouse, 1971) figured a ventral valve from GSC loc. 53720; Gorveatt and Nelson (1975) described this species from the "lower and middle Jungle Creek Formation" in the Peel River area. Outside the Yukon Territory, the species is common in the Asselian and Sakmarian stages of the Urals and Russian Platform and rare in the Upper Carboniferous (Kalashnikov, 1980). The species is also found in the Mt. Greene beds of northeastern British Columbia, and, possibly, the Lower Permian of southeastern Asia (Mansuy, 1913).

Genus *Domokhotia* Abramov and Grigor'yeva, 1983

Type species. (OD) *Domokhotia laticostata* Abramov and Grigor'yeva, 1983.

Diagnosis. Shell subrounded to subelliptical in outline, hinge narrower than shell width, interarea triangular; plicae well rounded, simple or branching, costae usually differentiated. Ventral umbonal thickening variably developed; adminicula short, separate, and diverging; delthyrial plate small, fused to valve floor in some species; ovarian impressions well developed over posterolateral valve floor.

Discussion. The diagnosis is translated and slightly modified from Abramov and Grigor'yeva (1983, p. 130). In their description of the genus, Abramov and Grigor'yeva did not provide details of the ventral plates, but these can be deduced from their drawings of thin sections and figured internal moulds of the type species. The umbonal region of *Domokhotia* is thickened, hiding the posterior portion of the dental plates and adminicula. The adminicula anteriorly diverge dorsally but do not extend beyond the interarea. The delthyrial plate appears to be small in the type species.

Domokhotia differs from *Purdonella* Reed in its generally broader ribs, much shorter and more divergent adminicula; from *Larispirifer* Enokjan and Poletayev in having a usually narrower hinge line, and shorter, more divergent adminicula; and from *Cartorhium* Cooper and Grant in possessing broader and nonfasciculate ribs.

Domokhotia junglensis n. sp.

Plate 27, figures 8-12; Plate 28, figures 1-5

Etymology. Named for Jungle Creek, northern Ogilvie Mountains.

Holotype. GSC 97589 from JBW loc. 109, Ettrain Creek; Ey zone, Jungle Creek Formation (Pl. 27, figs. 11, 12).

Diagnosis. Large, transversely elliptical and moderately convex shell with narrow costae over sulcus and fold; lateral costae broad, inner two to four pairs bifurcated, others simple.

Material.

Locality	Ventral	Dorsal	Conjoined
JBW loc. 11	1		
JBW loc. 60	1(em)		
JBW loc. 88	3(em)	1(em)	
JBW loc. 109	1(em), 1(im)	2(em)	1

Description. External. Shell large, transversely elliptical in outline, moderately biconvex, widest along midlength; anterior commissure prominently uniplicate. Ventral umbo small, moderately extended, moderately incurved over delthyrium; umbonal angle obtuse; hinge line slightly narrower than shell width; cardinal extremities bluntly rounded at about 120°; interarea low and wide, triangular, slightly concave under umbo; delthyrium proportionately narrow, delthyrial angle of 35°, no distinct delthyrial plate observed; anterolateral margins broadly convex and well rounded; sulcus commencing from near umbo, well differentiated from flanks by lateral costae in some specimens (Pl. 28, fig. 1), generally broad and shallow, anterior tongue short and moderately indenting dorsal valve, usually carrying five narrow and well rounded costae, 1 to 2 mm in diameter, median costa present (Pl. 28, figs. 1, 5); flanks bounding sulcus flatly convex, bearing eight or nine pairs of low, well rounded plicae, 2 to 3 mm across, measured at midlength, separated by narrower but prominent interspaces, inner three or four pairs usually weakly bifurcated over anterior two thirds of valve length (Pl. 28, fig. 5), occasionally trifurcated; lateral pairs of plicae remaining simple; primary costae usually twice as coarse as costae arising later. Dorsal valve equally convex, umbo blunt; fold prominent (Pl. 28, fig. 2), separated from flanks by prominent lateral grooves, low and well rounded on crest, carrying weak, irregularly branched costae; lateral plicae on flanks similar to those on ventral valve, but crests more angular. Micro-ornament consists of fine concentric lamellae, three or four in 1 mm.

Internal. Umbonal region of ventral valve moderately thickened, burying posterior portions of dental plates and adminicula (Pl. 28, fig. 4); dental plates low; adminicula slightly higher, diverging forward but confined to length of interarea, probably not reaching muscle field (Pl. 27, fig. 8; Pl. 28, fig. 4); muscle field partly exposed in holotype, well depressed, bisected by prominent myophragm, posterolaterally striated; ovarian impressions extensive over posterior floor (Pl. 27, fig. 11).

Dimensions (in mm).

Specimen	Valve	Length	Width	Height	Hinge width
GSC 97588	VIM	43	74	?10	70
GSC 97589	CON	?50	67	+16	60
GSC 97591	DOR	?50	80	?8	?70

Comparisons. Only two species have been assigned to *Domokhotia,* both from the Late Carboniferous (?"Kashmirian") Natalin Horizon of the Verchoyan Mountains. The type species, *D. laticostata* Abramov and Grigor'yeva (1983, p. 131, Pl. 27, figs. 7–14; Textfig. 49), is smaller than the Yukon material, with a rounded outline; its sulcus is narrower and plicae are less frequently costate. *Domokhotia varankini* (Abramov) (Abramov and Grigor'yeva, 1983, p. 132, Pl. 28, figs. 1–6; Pl. 29, figs. 1, 2) is about the size and shape of the Yukon species, but differs in its higher triangular interarea, less prominent plicae, and more extended, narrower umbo.

Occurrence. Ey zone, Tastubian.

Subfamily CHORISTITINAE Waterhouse, 1968

Genus *Larispirifer* Enokjan and Poletayev, 1986

Type species. Choristites jigulensis riphaeicus Einor (Aleksandrov and Einor *in* Einor, 1979).

Diagnosis. Broad-ribbed Choristitinae with denticulate hinge line and large, trapezoidal interarea; hinge line usually narrower than maximum width. Dental plates and adminicula strongly thickened posteriorly, widely spaced, fused together through prismatic layers in some species; adminicula slightly diverging from dental plates, anteriorly well spaced and subparallel, usually up to twice as long as dental plates; ovarian impressions distinct on posterolateral floors.

Discussion. This diagnosis is elaborated from that of Poletayev (1986, p. 61) based on present material. Figure 48 illustrates internal differences between type species of three choristitid genera: *Choristites* Fischer de Waldheim, 1853, *Larispirifer*, and *Purdonella* Reed, 1944.

Barchatova (1970) recognized four species groups of *Choristites* on the basis of shell shape and coarseness of costae. Her last group, typified by *Choristites jigulensis* (Stuckenberg) seems to correspond to *Larispirifer*. This group was distinguished from other groups of *Choristites* in having a large size, subquadrate or slightly transverse outline, and low, broad plicae (Barchatova, 1970). Having sectioned *Choristites jigulensis riphaeicus* Einor, Poletayev (1986) discovered that this broad-ribbed choristitid species also differed internally from typical *Choristites* (*s. s.*) in that the adminicula were well spaced and diverged forward, and were approximately twice as long as the dental plates (Fig. 48C). In *Choristites mosquensis* (Fischer de Waldheim) (see Fig. 48A), the type species of *Choristites*, the adminicula are usually close-spaced and about five times as long as the dental plates. In addition, ovarian impressions also differ

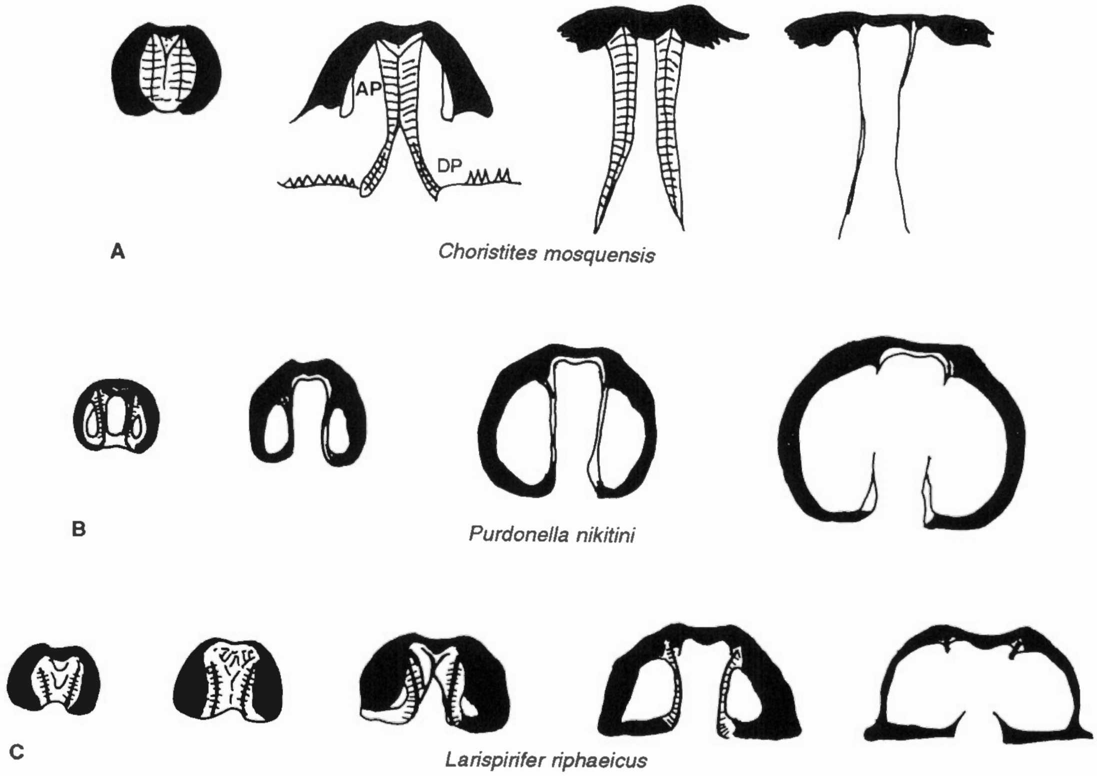


Figure 48. *Comparison of transverse serial sections of ventral valve between* ***Choristites mosquensis*** *(Fischer de Waldheim) (redrawn from Ivanova, 1960, Fig. 363, x2),* ***Purdonella nikitini*** *(Chernyshev) (redrawn from Poletayev, 1984, Fig. 1, x1), and* ***Larispirifer riphaeicus*** *(Einor) (redrawn from Poletayev, 1986, Fig. 5A, x1). AP, adminicular plate; DP, dental plate.*

between the two genera. These are mainly concentrated on the posterolateral portions of the ventral valve floor in *Larisipirifer*, whereas in typical *Choristites* they occupy a small area surrounding the muscle field. The ventral internal characteristics of *Larisipirifer* are similar in varying degrees to those of *Purdonella*, from which *Larispirifer* can be distinguished by other features, including a wider hinge line, a wide, trapezoidal interarea, and broader costae.

Ozaki (1931, p. 68) proposed *Neomunella* for *N. chaoi* Ozaki on the grounds that it has a hinge line wider than in *Purdonella* but narrower than in *Choristites*, and apically unfused, broadly diverging adminicula. Ivanova (1960) and Pitrat (1965) placed *Neomunella* in synonymy with *Choristites*. However, if we accept the criteria recognized by Poletayev (1984, 1986) in distinguishing homeomorphic forms of choristitid shells, *Neomunella* seems to be distinguishable from *Larispirifer*, *Choristites*, and *Purdonella* by its unfused, well separated, and broadly divergent adminicula.

Parachoristites Barchatova (1970, p. 145), as revised by Poletayev (1986), differs from *Larispirifer* in having an alate hinge line and more widely spread ovarian impressions on the posterior floor of the ventral valve.

Poletayev (1986) classed *Larispirifer* with the Spiriferinae, but this was not supported by his analysis of both external and internal characteristics of choristitid genera. It seems more logical to link this genus with *Choristites* rather than with *Spirifer* Sowerby, 1816. The latter, as discussed by Archbold and Thomas (1984b), has finer, more branching costae. Internally, *Spirifer* never has adminicula comparable either in length or in other details to those of *Larispirifer*, as clearly demonstrated by Poletayev (1986, Fig. 2).

Larispirifer ettrainensis n. sp.

Plate 26, figures 15–20; Plate 27, figures 1–7;
Figure 49

Etymology. Named for Ettrain Creek, northern Ogilvie Mountains.

Holotype. GSC 97596 from GSC loc. 53712, section 116H-1A; Ey zone, Jungle Creek Formation (Pl. 26, figs. 17, 18; Pl. 27, fig. 5).

Diagnosis. Large, subrounded shell with hinge width/shell width ratio at 0.85 to 0.9; sulcus shallow and broad; fold low and well rounded; ventral costae weakly branching, dorsal costae mostly simple.

Material.

Locality	Ventral	Conjoined
GSC loc. 53712	2	
GSC loc. 53954		2
GSC loc. 57053	1	
GSC loc. 57266		1
JBW loc. 9	1	
JBW loc. 11	1	
JBW loc. 56	1	
JBW loc. 57	3	
JBW loc. 88	1(im)	
JBW loc. 113	2, 1(em)	
JBW loc. 537	1(em)	

Description. External. Shell large, moderately to strongly convex, rounded to subrounded in outline, widest at midlength or just behind.

Ventral valve strongly convex, most inflated at midlength to posterior third; umbo prominent, moderately extended and incurved; umbonal angle 94°; umbonal slopes straight or gently swollen in profile, well rounded in section, high and steep; lateral and anterior margins well rounded; hinge line 85% to 90% of maximum width of shell; cardinal extremities broadly rounded, approximately at 115°; interarea well defined by sharp posterior margins and hinge line (Pl. 26, fig. 17), trapezoidal in shape, apsacline, marked by vertical striae; hinge denticulate in some specimens; delthyrium proportionately large, delthyrial angle 48, open, possibly closed apically by small umbonal thickening; sulcus prominent (Pl. 27, fig. 1), commencing from near umbo, initially narrow, sulcal angle close to 20°, not clearly separated from flanks by elevated costae, anteriorly rather broad and shallow, floor usually carrying two or three costae with or without median costa; flanks bounding sulcus broad and gently convex in transverse section, each carrying eight to 10 low, broad, well rounded plicae, 1.5 to 2 mm in diameter, separated by shallow, narrow interspaces, becoming weak or fading away toward cardinal extremities, inner one or two pairs bifurcated once within approximately 5 mm of curvature length from umbo (Pl. 27, figs. 1, 5), and again at midlength, distal pairs branching (bifurcated, occasionally trifurcated) at varying distances from umbo; costae slightly differentiated.

Dorsal valve slightly less convex than opposite valve, median portion broadly and moderately raised to form well rounded fold (Pl. 26, fig. 15); plicae low and wide, 1.5 to 2 mm across, simple except for inner two pairs, which bifurcate or trifurcate; fold has four costae of equal strength.

Micro-ornament of fine, poorly developed concentric lamellae.

Internal. Adminicula little curved from dental plates, widely spaced, posterior half buried and fused together by shell thickening (Pl. 28, figs. 3, 5, 6; Fig. 49), subparallel, approximately twice as long as dental plates, anterior ends curving as low ridges around posterior edge of muscle field (Pl. 27, fig. 6); muscle field elongate-oval in shape, well depressed

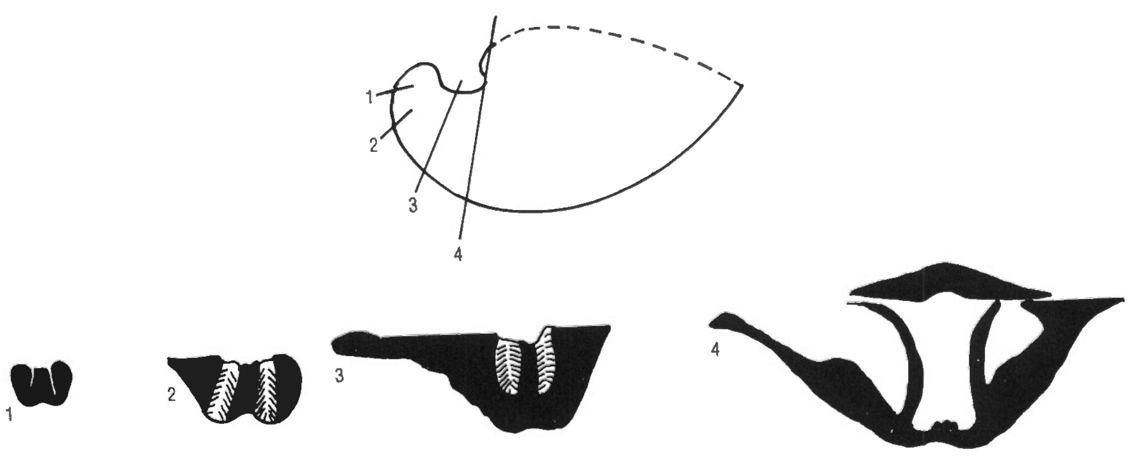


Figure 49. *Transverse serial sections of **Larispirifer ettrainensis** n. sp. (x1).*

below valve floor; adductor ridge at median location, narrow, slightly elevated, with few vertical striae, bisected by thin myophragm; diductor scars relatively large, vertically striated; posterolateral floor covered with well defined ovarian impressions (Pl. 27, figs. 4, 6), two or three in 1 mm, slightly extending forward near to muscle field.

Dimensions (in mm).

Specimen (Ventral valves)	Length	Width	Height	Hinge width
GSC 97596	55	+80	23	70
GSC 97597	65	+70	25	64

Comparisons. The new species is close to the type species *Larispirifer riphaeicus* (Einor) (Aleksandrov and Einor *in* Einor, 1979, p. 83, Pl. 32, fig. 3; Pl. 33, fig. 2) from the Upper Carboniferous of Bashkiria. The holotype of the Russian species is subelliptical in outline, with hinge line/shell width ratio at 0.73, as compared to the same ratio of 0.88 in the holotype of the new species. Another shell of *L. riphaeicus* (op. cit., Pl. 33, fig. 2) appears to have a wider hinge line as in the new species, but differs in possessing a broader umbo, well developed concentric lamellae, and probably a higher fold.

Choristites jigulensis Stuckenberg (1905, Pl. 6, figs. 4–6; Pl. 8, fig. 1) from the Upper Carboniferous of Samara Bend of the Russian Platform, also recorded by Barchatova (1970) from the Asselian Timan beds of northern Timan, is also a large broad-ribbed shell, but it is distinguished from the Yukon species by having a deeper sulcus and finer costae. Neither Stuckenberg nor Barchatova provided internal details for *C. jigulensis*, so its generic position is uncertain.

Occurrence. Ey, Eog, and Ej zones, Sakmarian to Early Artinskian.

Spiriferacea gen. et sp. indet.

Plate 26, figures 1, 2

Remarks. A single ventral valve was found at GSC loc. 53954. It is rather small, apparently elongate in shape, strongly convex, most inflated over posterior third; umbo attenuated posteriorly, strongly extended; umbonal angle close to 40°; umbonal slopes gently concave; hinge about half shell width at midlength; cardinal extremities very broadly rounded, merging well with lateral margins; sulcus narrow, groove-like, smooth; flanks elongate, broadly rounded, moderately steep toward lateral margins. Twelve pairs of costae present over flanks, low and rounded, with innermost pair bifurcated and other pairs simple, separated by fine interspaces. Micro-ornament not known; interior not revealed.

The specimen is distinguished by its small size, typically elongate-ovate outline, narrow, groove-like sulcus, and numerous small, low, rounded costae.

Superfamily RETICULARIACEA
Waagen, 1883

Family INGELARELLIDAE Campbell, 1959

Subfamily INGELARELLINAE Campbell, 1959

Genus *Tomiopsis* Benedictova, 1956

1956 (April) *Tomiopsis* (not Cope, 1893) Benedictova, p. 169.
1956 (December) *Ambikella* Sahni and Srivastava, p. 207.
1959 *Ingelarella* Campbell, p. 340.

Type species. (OD) *Brachythyris kumpani* Yanischevsky, 1935.

Discussion. There has been much debate recently on whether or not to recognize three Ingelarellidae genera: *Tomiopsis*, *Ambikella*, and *Ingelarella*. Waterhouse (1987a) and Clarke (1987) referred these genera to synonymy, in which *Tomiopsis* has priority. Archbold and Thomas (1986) argued for the validity of *Ingelarella* on the grounds that some hypotypes of *I. angulata* Campbell (type species of the genus) have "linear grooves with small C-shaped protuberances at the posterior end of the grooves." Waterhouse (1986) stressed that the holotype of *I. angulata* did not have C-shaped spines, but he also recognized the significance of the presence of C-shaped spines in some species of *Ingelarella* and grouped these forms into a new genus named *Homevalaria*, based on *Ingelarella ovata* Campbell.

Martiniopsis Waagen, 1883 is probably best restricted to warm-water forms lacking prominent sulcus, fold, and lateral plicae, as pointed out by Campbell (1959) and Clarke (1987). Most of *Martiniopsis* species occur in the warm waters of lower paleolatitudes.

Tomiopsis ovulum Waterhouse, 1971a

Plate 28, figures 6–8

1971a *Tomiopsis ovulum* Waterhouse, p. 73, Pl. 15, figs. 1–15; Pl. 16, figs. 1–15; Pl. 17, figs. 3, 6–8, 11, 12.

1971 *Tomiopsis ovulum* Waterhouse; Waterhouse *in* Bamber and Waterhouse, Pl. 12, figs. 14, 15.

Holotype. GSC 24802 from the Asselian Kindle Formation of northeastern British Columbia, figured by Waterhouse (1971a, Pl. 15, figs. 9, 13, 15).

Diagnosis. Moderately large, transversely ovate shell; sulcus and fold weak or not developed; lateral plicae absent or very weak; umbo low, broad; umbonal slopes evenly concave.

Material. One internal mould of conjoined shell from GSC loc. 53703 and one ventral external mould from GSC loc. 53818.

Description. External. Moderately large, transversely ovate in outline, slightly wider than long; moderately biconvex; widest along midlength.

Ventral umbo prominent, broad and incurved; umbonal slopes gently and evenly concave in profile; umbonal angle 100; interarea small (Pl. 28, fig. 8), low, wide, transversely striated; delthyrium open with delthyrial angle close to 80°; cardinal extremities broadly rounded at 130°; sulcus absent from posterior half of shell, anteriorly not known due to poor preservation; no lateral plicae.

Dorsal valve equally convex; interarea narrow and low, with small open notothyrium.

Internal. Teeth supported by thin, low dental plates, which are in turn supported by equally thin but prominent adminicula (Pl. 28, fig. 7); adminicula nearly twice as long as dental plates, diverging anteriorly by about 13°; umbonal thickening moderately developed; muscle field outlined by adminicula, small, vertically striated (Pl. 28, fig. 7). Inner socket ridges short and stout, supported by long, thin tabellae that diverge forward (Pl. 28, fig. 8); median ridge and adductor scars obscure.

Comparisons. Tomiopsis ovulum was described by Waterhouse (1971a); shell morphology and internal structures varied considerably among nearly 500 specimens. Most specimens exhibited a weakly to moderately developed sulcus and fold, and low lateral plicae. The conjoined shell described above appears to be identical to specimens of *T. ovulum* that lack a prominent sulcus and lateral plicae.

Waterhouse (1971a) compared the species with related forms. Comparisons with two newly described species from Western Australia may be added. *Tomiopsis notoplicatus* Archbold and Thomas (1986, p. 586, Figs. 3.1–3.11), from the Sakmarian Lyons Group to the lower part of the Callytharra Formation of Carnarvon Basin, is moderately close in overall appearance, but differs in being generally smaller and having more prominent plicae on the flanks. *Tomiopsis rarus* Archbold and Thomas (1986, p. 590, Figs. 4.1–4.5), from the Aktastinian High Cliff Sandstone of Perth Basin, is about the same size as the Yukon material and has weak plicae, like some shells of *I. ovulum* described by Waterhouse (1971a), but differs in possessing a prominent sulcus and fold.

Occurrence. Tomiopsis ovulum is known from the Eta, Ey, and Ej zones of the Jungle Creek Formation, of probably Late Asselian (Krumaian) to Early Artinskian (Aktastinian) age. Elsewhere the species is known only from its type locality — the Asselian Kindle Formation of northeastern British Columbia.

Family ELYTHIDAE Frederiks, 1924

Genus *Spirelytha* Frederiks, 1924

Type species. (OD) *Spirelytha parvlovae* Archbold and Thomas, 1984a.

Diagnosis. See Archbold and Thomas (1984a, p. 313).

Discussion. Spirelytha is externally very close to *Torynifer* Hall and Clarke, 1895 (senior synonym of *Stepanoviina* Zavodovskiy, 1968, according to Pavlova, 1969) and *Kitakamithyris* Minato, 1951. Archbold and Thomas (1984a) noted the significance of the presence of a delicate dorsal myophragm and of the absence of radial vascular markings in Permian *Spirelytha*. Klets (1987) indicated that the vascular system in *Spirelytha* was represented by "netlike" markings, in contrast to the radial pattern of *Kitakamithyris* and *Torynifer*.

Spirelytha sp.

Plate 28, figures 9–12

Material. One internal mould with valves conjoined from JBW loc. 505, and three internal moulds with valves conjoined from JBW loc. 545.

Description. External. Shell large for genus, subrounded to transversely ovate (Pl. 28, fig. 11), moderately convex; widest at posterior third of shell length; ventral umbo slightly extended with obtuse umbonal angle; intearea low, wide; cardinal extremities well rounded with lateral margins; anterior commissure rectimarginate or slightly deflected dorsally; no prominent sulcus or fold; concentric lamellae weakly preserved on internal moulds.

Internal. Dental plates high, supported by low and short adminicula (Pl. 28, fig. 9); muscle field large, elongate-oval in shape, bisected by low, ventral median septum (Pl. 28, fig. 11).

Cardinal process consists of two small, rounded and separate lobes (Pl. 28, fig. 9), each deeply pitted centrally; sockets small and narrow; inner socket ridges not supported by tabellae; myophragm obscure.

Comparisons. There are few species of this brachiopod group that compare in size and shape with the large Yukon shells, and detailed comparisons are hindered by the incomplete, poor preservation of the Yukon material. *Spirelytha kislakovi* Klets (1987, p. 33, Pl. 4, figs. 1-7), from the Lower Permian Khanalichan Suite of the southern Verchoyan Mountains, is close in overall appearance, but it has tabellae. *Spirelytha magna* Miloradovich (1936a, Pl. 2, fig. 3; Pl. 4, fig. 10), from a Lower Permian exposure in Novaya Zemlya and the Asselian-Sakmarian Olichan Suite of the southern Verchoyan Mountains (Abramov and Grigor'yeva, 1988), is more rounded than the Yukon species, and has strongly concave umbonal slopes.

Occurrence. Ey zone, Tastubian.

Spirelytha fredericksi Archbold and Thomas, 1984a

Plate 28, figures 13-21

1984a *Spirelytha fredericksi* Archbold and Thomas, p. 314, Figs. 1A-R, 2A-K.

1987 *Spirelytha fredericksi* Archbold and Thomas; Klets, p. 34, Pl. 4, figs. 8-12.

Holotype. CPC 19931 figured by Archbold and Thomas (1984a, Figs. 1A-C) from the late Sakmarian (Sterlitamakian) Callythara Formation, Carnarvon Basin, Western Australia.

Diagnosis. Medium to large *Spirelytha*, with broad, distinct, shallow sulcus, and low wide fold. Adminicula and ventral median septum prominent. No tabellae; dorsal median septum fine. Anterior commissure uniplicate.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53720			1
JBW loc. 24	1	1(em)	
JBW loc. 89	1(im)		
JBW loc. 558			1(em), 1(im)

Description. External. Shell medium-sized, subrounded, slightly wider than long; widest along midlength; moderately biconvex; anterior commissure broadly uniplicate.

Ventral valve evenly inflated; umbo short, slightly incurved, umbonal angle 110°; umbonal slopes straight or slightly concave; interarea low, broadly triangular in shape; delthyrium distinct, delthyrial plate obscure, delthyrial angle about 55°; cardinal extremities bluntly rounded at about 100°; sulcus commencing from midlength, generally shallow and broad, indistinct in some specimens (Pl. 28, figs. 15, 17).

Dorsal valve equally or slightly less convex; no distinct fold except for broad median swelling in some specimens (Pl. 28, fig. 20). Shell ornament of about evenly spaced, flatly rounded concentric bands, each bearing single row of biramous spines along anterior edge, one or two in 1 mm (Pl. 28, figs. 19, 21).

Internal. Dental plates thin, supported by equally thin, long adminicula which diverge forward at about 40° (Pl. 28, figs. 13, 15); median septum thin and long, extending over posterior half of shell length, at least twice as long as dental plates; muscle field outlined posteriorly by adminicular ridges, smooth, weakly impressed and faintly striated anterior; posterolateral floor irregularly pitted.

Cardinal process small, subrounded, vertically striated by 16 thin, blade-shaped ridges (Pl. 28, fig. 16); sockets small and narrow, no tabellae; adductor scars poorly impressed, anteriorly delimited by pair of vertical ridges, bisected by thin, discontinuous myophragm (Pl. 28, fig. 16).

Dimensions (in mm).

Specimen	Valve	Length	Width	Height	Hinge width
GSC 97605	CON	23	29	+8	22
GSC 97608	DOR	+23	35	—	30
GSC 97609	CON	23	30	+8	18
GSC 97610	VIM	17	22	8	16

Comparisons. Spirelytha fredericksi Archbold and Thomas, 1984a from the Callythara Formation of Western Australia appears to be variable in size, development of sulcus and fold, length of ventral median septum relative to the length of adminicula, and umbonal thickening. Examination of the type material of the Western Australian species at the Geology Department of the University of Melbourne has shown that in smaller specimens (Archbold and Thomas, 1984a, Figs. 1O, P, 2C–F) the sulcus is weakly developed, the umbonal slopes straight or gently convex, the ventral median septum much longer than adminicula, and the umbonal thickening weakly developed. Larger specimens (Archbold and Thomas, 1984a, Figs. 1A–M) show more concave umbonal slopes, longer and better-defined sulcus, shorter, ventral median septum with respect to adminicula, and conspicuously thickened umbo with a small delthyrial plate. The Yukon material is strikingly similar to those small, probably immature, specimens of the Western Australian species. This implies that the present material is perhaps an immature representative of *S. fredericksi*. The specimens figured as *S. fredericksi* by Klets (1987), from the Sakmarian Sigian Suite of the southern Verchoyan Mountains, are also smaller than mature Western Australian specimens and appear to be identical to the Yukon material.

Liu and Waterhouse (1985, p. 38, Pl. 11, fig. 8; Pl. 12, figs. 2, 4) referred to *Phricodothyris lineata* Prendergast (now *Spirelytha fredericksi*) and noted that the umbonal slopes were more concave in their "*Kitakamithyris*" *ovata* from the Sakmarian Houtoumiao Formation of Inner Mongolia, northeastern China. Like the Yukon material and some small Western Australian specimens, the Chinese species is medium-sized and has a thin dorsal myophragm and a pair of thin ridges delimiting dorsal adductors. However, the ventral median septum of the Chinese species was said to extend only for the posterior quarter of the shell length — appearing to be much shorter than any Western Australian specimens or any Yukon material. The relative length of the ventral median septum is variable in *S. fredericksi*, as indicated above, so the Chinese species may prove to have a longer ventral median septum in larger specimens.

Occurrence. In northern Yukon Territory, *S. fredericksi* is confined to the Ey zone, of Early Sakmarian (Tastubian) age. This species was originally described from the Sterlitamakian fauna of the Callythara Formation in Carnarvon Basin, Western Australia. The same species has also been discovered from the Sakmarian Sigian Suite of the southern Verchoyan Mountains in northeastern Siberia.

Superfamily MARTINIACEA Waagen, 1883

Family BRACHYTHYRIDIDAE Frederiks, 1924

Genus *Brachythyris* M'Coy, 1884

Type species. (OD) *Spirifer ovalis* Philips, 1836.

Brachythyris sp.

Plate 29, figures 1–4

Material. One ventral valve from GSC loc. 57052; one ventral valve from JBW loc. 113.

Description. Medium in size, moderately convex, widest along midlength; umbo prominent, narrow, strongly extended; beak moderately incurved over apex of delthyrium; umbonal angle 80°, umbonal slopes gently concave, well rounded in section; cardinal extremities broadly emerging with lateral margins; interarea small, triangular, moderately concave; delthyrium filled with sediments, delthyrial angle about 55°; sulcus commencing at 5 mm from umbo with sulcal angle close to 25°, generally shallow and narrow, carrying two low, well rounded costae; flanks moderately spreading and sloping laterally, each bearing six broad and simple costae. No interior recorded.

Comparisons. The two ventral valves are very close to specimens commonly referred to as *Brachythyris ufensis* (Chernyshev, Pl. 38, figs. 6–8; not Pl. 13, figs. 5 and Pl. 39, figs. 1–3) from the Sakmarian beds of the southern Urals, but appear to differ in possessing narrower, lower costae.

Occurrence. Ey and Ej zones, of Sakmarian to Early Artinskian (Aktastinian) age.

Brachythyridid or Syringothyridid gen. et sp. indet.

Plate 23, figure 10

Remarks. The one incompletely preserved dorsal internal mould from JBW loc. 113 is rather large in size, with low, but well defined, smooth fold and nine broad, simple, lateral costae.

Family MARTINIIDAE Waagen, 1883

Genus *Tiramnia* Grunt, 1977

Type species. (OD) *Martinia uralica* Chernyshev, 1902.

Diagnosis. Martiniid shells with small, well defined, deeply depressed, and rhomb-shaped muscle field bisected by strong median groove, which may extend beyond midlength of shell; lateral pallial markings few and prominent, not branching. Shell micro-ornament not known.

Discussion. Waterhouse (1981) discussed the potential difficulties in distinguishing three allied genera: *Martinia* M'Coy, 1844 with type species *M. glabra* (Sowerby), *Spinomartinia* Waterhouse, 1968a with type species *S. spinosa* Waterhouse, and *Tiramnia* Grunt, 1977. The minute surface spinules initially used to characterize *Spinomartinia* may have been obscured through preservation, or even lost. Thus, internal structures, especially the nature of the ventral muscle field and pallial markings, may be more applicable taxonomically. Comparison of shape, size, and location of ventral muscle field, and the pattern of ventral pallial markings between the type species of the three genera, is shown in Figure 50. *Tiramnia* appears to be distinguished from the other two by its small, deeply depressed, narrow-elongate, and apically placed muscle field that is bisected by a long, prominent median groove, in conjunction with the few, prominent simple lateral pallial grooves. Its micro-ornament is still to be clarified.

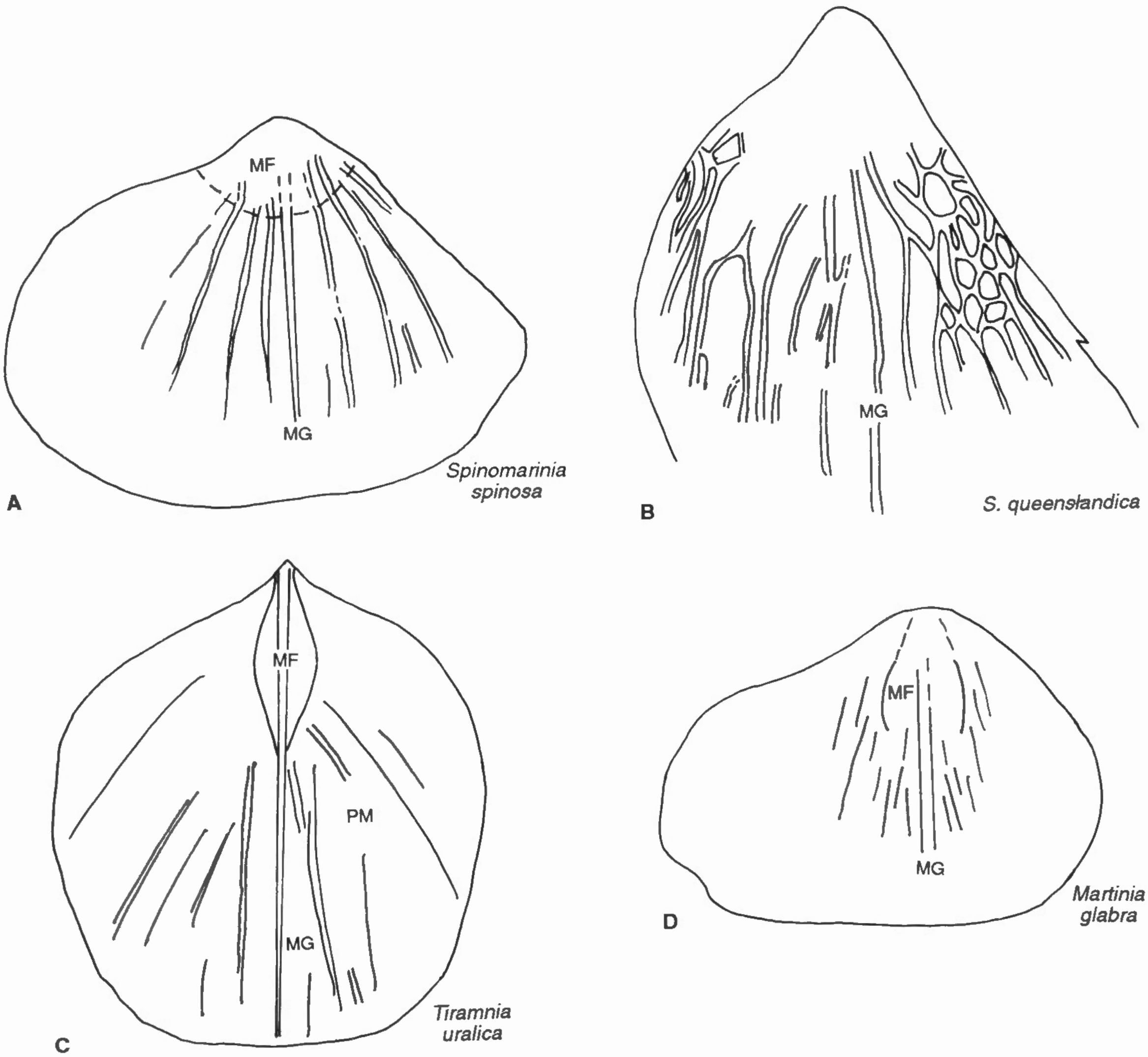


*Figure 50. Comparison of ventral muscle field and patterns of ventral pallial markings (all approx. x1). A, **Spinomartinia spinosa** Waterhouse (redrawn from Waterhouse, 1968, Pl. 9, fig. 7); B, **Spinomartinia queenslandica** Waterhouse (redrawn from Armstrong, 1970, Fig. 1D, then figured as **Martinia** sp.); C, **Tiramnia uralica** (Chernyshev) (redrawn from Grunt and Dmitrev, 1973, Fig. 42); D, **Martinia glabra** (Sowerby) from England (redrawn from Waterhouse, 1981, Pl. 30, fig. 3). MF, muscle field; MG, median groove; PM, pallial markings.*

Tiramnia canadica n. sp.

Plate 29, figures 5-19

1971 *Martinia* sp. Waterhouse *in* Bamber and Waterhouse, Pl. 16, figs. 11, 12.

Etymology. For Canada.

Holotype. GSC 97619 from JBW loc. 109, Ettrain Creek; Ey zone, Jungle Creek Formation (Pl. 29, fig. 5).

Diagnosis. Medium-sized to moderately large *Tiramnia* with strongly convex ventral valve and moderately convex dorsal valve; ventral umbo strongly incurved; maximum width at midlength; sulcus weakly developed over anterior third of ventral valve; anterior commissure rectimarginate to gently deflected dorsally.

Material.

Locality	Ventral	Dorsal	Conjoined
GSC loc. 53720	2		
GSC loc. 53947	17, 1(im)	7	3
GSC loc. 53951	1		
GSC loc. 53952	1		
GSC loc. 57053	1		
GSC loc. 57141	1		
GSC loc. 57255	4		
GSC loc. 57266	3, 1(im)	2	
JBW loc. 24	2, 1(im)		
JBW loc. 56	2		
JBW loc. 109	1		
JBW loc. 113	1, 3(im)		
JBW loc. 508	2	1	

Description. External. Shell medium to moderately large, slightly wider than long, subrounded in outline; widest at midlength (Pl. 29, fig. 5).

Ventral valve strongly convex (Pl. 29, fig. 8), most inflated over midlength or slightly behind it; umbo prominent, strongly extended and discriminated from rest of valve with beak strongly incurved over apex of delthyrium; umbonal angle between 80° and 90°; umbonal slopes gently and evenly concave in outline, well rounded in section; hinge line usually two thirds of shell width; cardinal extremities merging with lateral margins; lateral and anterior margins well rounded; palintrope small, triangular, strongly and evenly concave; delthyrium open, delthyrial angle about 50°; sulcus absent in some specimens, very weakly defined and anteriorly placed in others, especially in large specimens (Pl. 29, figs. 5, 12); anterior commissure gently deflected dorsally (Pl. 29, fig. 12).

Dorsal valve gently to moderately convex, more arched in transverse direction than longitudinal; umbo blunt; fold either not developed or forming low median swelling restricted to anterior quarter of valve length.

Shell smooth except for rather fine concentric growth lines, best defined on posterolateral slopes of ventral valve (Pl. 29, fig. 18).

Internal. Teeth small, indistinct, not supported by prominent dental plates (Pl. 29, fig. 8); muscle field moderately large (Pl. 29, figs. 14, 15), well formed, deeply depressed just under apex of umbo, rhomboid in shape, approximately 6 mm wide and 10 mm long; adductor field moderately differentiated, located in broad, prominent median groove, which is faintly striated vertically; diductor scars less depressed, marked by oblique striae; median groove continuing forward well into anterior third of shell length, near anterior margin in some specimens, gradually tapering anteriorly; three to five pallial grooves dispersed on each side of median groove, thin but prominent, simple, most commencing slightly in front of muscle field, slightly convex toward lateral margins, with few (one or two) additional short grooves anteriorly intercalated.

Dimensions (in mm).

Specimen (Ventral valves)	Length	Width	Height
GSC 97617	26	30	13
GSC 97618	35	38	15
GSC 97622	23	25	11
GSC 97623	12.5	15	5

Comparisons. The general size and shape, and the weak sulcus in some specimens, are similar to several species. *Tiramnia yakutica* Solomina (1978, p. 121, Pl. 11, figs. 12-15), from the Upper Carboniferous Khaldan Suite of Verchoyan Mountains, resembles the new species in size and in the indistinct sulcus in some larger specimens, but differs in being subtriangular in shape, with the maximum width placed in front of midlength, in being less convex in the ventral valve, and in having a slightly incurved ventral umbo. *Tiramnia semiglobosa* (Chernyshev, 1902, p. 564, Pl. 17, figs. 6-10, 12, 13) from the Sakmarian Stage of the Urals is similar in size, in outline, and in the ill defined anterior sulcus, but is distinguished by its slightly elongate outline and shorter, broader umbo. *Tiramnia uralica* (Chernyshev, 1902, p. 566, Pl. 18, figs. 1–4), from the Sakmarian Stage of the Urals, approaches the Yukon species in its overall appearance, especially the strongly incurved umbo and gently inflated dorsal valve, but differs in its large size, elongate outline, and strongly convex ventral valve. Grunt and Dmitriev (1973, p. 142, Pl. 11, figs. 2–5; Pl. 15, fig. 3; Textfigs. 42, 43) recorded *T. uralica* from the Sakmarian Bazardar Suite of southeastern Pamir. The Pamiran specimens are less elongate and slightly smaller than types of *T. uralica* from the Urals, and thus more similar to the Yukon material, but they appear to have a more inflated ventral valve and a smaller muscle field.

Occurrence. Ey, Eog, and Ej zones, Sakmarian to Early Artinskian.

Order SPIRIFERINIDA Cooper and Grant, 1976

Suborder SPIRIFERINIDINA Ivanova, 1972

Superfamily SPIRIFERINACEA Davidson, 1884

Family CRENISPIRIFERIDAE Cooper and Grant, 1976

Genus *Spiriferellina* Frederiks, 1924

Type species. (OD) *Terebratulites cristatus* Schlotheim, 1816.

Spiriferellina? sp.

Plate 29, figures 20–23

Material. One dorsal external mould from JBW loc. 89; two ventral external moulds, one dorsal external mould, and one dorsal internal mould from JBW loc. 559.

Description. External. Shell small to medium, up to 20 mm wide and 15 mm long; slightly transverse; cardinal extremities obtusely rounded; maximum width at hinge line; sulcus and fold distinct, nonplicate; sulcus delimited by high lateral plicae, deep, floor angular; fold with angular crest, as wide as or slightly wider than lateral plicae; three pairs of high, narrowly rounded plicae on flanks of both valves, diminishing in size toward cardinal extremities, separated by equally wide, narrowly rounded interspaces; concentric lamellae distinct, consisting of fine growth increments, approximately three or four in 1 mm; surface pustules coarse and prominent (Pl. 29, fig. 23), rounded and hollow inside, mainly concentrated on slopes of plicae where there are three or four in 1 mm, less numerous over crests of plicae and floors of interspaces and sulcus.

Internal. Ventral interior not known. Cardinal process large (Pl. 29, fig. 22), knob-like; sockets narrow, triangular, with wide anterior ends, bordered at inner side by prominently high inner socket ridges joined by narrow platform-like crural plates; muscle field obscure; endopunctae dense, eight to 10 in 1 mm.

Comparisons. This species is distinguished by its weakly transverse outline and three pairs of high, narrowly rounded plicae. No species are known to be particularly comparable.

Occurrence. Ey zone, Tastubian.

Order TEREBRATULIDA Waagen, 1883

Superfamily DIELASMATACEA Schuchert, 1913

Family DIELASMATIDAE Schuchert, 1913

Subfamily DIELASMATINAE Schuchert, 1913

Genus *Dielasma* King, 1859

Type species. (OD) *Terebratulites elongatum* Schlotheim, 1816.

Dielasma rectimarginatum Cooper, 1957

Plate 29, figures 24–30; Figure 51

1957 *Dielasma rectimarginatum* Cooper, p. 67, Pl. 12C, figs. 27–31.

Holotype. USNM 125414 figured by Cooper (1957, Pl. 12C, figs. 27–31) from the Sakmarian to Kungurian Coyote Butte Formation of central Oregon.

Diagnosis. Moderately large shell with maximum width placed at midlength; dorsal valve moderately convex; no sulcus or fold, anterior commissure rectimarginate.

Material. One conjoined shell, two ventral valves, one ventral internal mould, and one dorsal internal mould from GSC loc. 53999.

Description. External. Shell of average size for genus, up to 27 mm wide, 40 mm long, and 8 mm high, length/width ratio 1.78; moderately convex, most inflated over midlength, ventral valve slightly more convex than dorsal valve; widest along midlength; anterolateral margins broadly rounded.

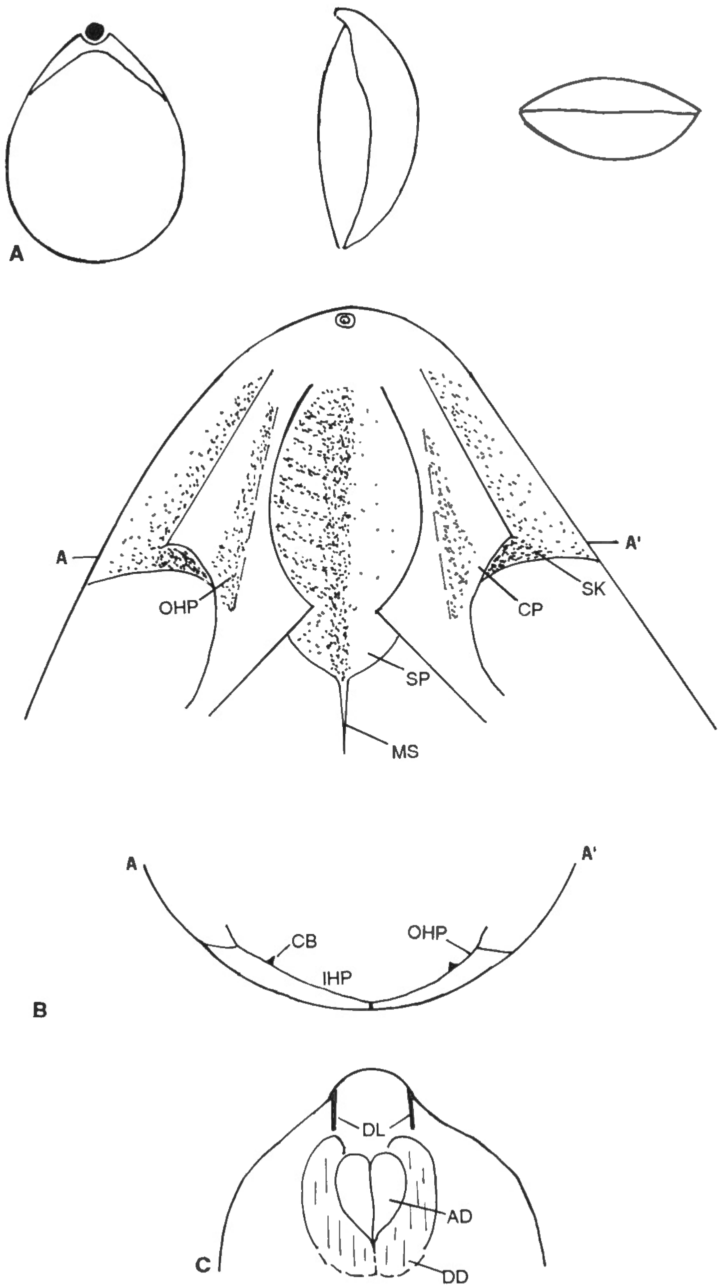


Figure 51. ***Dielasma rectimarginatum*** *Cooper. A, showing dorsal, lateral, and anterior views of a conjoined shell (GSC 97634, x1); B, reconstruction of cardinalia and transverse section based on GSC 97634 (approx. x5), showing dorsal plates; C, ventral internal mould (GSC 97635, x2.5), showing dental lamellae and muscle scars. AD, adductor; DD, diductor; CB, crural base; CP, crural plate; DL, dental lamellae; IHP, inner hinge plate; MS, median septum; OHP, outer hinge plate; SK, socket; SP, spondylium.*

Ventral umbo prominent, suberect, apical angle 100°, truncated by circular foramen, 4 mm across and slightly labiate (Fig. 51A); umbonal ridges narrowly rounded; no distinct sulcus observed except for shallow median depression seen from GSC 97635 (Pl. 29, fig. 27), which may have resulted from crushing; anterior commissure entirely rectimarginate in conjoined specimen (Fig. 51A).

Dorsal valve moderately swollen medianly and well rounded in section (Pl. 29, fig. 29). Surface ornament of indistinct concentric growth lines; punctae 100 to 150 in 1 mm^2 (Pl. 29, fig. 30).

Internal. Dental lamellae prominent, 0.3 mm in diameter, extending subparallel forward for posterior sixth to seventh of shell length; muscle field impressed (Pl. 29, fig. 27; Fig. 51C), adductor scars medianly located, ovate in shape, bisected by thin myophragm, smooth; large diductor imprints surrounding adductor scars, weakly striated vertically.

Inner socket ridges and crural bases prominent; inner hinge plates meeting posteriorly along middle line of valve floor and meeting anteriorly along very thin, low median ridge, forming sessile, broadly rounded, spoon-shaped brachidium posteriorly (Pl. 29, fig. 25; Fig. 51B), marked inside by anteriorly convex ridges and grooves of adductor scars, extending over posterior fourth to fifth of shell length; median ridge less than 1 mm in diameter, extending forward for 2 to 4 mm beyond brachidium, not reaching midlength.

Comparisons. The Yukon material appears conspecific with *Dielasma rectimarginatum* Cooper, 1957 from the Coyote Butte Formation of central Oregon.

Dielasma rectimarginatum is similar to *D. dubium* Chernyshev (1902, p. 437, Pl. 1, fig. 3), from the probably Sakmarian Stage of Timan, in size and shape, but the Russian species has a strongly sulcate anterior commissure.

Occurrence. Dielasma rectimarginatum is confined to the Eog zone in northern Yukon Territory, of Late Sakmarian (Sterlitamakian) age. Elsewhere, this species is known only from the Sakmarian to Kungurian Coyote Butte Formation of central Oregon.

Dielasma brevicostatum Cooper, 1957

Plate 30, figures 1–12

1957 *Dielasma brevicostatum* Cooper, p. 66, Pl. 12D, figs. 32–41.

Holotype. USNM 125413a figured by Cooper (1957, Pl. 12D, figs. 32–36) from the Coyote Butte Formation of central Oregon.

Diagnosis. Comparatively small, elongate-triangular *Dielasma* with strongly sulcate anterior commissure and prominent ventral median groove; maximum width placed at anterior third of shell length.

Material. Four conjoined specimens and one ventral valve from GSC loc. 53714 and one immature shell from GSC loc. 57053.

Description. External. Shell small to medium-sized, up to 19 mm wide and 20 mm long, elongate-triangular in outline, widest at anterior third of shell length (Pl. 30, fig. 5); anterior commissure prominently uniplicate.

Ventral valve strongly convex longitudinally, anterolateral margins broadly rounded; umbo prominent, long and suberect with apical angle close to 60°; umbonal ridges narrowly rounded; foramen large (Pl. 30, fig. 9), 3 mm across, permothyrid-type, slightly labiate; median groove narrow and prominent (Pl. 30, figs. 6, 8), running full length of ventral valve; sulcus beginning from anterior third of shell length, deepening forward, floor broadly rounded in immature specimens, median grooved in mature shells, moderately indenting dorsal valve; anterior commissure flexed dorsally to accomodate short ventral tongue.

Dorsal valve flatly convex longitudinally, moderately to strongly arched in section due to broad median swelling; no distinct fold.

Internal. Pedicle collar prominent; dental lamellae very thin (Pl. 30, fig. 10), 0.2 to 0.3 mm in diameter; ventral median groove reflected internally as low median ridge running from near umbo to anterior margin in some specimens (Pl. 30, figs. 5, 6); muscle field obscure.

Inner socket ridges meet in centre, on valve floor (Pl. 30, fig. 12); septalium entirely sessile, floor broadly rounded, anterior section V-shaped, extending for posterior third to quarter of shell length, bearing fine ridges of adductor impressions; median ridge absent or poorly defined.

Comparisons. These shells are externally identical to *Dielasma brevicostatum* Cooper, 1957 from the Coyote Butte limestone of central Oregon. The internal details were not known in the Oregon specimens, but are shown in the Yukon material.

Chernyshev (1902, p. 454, Pl. 1, figs. 4, 5) named two specimens, from the Schwagerina Horizon of the Ufa Plateau, *Dielasma curvatum* Chernyshev. His Plate 1, figure 4 shows a ventral internal mould, which is slightly larger and more elongate than *D. brevicostatum*, and has a feeble median ridge rather than a groove. His Plate 1, figure 5 shows a specimen identical to the present species in size, shape, and presence of an anterior sulcus, but its septalium seems broadly V-shaped in section.

Dielasma brevicostatum clearly differs from *D. rectimarginatum* Cooper in its well developed sulcus, triangular outline, uniplicate anterior commissure, prominent ventral median groove, and narrower umbo.

Occurrence. Dielasma brevicostatum is restricted to the Ey zone in northern Yukon Territory, of Early Sakmarian (Tastubian) age. Outside the Yukon Territory, this species is known only from its type locality in central Oregon, from the Sakmarian to Kungurian Coyote Butte Formation.

Phylum MOLLUSCA, Linne, 1758

Class BIVALVIA Linne, 1758

Order OSTREOIDA Ferussac, 1822

Suborder PECTININA Waller, 1978

Superfamily AVICULOPECTINACEA Meek and Hayden, 1864

Family DELTOPECTINIDAE Dickins, 1957

Genus *Deltopecten* Etheridge Jr., 1892

Type species. (OD) *Pecten illawarrensis* Morris, 1845.

Deltopecten? sp.

Plate 30, figure 13

Remarks. A single internal mould of a right valve from JBW loc. 537 is similar to *Deltopecten* or an allied genus. It is moderately large and convex, slightly higher than long; surface plicae mirrored on internal mould, approximately 10 in total, strong, separated by equally wide and broadly rounded interspaces; auricular areas not costate but with prominent growth lines; byssal notch distinct; ligament area not preserved.

Family AVICULOPECTINIDAE Meek and Hayden, 1864

Subfamily AVICULOPECTININAE Meek and Hayden, 1864

Genus *Acanthopecten* Girty, 1903

Type species. (OD) *Pecten carboniferus* Stevens, 1858.

Acanthopecten licharewi (Frederiks, 1915b)

Plate 30, figures 14–16

1915b *Pterinopecten licharewi* Frederiks, p. 28, Pl. 1, fig. 14.
1927 *Aviculopecten* (*Acanthopecten*?) *licharewi* (Frederiks); Likharev, p. 91, Pl. 6, fig. 24.
?1963 *Acanthopecten*? sp. Dickins, p. 86, Pl. 13, figs. 5, 6, 9; *non cet.*
1984 *Acanthopecten licharewi* (Frederiks) (partim); Muromtseva, p. 66, Pl. 25, fig. 14; *non cet.*

Holotype. The left valve figured by Frederiks (1915b, Pl. 1, fig. 15) from the Sakmarian Stage of the southern Urals.

Diagnosis. Moderately large, orbicular in outline; costae and lamellae distinct; first-order costae extending ventrally in prominent spines.

Material. One external mould of left valve from GSC loc. 56923; one left valve from JBW loc. 109; one internal mould of left valve from JBW loc. 113.

Description. External. Shell of medium size, about 28 mm long, 26 mm high, and 7 mm thick (measured from left valve); acline, orbicular in outline, moderately convex, umbonal angle 95°; left valve covered with 15 to 18 low costae, crests angular or narrowly rounded, separated by broad and shallow interspaces with well rounded floor; first-order lamellae coarse, widely spaced, separated by much finer secondary growth lamellae, projecting ventrally between costae in short but distinct spines which extend over approximately one third of interlamellar space; posterior auricle larger and longer than anterior one, both lack costae but growth lines prominent on posterior auricle; byssal notch prominent, moderately deep.

Internal. Narrow, but distinct, smooth, flat ligament area and poorly preserved resilifer observed from GSC 96844 (Pl. 30, fig. 15).

Comparisons. The holotype of *Acanthopecten licharewi* (Frederiks) is a left valve that appears to have been abraded on the surface, but clearly shows low, narrow costae and distinct concentric lamellae. It is 26 mm long and 13 mm high, acline and orbicular in outline. Apart from the poorly preserved projecting spines between costae in the holotype, the Soviet species is comparable in all other observable features with the Yukon material.

Material from the Kungurian fauna of the Pechora Basin identified as *Acanthopecten licharewi* by Muromtseva (1984, Pl. 28, figs. 7, 8, 11, 12) probably belongs to another species. It varies greatly from the holotype in their small size (half or less the size of the holotype) and greater height. Muromtseva included in her synonymy of *A. licharewi* several specimens from the Sterlitamakian fauna of Western Australia that were originally tentatively assigned to *Acanthopecten* by Dickins (1963, p. 86, Pl. 13, figs. 5–9). One of Dickins' specimens (Pl. 13, figs. 7, 8) is not likely to be conspecific as it has a much larger size (double or more the size of the holotype of *A. licharewi*) and fewer (12) costae. Other specimens could be conspecific judging from their size and outline, but the ornament is poorly preserved in Dickins' Plate 13, figures 5 and 9. Dickins' Plate 13, figure 6 is a fragment from a different locality; it shows prominent costae and concentric lamellae that extend ventrally in distinct spines, approaching the Yukon material.

Occurrence. In the Urals, *A. licharewi* occurs mainly in the Sakmarian stage. Muromtseva (1984) reported this species from the Early Artinskian (Aktastinian) lower Echii Suite of the Verchoyan Mountains. Allied specimens occur in the upper Sakmarian (Sterlitamakian) fauna of the Callytharra Formation in Western Australia. In northern Yukon Territory, this species is present in the Ey zone of the Tatonduk River Formation, of Early Sakmarian (Tastubian) age.

Subfamily ETHERIPECTININAE Waterhouse, 1982

Genus *Etheripecten* Waterhouse, 1963

Type species. (OD) *Etheripecten striatura* Waterhouse, 1963.

Etheripecten sp. A

Plate 30, figures 17, 18

Remarks. One fragment of a possible left valve external mould from JBW loc. 2 indicates the presence of *Etheripecten*. It is distinguished by its complex radial ornament and coarse spines arising from primary costae, 0.5 to 0.8 mm across, frequently interrupted by suberect spines; secondary costae intercalated between primary costae, with two to three further orders of costellae arising by intercalation between secondary and primary costae, one more order of costellae may further arise near the anterior margin; concentric ornament of very fine growth lines, passing straight over secondary costae and subsequent costellae with fine lamellae arising from conjunctions, and possibly passing straight over primary costae where coarse spines are developed.

Etheripecten sp. B

Plate 30, figures 19, 20

Remarks. One ventral external mould of a left valve was found at JBW loc. 113; one internal mould of a left valve at GSC loc. 57053. The two specimens are similar in size, shape, and convexity; moderately convex with umbo near midlength, umbonal angle at 83°; anterior umbonal wall low and gently convex in section; posterior wall low but steep, nearly vertical in section; anterior auricle flatly convex near hinge line, well demarcated from umbo by steep umbonal wall, with acute cardinal extremities extending as far as anterior margin; left posterior auricle slightly longer, flat near hinge line, very gently concave just below umbonal wall; cardinal angle about 60; primary costae prominent, crests narrowly rounded; secondary costae arising by intercalation, prominent near ventral margin; costae separated by wide flat interspaces; auricle also costate in one order, five or six on anterior auricle and eight on posterior auricle; concentric ornament of rather fine, indistinct growth lines passing straight over costae and slightly arching hingeward in between; growth lines best developed on auricles where they pass straight over costae.

Ligament area striated with shallow, low, long chondrophore under umbo. The Yukon material is poorly preserved and incomplete. No particular species is comparable.

Occurrence. Ey zone, Tastubian.

Subfamily STREBLOCHONDRIINAE Newell, 1938

Genus *Streblochondria* Newell, 1938

Type species. (OD) *Aviculopecten sculptilis* Miller, 1891.

Streblochondria sp.

Plate 30, figures 21, 22

Remarks. This genus is represented by one left valve from JBW loc. 24. It is 30 mm long, 37 mm high, markedly opisthocline, flatly convex on the dorsal half and ventrally flattened; umbo tiny, slightly extended, weakly opisthogyrous; anterior umbonal wall steep, straight in outline, inclined from hinge at about 45°, posterior wall lower and gently concave in outline; anterior auricle long, flat, with obtuse cardinal extremity at 110°, well demarcated from umbo; byssal sinus indistinct; posterior auricle conspicuously shorter and less defined, flat; anterior and posterior margins gently rounded. Ornament of network of very fine costellae crossed by fine concentric filae; four or five costellae in 1 mm on umbonal region with rounded crests and equally wide interspaces, slightly undulating in course, increasing anteriorly by intercalation; four or five concentric filae in 1 mm on average, sharper than radial ornament.

The Yukon material is incomplete. No species are known to be particularly comparable.

Order PHOLADOMYOIDA Gray, 1847

Superfamily PHOLADOMYOIDACEA Gray, 1847

Family CHAENOMYINAE Waterhouse, 1966

Subfamily VACUNELLINAE Astaf'yeva-Urbaytis, 1973

Genus *Exochorhynchus* Meek and Hayden, 1864

Type species. (OD) *Allorisma? altirostrata* Meek and Hayden, 1858.

Discussion. Astaf'yeva-Urbaytis (1981) discussed the genus in detail and provided comparisons with allied genera.

Exochorhynchus similis (Lyutkevich and Lobanova, 1960)

Plate 30, figures 23–27; Plate 31, figures 1–14; Figure 52

1960 *Allorisma similis* Lyutkevich and Lobanova (partim.), p. 83, Pl. 10, fig. 8.

1980 *Exochorhynchus similis* (Lyutkevich and Lobanova); Solomina and Astaf'yeva-Urbaytis, p. 31, Pl. 3, figs. 1-3.

1984 *Vacunella similis* (Lyutkevich and Lobanova) (partim.); Muromtseva, p. 96, Pl. 43, figs. 1, 2, 6.

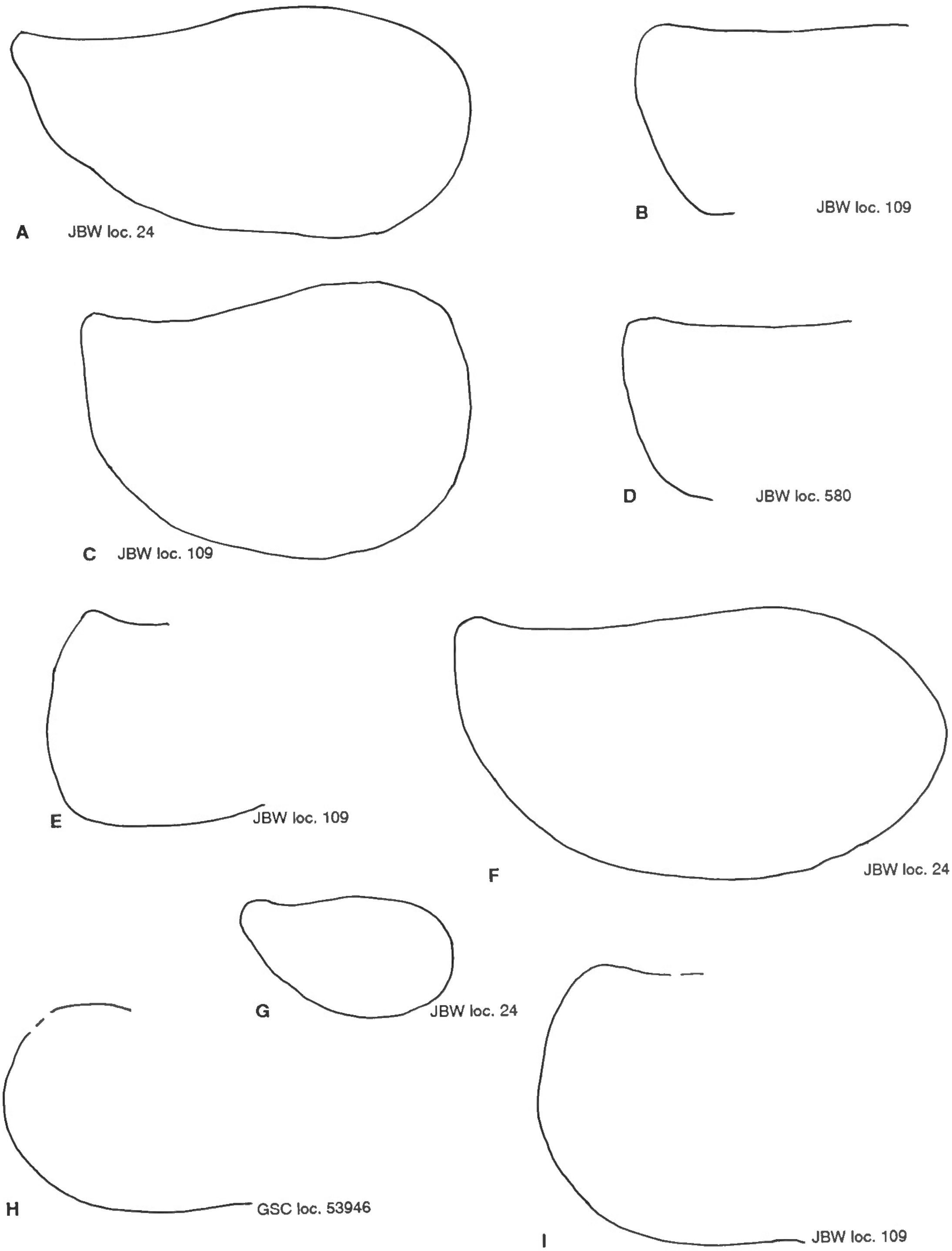


Figure 52. *Variation of umbonal shape of left valves in* ***Exochorhynchus similis*** *(Lyutkevich and Lobanova) (all x1). A–D, F, G are moderately to strongly prosocline, whereas E, H, I are orthocline to slightly opisthocline. This variation is clearly shown by specimens from the same locality, notably JBW loc. 109 (see B, C, E, I).*

Holotype. CNIGR Museum 181/7443 figured by Lyutkevich and Lobanova (1960, Pl. 10, fig. 8) from the Permian of central Taimyr, northern Russia.

Diagnosis. Large, long, moderately convex, with distinct concentric ridges and usually well defined umbo; umbos varying from slightly opisthocline to conspicuously prosocline; no sulcus; posterior gape narrow or ill defined.

Material.

Locality	Left	Right	Conjoined
GSC loc. 53858			1
GSC loc. 53946			1
JBW loc. 14			1
JBW loc. 54			1
JBW loc. 109	?1(em)	1(em)	5
JBW loc. 113			1
JBW loc. 537			2
JBW loc. 580			1(im)

Description. External. Shell large for genus, moderately inflated (Pl. 31, fig. 8), greatest convexity at anterior third of shell length behind umbos; higher toward posterior margin; subrectangular in lateral view; normally prosocline with prosogyrous umbos, but varying from prosocline through orthocline to slightly opisthocline (Fig. 52), even for specimens from same locality such as JBW loc. 109; beak commonly terminal and sometimes strongly drawn out, cardinal angle between 54° and 80°, often at about 70; umbos blunt, arising moderately above hinge line; dorsal margin concave in outline (Pl. 31, fig. 2), anterior margin merging well with ventral margin, posterior margin well rounded; posterior gape absent in some shells, narrow in others in which it extends from midlength of dorsal margin to middle height of posterior margin (Pl. 31, fig. 3), about 5 mm wide; umbonal ridge not developed or ill defined; posterior dorsal face not defined. Concentric ridges prominent (Pl. 31, fig. 7), crossing entire shell, usually low and broadly rounded, seven or eight in 10 mm near umbos, five in 10 mm at midlength, more closely spaced toward ventral and anterior margins, separated by slightly narrower, flattened or depressed interspaces, increasing posteriorly mainly by intercalation, occasionally superimposed by fine growth striae, especially near posterior and posteroventral margins (Pl. 31, fig. 7); fine granules numerous and prominent, two or three in 1 mm, arranged in more or less concentric rows (Pl. 30, fig. 26).

Internal. Escutcheon prominent (Pl. 31, figs. 3, 13), narrow, elongate, extending backward from umbos as far as about midlength, concave and smooth, separated from rest of shell by slightly elevated escutcheon ridges.

Dimensions (in mm).

Specimen	Length	Height	Width
GSC 97644	65	34	26
GSC 97645	72	41	30
GSC 97648	56	40	25

Comparisons. Though variable in outline, the Yukon specimens are consistent with *Exochorhynchus similis* (Lyutkevich and Lobanova, 1960) in their large size, usually elongate shape with well defined umbos and poorly defined posterior gape, distinct concentric ridges and fine granules, and lack of posterior umbonal ridges. In their illustrations, Lyutkevich and Lobanova (1960, Pl. 10, figs. 6, 7) included two specimens in *E. similis* other than the holotype are much more convex than the holotype that and, in particular, possess prominent umbonal ridges and large concave posterior dorsal faces, suggesting *Vacunella* Waterhouse, 1965, as also noted by Solomina and Astaf'yeva-Urbaytis (1980, p. 31). Muromtseva (1984) further broadened the concept of *Exochorhynchus similis*. She included in this species a great variety of specimens. Her specimens (her Pl. 43, figs. 1, 2, possibly fig. 6) appear to be conspecific with the holotype of *E. similis*, judging from their prominent prosocline umbos, moderate convexity, ill defined umbonal ridges, and the absence of a sulcus. Another specimen (her Pl. 43, fig. 7) is similar to some smaller Yukon specimens from JBW loc. 109 in having orthocline umbos, but it has higher and more widely spaced concentric ridges. Muromtseva's other specimens are readily distinguished from the holotype either by possessing poorly developed concentric ridges (Pl. 43, figs. 5, 8; Pl. 49, fig. 13), prominent opisthocline umbos (Pl. 45, figs. 10, 11; Pl. 50, fig. 14), high convexity and prominent umbonal ridges coupled with well developed posterior umbonal faces (Pl. 43, figs. 3, 4) or well developed sulcus (Pl. 43, figs. 10, 11).

Exochorhyncus curtus Astafy'eva-Urbaytis (1981, Pl. 3, figs. 4, 5), from the Upper Carboniferous Gshelian and Kasimovian stages of the Moscow Basin, is subrounded and more convex than the present species. *Exochorhyncus obliquarus* Astaf'yeva-Urbaytis and Ramovs (1985, Pl. 3, fig. 1), from the Gshelian fauna of Yugoslavia, is much smaller and more prosocline than the holotype of *E. similis*, and its concentric ridges are apparently higher and broader.

Figure 53. Pattern of suture line in ***Tabantalites bifurcatus*** *Ruzhencev (GSC 97642, x2).*

Occurrence. Exochorhynchus similis was originally described from an outcrop of unknown age in central Taimyr, possibly Permian (Muromtseva, 1984) . It has since been recorded from the late Artinskian (Baigendzinian) Talatin Suite of the Pechora Basin, northern Urals. In northern Yukon Territory, this species is known from the Ey and Ej zones of Sakmarian to early Artinskian (Aktastinian) age.

Class CEPHALOPODA Cuvier, 1797

Subclass AMMONOIDEA Zittel, 1884

Family MARATHONITIDAE Ruzhencev, 1938

Subfamily MARATHONITINAE Ruzhencev, 1938

Genus *Tabantalites* Ruzhencev, 1952

Type species. (OD) *Tabantalites bifurcatus* Ruzhencev (1952).

Tabantalites bifurcatus Ruzhencev, 1952

Plate 30, figure 28; Figure 53

1952 *Tabantalites bifurcatus* Ruzhencev, p. 77, Pl. 6, figs. 3-7; Figs. 24, 25.
1971 *Tabantalites bifurcatus* Ruzhencev; Nassichuk, p. 1012, Pl. 126, fig. 8; Textfig. 8.

Holotype. PIN 591/2072 figured by Ruzhencev (1952, Pl. 6, fig. 7) from the Tastubian Substage of the southern Urals.

Remarks. A single, crushed, incomplete internal mould from GSC loc. 57053. Conch over 30 mm, whorl about 28 mm high, 25 mm wide; suture pattern as shown in Figure 53.

Though poorly preserved, this single specimen appears to be identical to another Yukon specimen, identified as *Tabantalites bifurcatus* by Nassichuk (1971).

Occurrence. Tabantalites bifurcatus is known from the Upper Asselian (Krumaian) to Lower Sakmarian (Tastubian) stages in the Urals and the Sakmarian Ey and Eog zones in northern Yukon Territory.

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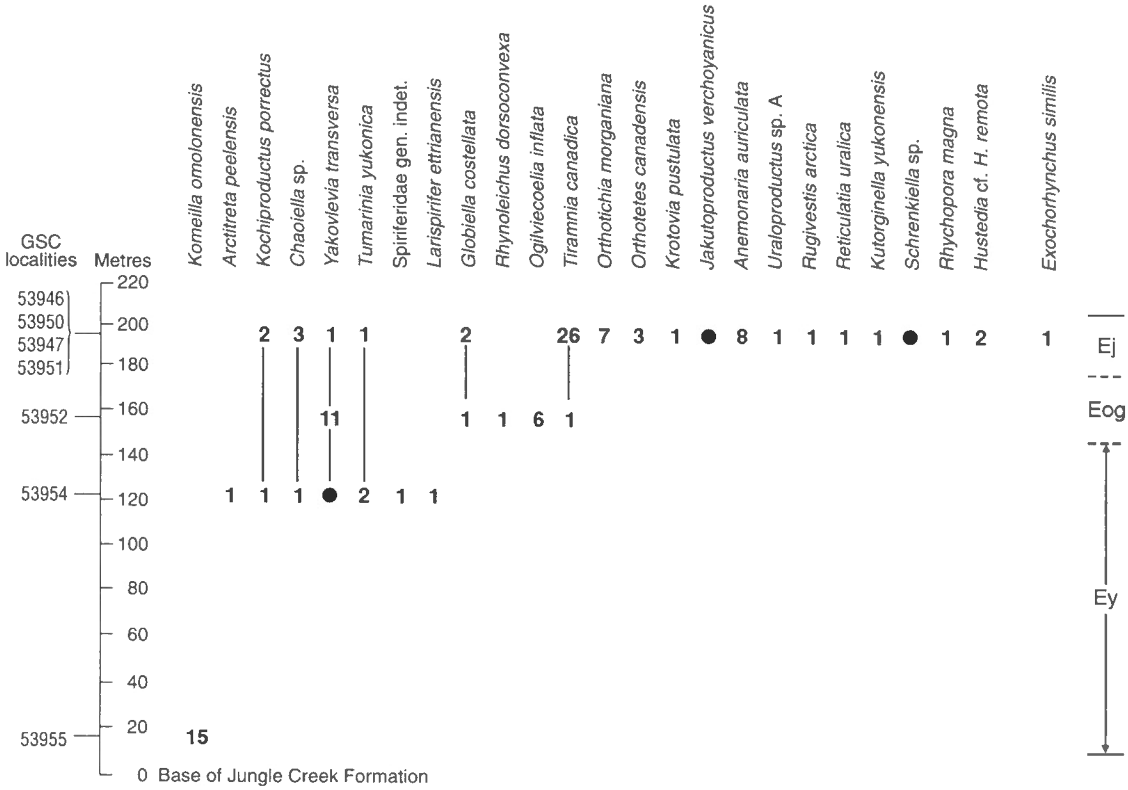
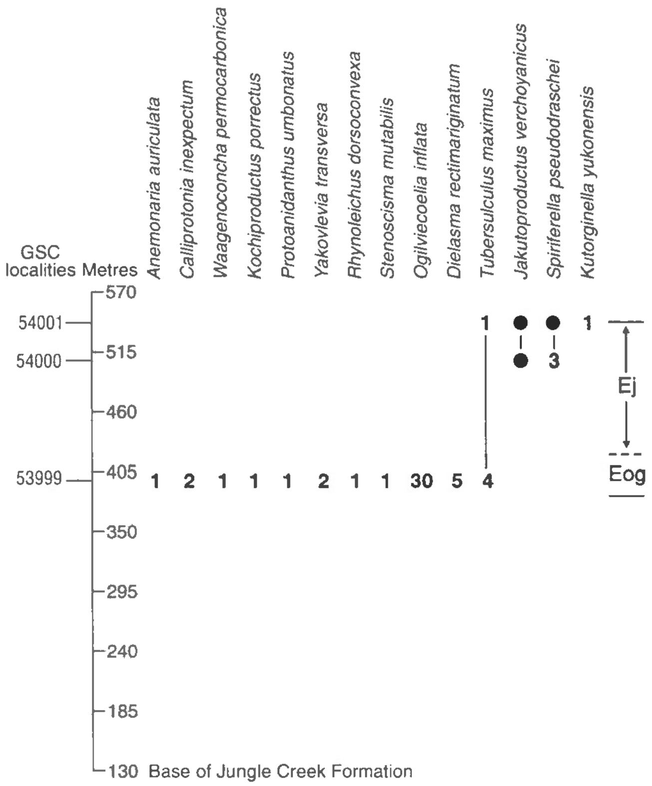
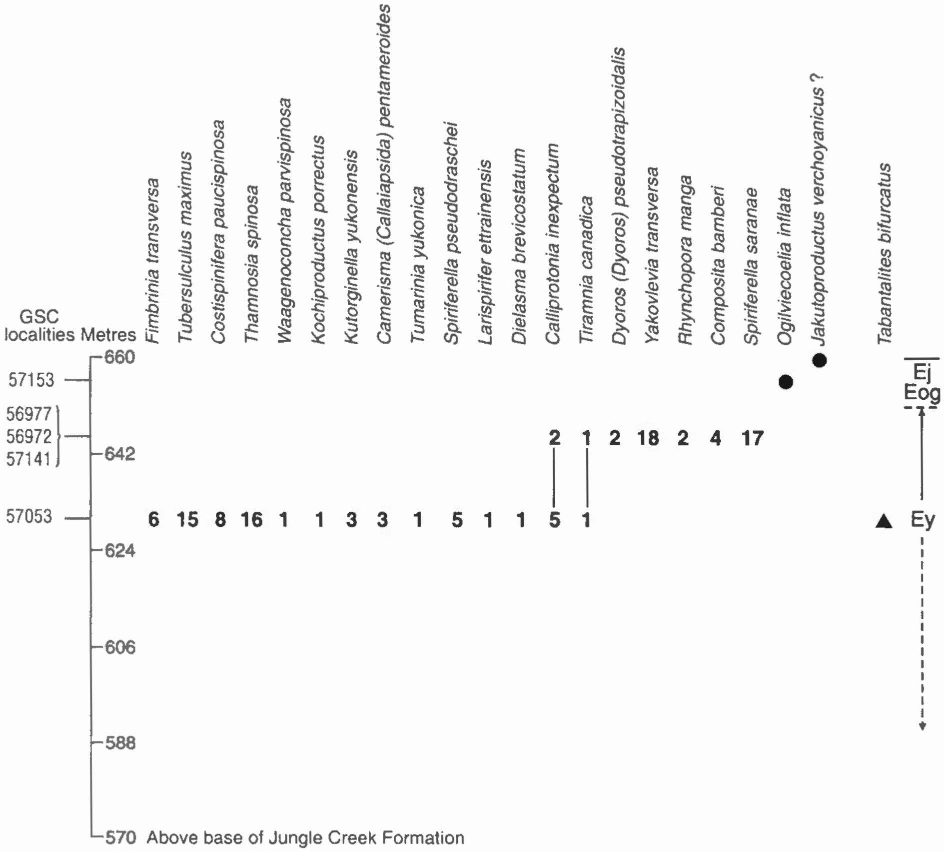
Appendix Figures



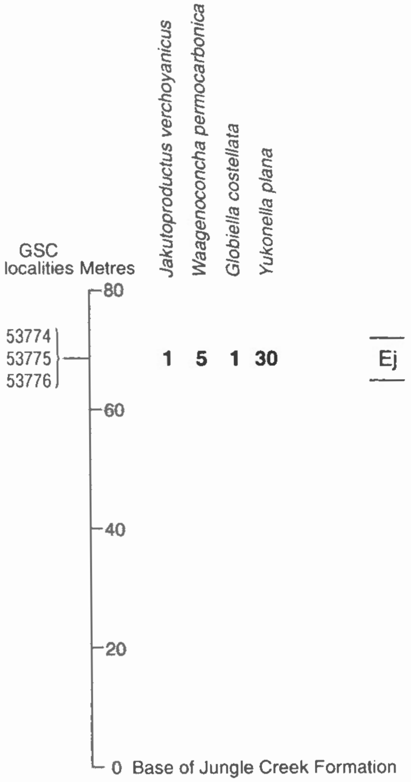
Appendix Figure 1. *Range of brachiopod species in section 116C-1, Tatonduk River, with number of individuals and black dots based on data in Bamber and Waterhouse (1971).*



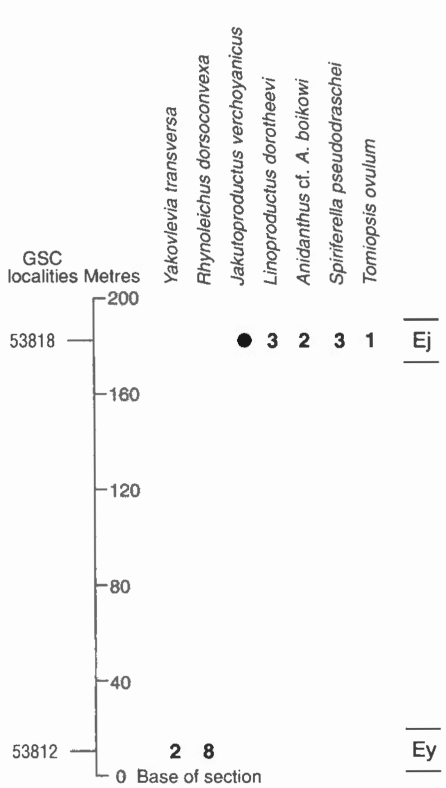
Appendix Figure 2. *Stratigraphic column of section 116F-9, northern Ogilvie Mountains, with number of individuals and black dots based on data in Bamber and Waterhouse (1971).*



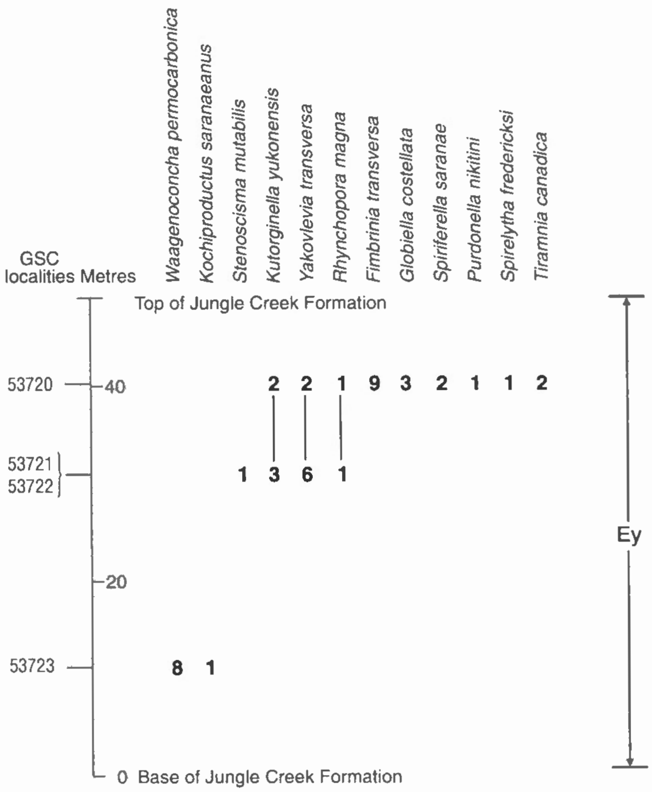
Appendix Figure 3. *Range of brachiopod species in section 116F-16, northern Ogilvie Mountains, with number of individuals and black dots based on data in Bamber and Waterhouse (1971).*



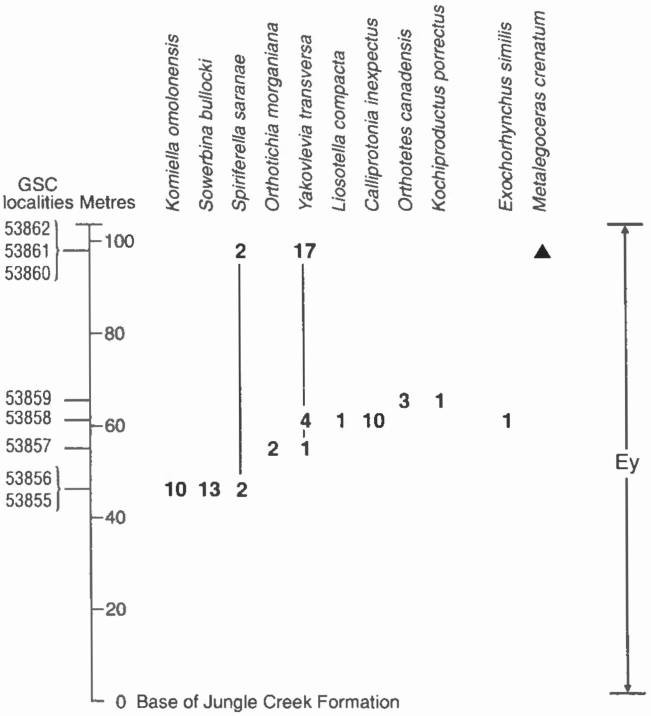
Appendix Figure 4. *Range of brachiopod species in section 116G-5, Nahoni Range East, northern Ogilive Mountains, with number of individuals.*



Appendix Figure 5. *Range of brachiopod species in section 116H-17, Peel River, southern Eagle Plain, with number of individuals and black dots based on data in Bamber and Waterhouse (1971).*



Appendix Figure 6. *Range of brachiopod species in section 116H-1B, Peel River, southern Eagle Plain, with number of individuals.*



Appendix Figure 7. *Range of brachiopod species in section 116P-10, northern Richardson Mountains, with number of individuals.*

Appendix Tables

Appendix Table 1

Location of GSC sections studied

Section	Location	Figures in text
116C-1	64°58.5′, 140°54′	5
116C-2	64°58.5′, 140°54′	5
116F-9	65°23′, 140°40′	4
116F-16	65°17.5′, 140°42.5′	4
116G-5	65°38.5′, 138°34.5′	
116H-1A	65°53′, 136°08′	
116H-1B	65°53′, 136°05.5′	2
116H-17	65°49.5′, 136°32.5′	3
116P-10	63°31′, 136°32.5′	

Appendix Table 2

Details of Geological Survey of Canada collections (GSC localities) examined in this study

GSC locality	Section	Formation	Brachiopod zone
53703	116H-1A	Jungle Creek	Ey
53704	116H-1A	Jungle Creek	Ey
53705	116H-1A	Jungle Creek	Ey
53710	116H-1A	Jungle Creek	Ey
53712	116H-1A	Jungle Creek	Ey
53713	116H-1A	Jungle Creek	Ey
53714	116H-1A	Jungle Creek	Ey
53715	116H-1A	Jungle Creek	Eog
53716	116H-1A	Jungle Creek	Eog
53718	116H-1A	Jungle Creek	Ej
53720	116H-1B	Jungle Creek	Ey
53721	116H-1B	Jungle Creek	Ey
53722	116H-1B	Jungle Creek	Ey
53723	116H-1B	Jungle Creek	Ey
53774	116G-5	Jungle Creek	Ej
53775	116G-5	Jungle Creek	Ej
53776	116G-5	Jungle Creek	Ej
53812	116H-17	Jungle Creek	Ey
53818	116H-17	Jungle Creek	Ej
53855	116P-10	Unnamed carbonate unit	Ey
53856	116P-10	Unnamed carbonate unit	Ey
53857	116P-10	Unnamed carbonate unit	Ey
53858	116P-10	Unnamed carbonate unit	Ey
53859	116P-10	Unnamed carbonate unit	Ey
53860	116P-10	Unnamed carbonate unit	Ey
53861	116P-10	Unnamed carbonate unit	Ey
53862	116P-10	Unnamed carbonate unit	Ey
53946	116C-1	Jungle Creek	Ej
53947	116C-1	Jungle Creek	Ej
53950	116C-1	Jungle Creek	Ej
53951	116C-1	Jungle Creek	Ej
53952	116C-1	Jungle Creek	Eog
53954	116C-1	Jungle Creek	Ey
53955	116C-1	Jungle Creek	Ey
53999	116F-9	Jungle Creek	Eog
54000	116F-9	Jungle Creek	Ej
54001	116F-9	Jungle Creek	Ej
56917	116C-2	Tahkandit	Ej
56922	116C-2	Tahkandit	Ej
56923	116C-2	Jungle Creek	Ey
56935	116C-2	Jungle Creek	Ey
56937	116C-2	Jungle Creek	Ej
56942	116C-2	Jungle Creek	Ey
56972	116F-16	Jungle Creek	Ey
56977	116F-16	Jungle Creek	Ey
57049	116C-2	Jungle Creek	Ey
57052	116C-2	Tahkandit	Ej
57053	116F-16	Jungle Creek	Ey
57059	116C-2	Jungle Creek	Ey
57141	116F-16	Jungle Creek	Ey
57154	116C-2	Jungle Creek	Ey
57255	116C-2	Jungle Creek	Ej
57266	116C-2	Jungle Creek	Eog
57273	116C-2	Jungle Creek	Ey
57275	116C-2	Tahkandit	Ej

Appendix Table 3

J.B. Waterhouse collections (JBW localities) from the Ettrain Creek area, northern Yukon Territory (all localities are shown in Figure 4)

JBW locality	Location in Figure 4	Brachiopod zone
2	Ridge 36 north of 116F–16	Ej
9	Ridge 42 north of 116F–16	Ey
11	Ridge 42 north of 116F–16	Ey
14	27.4 m from crest of Ridge 42, north of 116F–16	Ey
15	39.6 m from crest of Ridge 42, north of 116F–16	Ey
24	24 m below crest of Ridge 42, north of 116F–16	Ey
54	Ridge 39 north of 116F–16	Ey
56	JBW section 39, Ridge 39	Ej
57	JBW section 39, Ridge 39	Eog
58	JBW section 39, Ridge 39	Ey
59	JBW section 39, Ridge 39	Ey
60	JBW section 39, Ridge 39	Ey
63	Ridge 39 north of 116F–16	Ey
64	Ridges 34–42 north of 116F–16	Ey
88	JBW section 44, Ridge 44	Ey
89	JBW section 44, Ridge 44	Ey
109	Section 116F–9	Ey
110	Section 116F	Ey
111	Ridge 42 north of 116F–16	Ey
113	Section 116F–9	Ey
131	Section 116F–9	Eog
505	Ridge 44 southwest of 116F–16	Ey
506	Ridge 44 southwest of 116F–16	Ey
507	Ridge 44 southwest of 116F–16	Ey
508	Ridge 44 southwest of 116F–16	Ey
512	JBW section 44, Ridge 44	Ej or Eog
526	Ridge 44 southwest of 116F–16	Ej
537	Ridge 44 southwest of 116F–16	Ej
541	Ridge 33 southwest of 116F–16	Ej
542	Ridge 33 southwest of 116F–16	Ej
545	Ridge 33 southwest of 116F–16	Ej
546	Ridge 33 southwest of 116F–16	Ej
558	Ridge 44 southwest of 116F–16	Ej
559	Immediately below JBW loc. 558	Ej
590	Ridge 26	Ey

PLATE 1

Figure 1. *Orbiculoidea* sp. GSC 97348, GSC loc. 53714.

Figures 2–18. *Orthotichia morganiana* (Derby)

2. Latex cast, ventral interior, showing adminicula, GSC 96854, JBW loc. 89.
3. Ventral internal mould, GSC 96854, JBW loc. 89.
4. Ventral internal mould, showing thick adminicula and median septum, GSC 96852, JBW loc. 24.
5. Latex cast, ventral internal mould, showing ventral internal plates and muscle field, GSC 96856, GSC loc. 53946.

6, 18. Ventral view, ventral valve, GSC 96855, JBW loc. 24; fig. 18 enlarged (x5) to show uninterrupted costellae.

7, 11. Exterior and internal mould, dorsal valve, showing dorsal cardinalia and muscle field, GSC 96853, JBW loc. 24.

8. Abraded ventral valve, GSC 96858, GSC loc. 53946.

9, 13–15. Lateral, posterior, ventral, and dorsal views, conjoined shell, GSC 96849, GSC loc. 53857.

10. Ventral view, ventral valve, GSC 96857, GSC loc. 53946.

12. Dorsal internal mould, showing muscle field, GSC 96851, JBW loc. 24.

16. Latex cast, dorsal internal mould, showing cardinalia and muscle field, GSC 96850; JBW loc. 590; x2.

17. Latex cast, dorsal internal mould, showing cardinalia and muscle field, GSC 96896, JBW loc. 590; x2.

Figures 19–24. *Arcitreta peelensis* n. sp.

19. Dorsal valve, showing costellae, GSC 96861, GSC loc. 53703.

20, 21, 24. Ventral internal mould and latex cast, showing a deeply depressed muscle field, GSC 96863, GSC loc. 56942; fig. 24 enlarged to show endopunctae (x3).

22. Ventral internal mould, GSC 96862, GSC loc. 53703.

23. Dorsal–posterior view, conjoined specimen, holotype, GSC 96860, GSC loc. 53713.

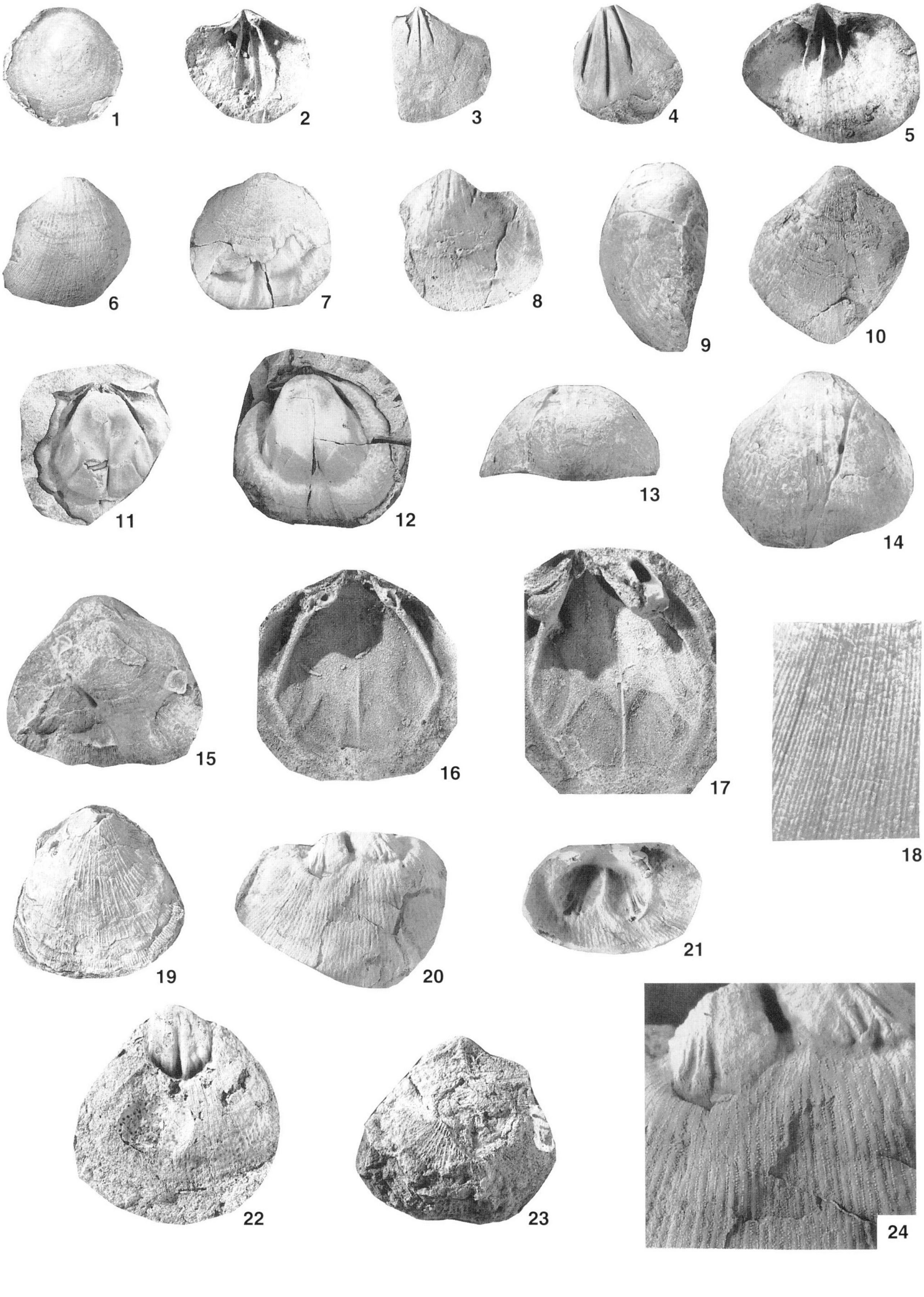

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PLATE 2

Figures 1–10. *Orthotetes canadensis* n. sp.

1, 2. Latex cast, dorsal internal mould, GSC 96864, GSC loc. 56922; fig. 2 shows cardinal process and recurved crural plates (x3).

3, 6. Latex cast and dorsal internal mould, GSC 96870, JBW loc. 109.

4. Latex cast, dorsal external mould, GSC 96873, JBW loc. 88.

5. Ventral internal mould, GSC 96882, JBW loc. 113.

7. Dorsal internal mould, GSC 96879, JBW loc. 109.

8. Latex cast, dorsal internal mould, GSC 96876, JBW loc. 109.

9. Dorsal internal mould, holotype, GSC 96877, JBW loc. 109.

10. Abraded dorsal valve, GSC 96871, GSC loc. 53859.

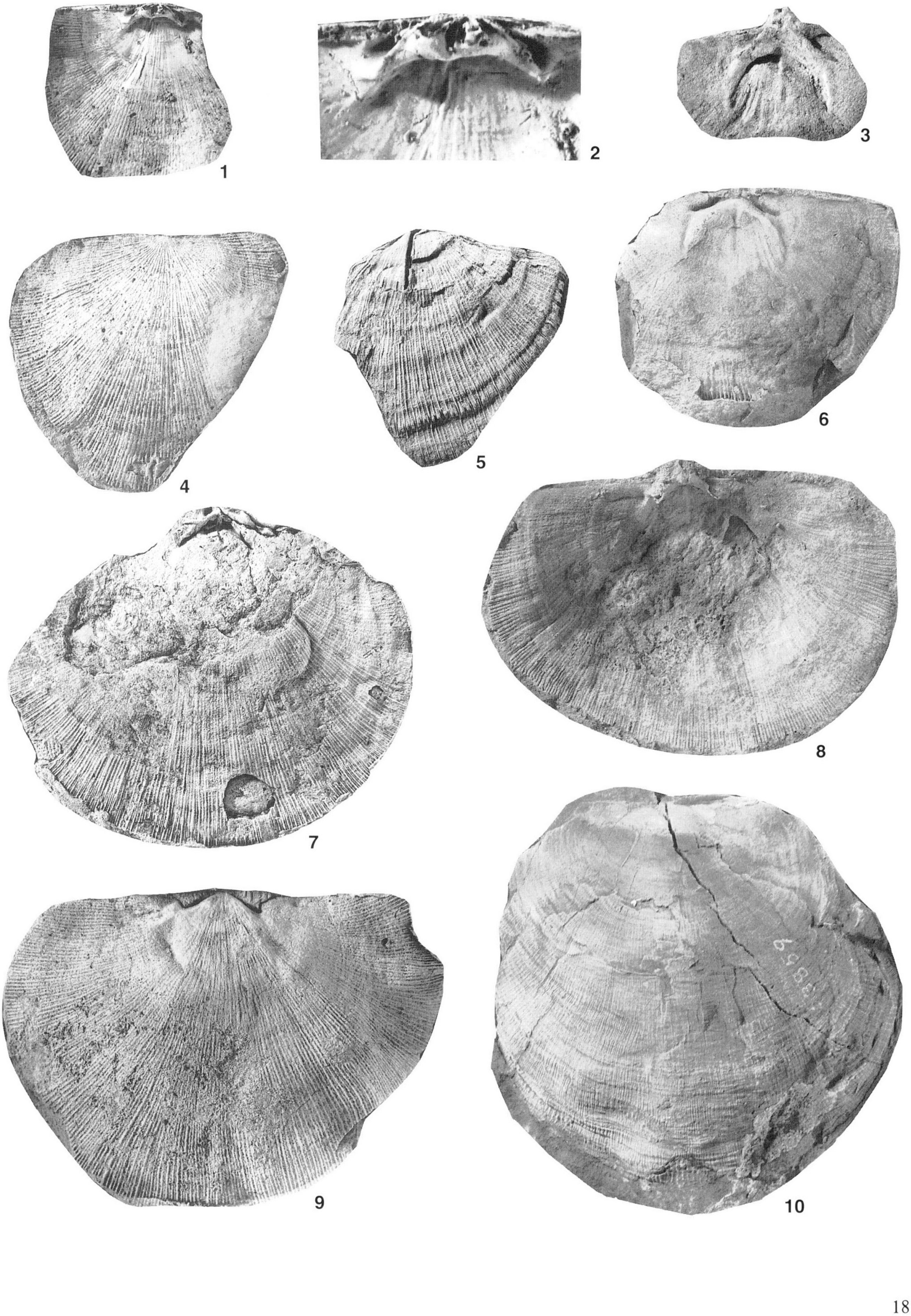
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PLATE 3

Figures 1–9, 11. *Orthotetes canadensis* n. sp.

1. Posterior view, ventral internal mould, showing interarea and dental plates, GSC 96866, JBW loc. 88.

2, 3. Ventral internal mould and latex cast, GSC 96866, JBW loc. 88; fig. 3, x2.

4. Abraded dorsal internal mould, GSC 96868, JBW loc. 88.

5, 7. Ventral and posterior views, latex cast, ventral external mould, GSC 96878, JBW loc. 109.

6. Posterior view, latex cast, dorsal internal mould showing cardinal process, GSC 96864, GSC loc. 56922; x5.

8. Posterior view, latex cast, dorsal internal mould, GSC 96893, JBW loc. 88; x4.

9. Dorsal internal mould, GSC 96865, GSC loc. 53714.

11. Ventral internal mould, GSC 96874, JBW loc. 89.

Figure 10. *Dyoros* (*Dyoros*) *pseudotrapezoidalis* (Miloradovich)

Latex cast, dorsal internal mould, GSC 96894, JBW loc. 54; x5.

Figures 12–23. *Komiella omolonensis* (Likharev)

12. Internal mould, ventral valve (above) and dorsal valve (below), GSC 96889, GSC loc. 53955; x2.

13. Ventral internal mould, GSC 96892, GSC loc. 53705; x3.5.

14. Latex cast, dorsal internal mould, GSC 96886, GSC loc. 53703.

15. Dorsal–posterior view, conjoined shell, GSC 96887, JBW loc. 113; x3.5.

16. Ventral valve, GSC 96890, JBW loc. 113; x4.

17. Ventral interior, GSC 96888, GSC loc. 53955; x4.

18. Dorsal view, broken conjoined shell, GSC 96895, GSC loc. 53856; x2.5.

19. Ventral valve, GSC 96883, GSC loc. 53705.

20. Dorsal internal mould, GSC 96885, JBW loc. 113; x3.5.

21, 23. Abraded ventral valve, GSC 96891, GSC loc. 53856; fig. 23 shows hinge spines (x7).

22. Ventral valve, GSC 96884, GSC loc. 53704.

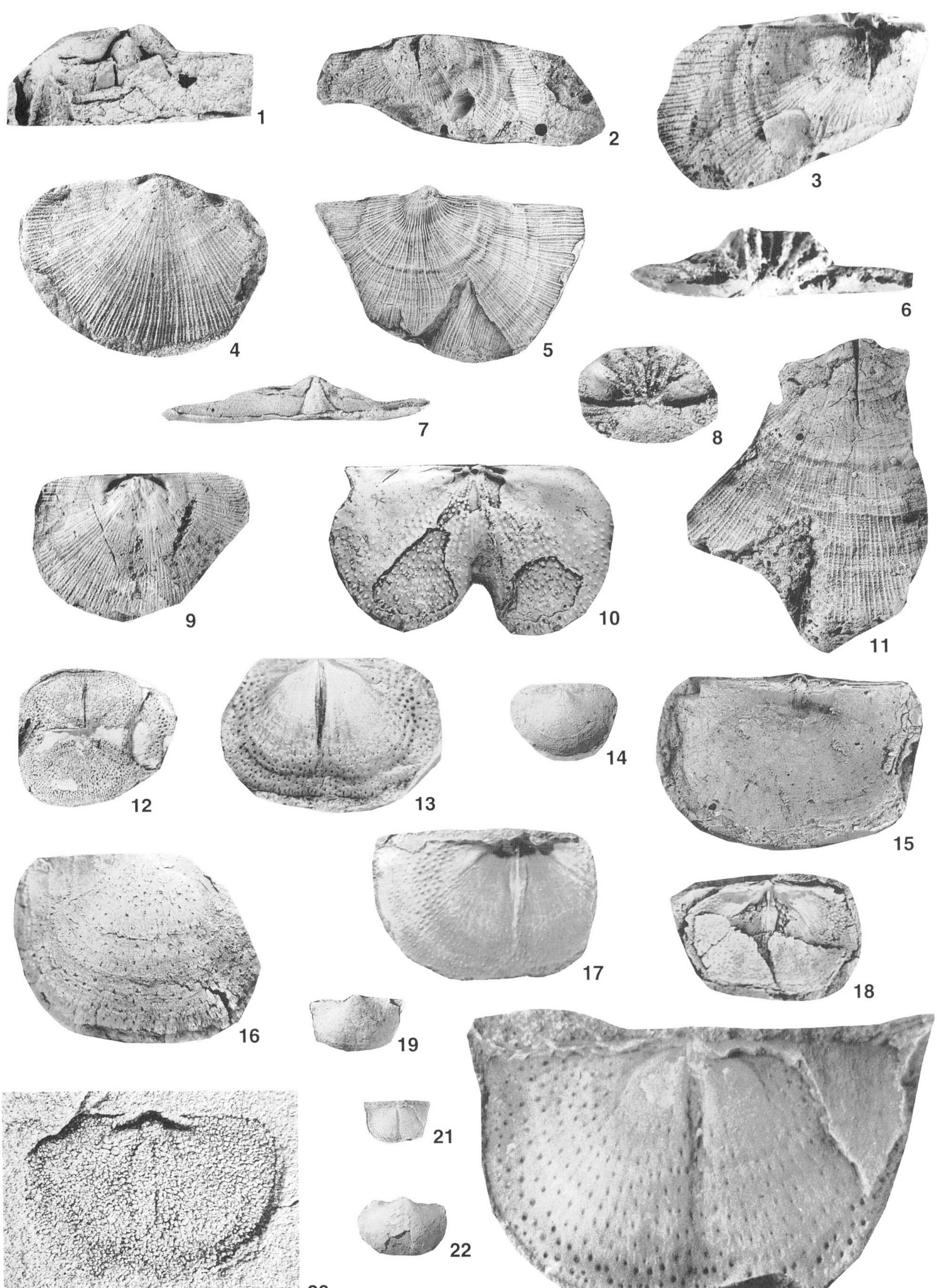
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PLATE 4

Figures 1–6. *Dyoros* (*Dyoros*) *pseudotrapezoidalis* (Miloradovich)

1, 2. Ventral and posterior views, ventral valve, GSC 97087, GSC loc. 56922; x2; in fig. 2 rotated to show sulcus.

3, 5. Posterior–lateral and posterior views, ventral valve, GSC 97086, GSC loc. 57141; x2.

4. Ventral valve, GSC 97088, GSC loc. 57141; x2.

6. Ventral internal mould, GSC 97089, JBW loc. 109.

Figures 7, 8. *Rugaria*? sp.

7. Ventral interior, GSC 96897, JBW loc. 109; x2.

8. Abraded dorsal interior, GSC 96898, JBW loc. 109; x2.

Figures 9–20. *Fimbrinia transversa* n. sp.

9. Posterior view, ventral internal mould, GSC 97096, JBW loc. 88; x2.

10. Lateral view, ventral internal mould, GSC 97094, JBW loc. 109; x2.

11, 17. Ventral and dorsal views, conjoined shell, holotype, GSC 97092, GSC loc. 53720; x2.

12. Dorsal view of latex cast, dorsal external mould with ventral umbo, GSC 97093, JBW loc. 88; x2.

13. Abraded ventral valve, GSC 97094, JBW loc. 109; x2.

14. Latex cast, juvenile ventral valve, GSC 97092, GSC loc. 53720; x4.

15, 16. Posterior and lateral views, ventral valve, GSC 97095, GSC loc. 57266; x2.

18. Ventral internal mould, GSC 97097, GSC loc. 53999; x2.

19. Dorsal internal mould, GSC 97090, JBW loc. 88; x2.

20. Latex cast, dorsal internal mould, GSC 97090; x6.

Figures 21–23. *Krotovia pustulata* (Kerserling)

21. Ventral valve, GSC 96899, JBW loc. 113.

22. Latex cast, ventral external mould, GSC 96901, GSC loc. 57266.

23. Dorsal external mould, GSC 96900, GSC loc. 53951.

Figures 24–29. *Tubersulculus maximus* Waterhouse

24. Ventral internal mould, GSC 96903, JBW loc. 60; x2.

25. Dorsal internal mould, GSC 96902, JBW loc. 89; x2.

26, 29. Posterior and anterior views, dorsal external mould, GSC 96907, GSC loc. 57053; x2.

27. Dorsal internal mould, GSC 96912, JBW loc. 89; x2.

28. Dorsal external mould, GSC 96904, JBW loc. 54.

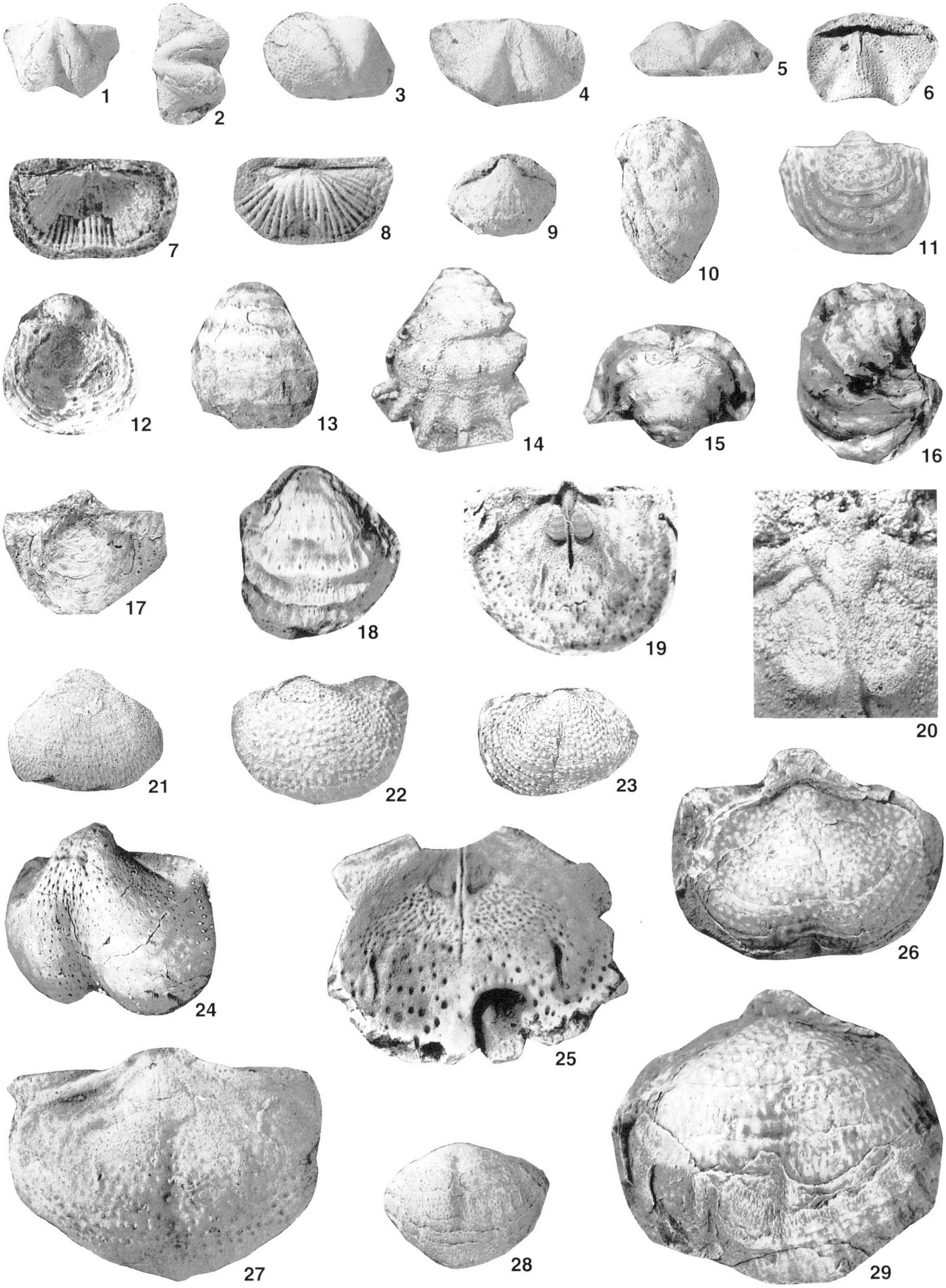
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PLATE 5

Figures 1–9. *Tubersulculus maximus* Waterhouse

1. Posterior view, ventral valve, GSC 96911, JBW loc. 54.
2. Anterior view, ventral valve, GSC 96906, GSC loc. 57053.
3. Dorsal external mould, GSC 97100, GSC loc. 57052.
4. Ventral internal mould, GSC 96905, JBW loc. 24.
5. Latex cast, dorsal internal mould, GSC 96913, JBW loc. 88; x2.
6. Ventral valve, GSC 96910, GSC loc. 57275.
7. Dorsal external mould, GSC 97101, JBW loc. 60.
8. Dorsal external mould, GSC 96908, JBW loc. 88.
9. Posterior view, ventral valve, GSC 96909, JBW loc.89.

Figures 10–23. *Jakutoproductus verchoyanicus* (Frederiks)

10. Ventral view, ventral valve, GSC 96914, GSC loc. 53718.
11. Ventral view, ventral valve, GSC 96922, GSC loc. 53718.
12. Ventral view, ventral valve, GSC 96922, GSC loc. 53718.
13. Ventral view, ventral valve, GSC 96915, GSC loc. 53718.
14. Dorsal internal mould, showing lanceolate median septum and brachial ridges, GSC 96916, GSC loc. 53718; x2.
15. Ventral internal mould, showing ventral muscle scars, GSC 96917, GSC loc. 53718.
16. Anterior view, crushed ventral valve, GSC 96923, GSC loc. 53718.
17. Dorsal view, dorsal valve, GSC 96926, GSC loc. 53718.
18. Dorsal external mould, GSC 96919, GSC loc. 53718.
19. Anterior view, ventral valve showing geniculated marginal band, GSC 96924, GSC loc. 53718; x2.

20–22. Dorsal, ventral, and anterior views, conjoined shell, GSC No. 96926, GSC loc. 53718.

23. Ventral internal mould, showing ventral muscle scars, GSC 96920, GSC loc. 53718.

Figures 24–29. *Kozlowskia* sp.

24. Anterior view, abraded conjoined shell, showing dorsal marginal ridge, GSC 96931, JBW loc. 57; x2.
25. Posterior view, ventral valve, GSC 96929, JBW loc. 109; x2.

26–28. Anterior, lateral, and lateral views, ventral valve, showing spine pattern, GSC 96928; JBW loc. 109; x2.

29. Posterior view, ventral valve, GSC 96930, JBW loc. 57; x2.

Figures 30, 31. *Liosotella compacta* n. sp.

30. Anterior view, ventral valve, GSC 96952, GSC loc. 53858; x2.
31. Anterior view, ventral valve, GSC 96947, JBW loc. 2; x2.

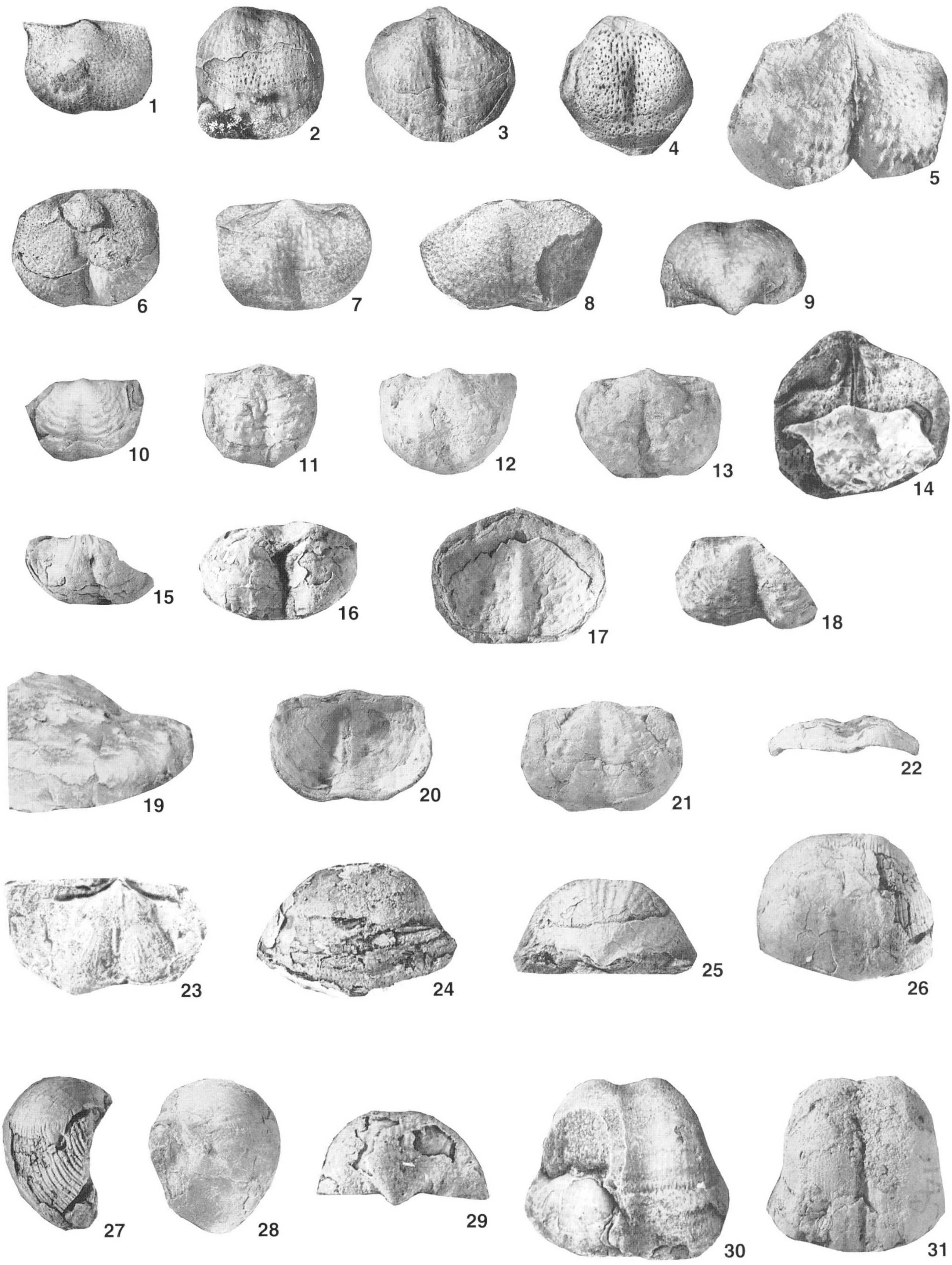
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PLATE 6

Figures 1–9. *Liosotella compacta* n. sp.

1. Dorsal external mould, GSC 96948, JBW loc. 2.
2. Dorsal external mould, GSC 97652, JBW loc. 2; x2.
3. Dorsal interior, GSC 96951, JBW loc. 2; x2.

4–6. Posterior, lateral, and anterior views, ventral valve, holotype, GSC 96944, JBW loc. 2; x2.

7. Ventral internal mould, GSC 96953, JBW loc. 57; x2.
8. Ventral internal mould, GSC 96945, JBW loc. 2; x2.
9. Dorsal interior, GSC 96950, JBW loc. 2; x2.

Figures 10–28. *Anemonaria auriculata* n. sp.

10, 11, 28. Latex cast, dorsal internal mould, GSC 96941, JBW loc. 63; fig. 28, x2.

12. Latex cast, dorsal internal mould, GSC 96942, JBW loc. 63.

13. Lateral view, ventral valve, GSC 96939, GSC loc. 56917.

14. Ventral internal mould, GSC 96933, GSC loc. 56917.

15, 16. Anterior and lateral views, ventral internal mould, GSC No. 96940, GSC loc. 53946.

17–19, 23. Dorsal, lateral, ventral, andposterior views, conjoined shell, holotype, GSC 96932, GSC loc. 53947.

20. Abraded dorsal internal mould, GSC 96938, GSC loc. 56917.

21. Dorsal view, reticulate shell, GSC 96936, JBW loc. 113.

22. Ventral valve, GSC 96943, GSC loc. 56917.

24, 26. Anterior and posterior views, ventral valve, GSC 96937, GSC loc. 56917.

25. Ventral valve, GSC 96934, GSC loc. 53946.

27. Ventral valve, GSC 96935, GSC loc. 57052.

Figures 29–39. *Costispinifera paucispinosa* n. sp.

29. Abraded ventral valve, GSC 96956, GSC loc. 57053.

30. Fragment of dorsal interior showing cardinal and lateral ridges, GSC 96957, GSC loc. 57053; x2.

31, 34–37. Posterior-lateral, anterior-lateral, posterior, anterior, and lateral views, ventral valve, GSC 96954, GSC loc. 57053; x2.

32, 33, 39. Posterior, dorsal, and anterior views, conjoined shell, holotype, GSC 96955, GSC loc. 57053; x2.

38. Dorsal external mould, holotype, GSC 96955a, GSC loc. 57053; x2.

Figures 40–42. *Uraloproductus* sp. A.

Dorsal (x2), anterior, and posterior views, conjoined shell, GSC 96980, GSC loc. 53951.

Figure 43. *Uraloproductus* sp. B.

Posterior view, crushed ventral valve, GSC 96981, GSC loc. 57266.

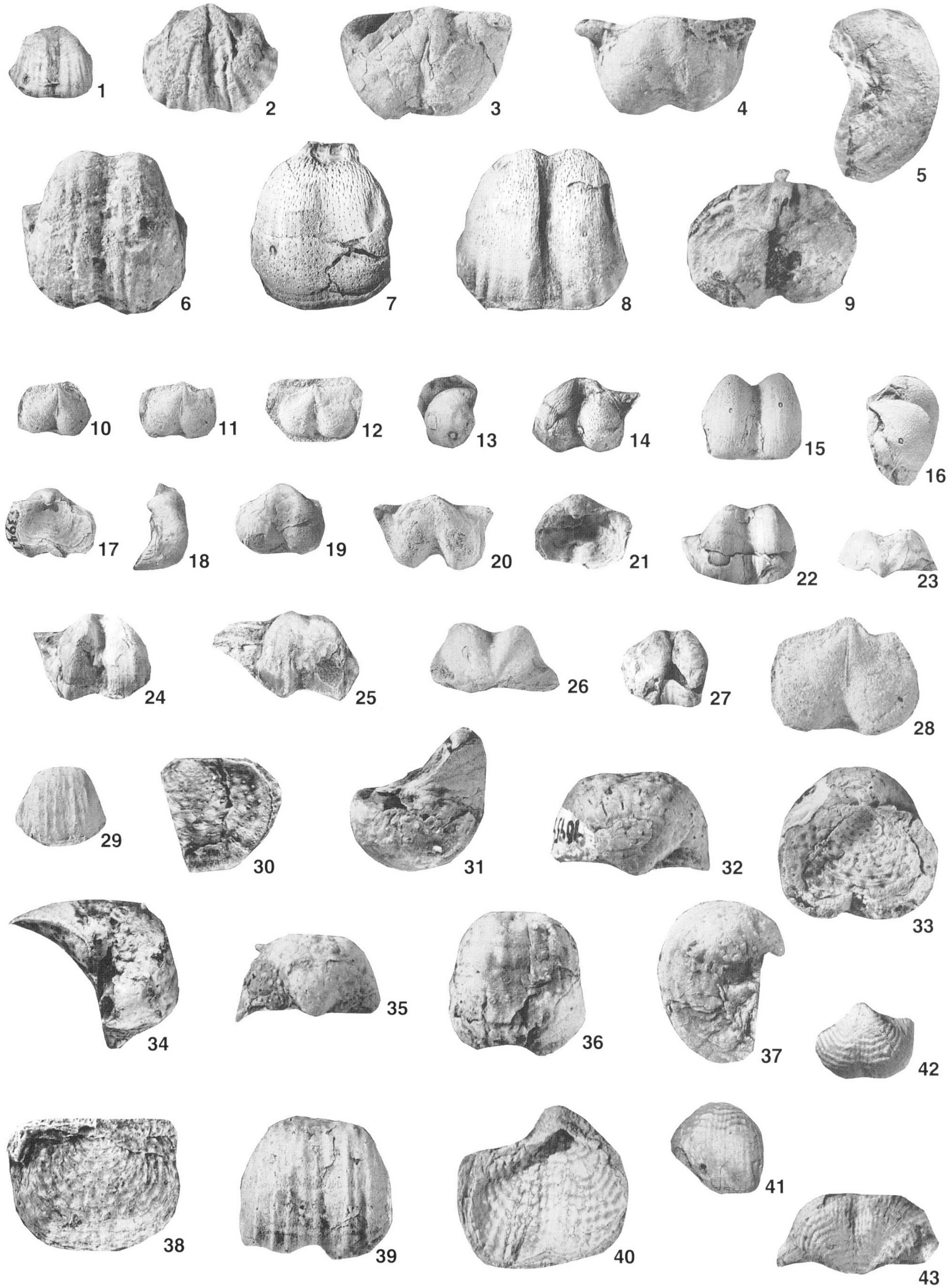
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PLATE 7

Figures 1–19. *Kutorginella yukonensis* Sarytcheva and Waterhouse

1, 2. Dorsal and ventral views, conjoined internal mould, GSC 96962, JBW loc. 24.

3. Dorsal internal mould, GSC 96973, JBW loc. 109.

4. Ventral valve, GSC 96965, JBW loc. 109.

5. Latex cast, dorsal internal mould, GSC 97012, JBW loc. 88.

6–7. Posterior-lateral and ventral views, latex cast, ventral external mould, GSC 96961, JBW loc. 88.

8. Ventral internal mould, GSC 96960, JBW loc. 88.

9–11. Lateral, dorsal, and ventral views, conjoined shell, GSC 96959, JBW loc. 508.

12. Latex cast, dorsal internal mould, GSC 96964, GSC loc. 57052.

13. Ventral internal mould, GSC 96963, JBW loc. 88.

14. Ventral internal mould, GSC 96963, JBW loc. 88.

15. Lateral view, ventral valve, GSC 96958, GSC loc. 53722.

16, 17, 19. Posterior, dorsal, and lateral views, conjoined shell, GSC 26354, GSC loc. 53720.

18. Ventral internal mould, GSC 96966, JBW loc. 88; x2.

Figures 20–22. *Thamnosia spinosa* n. sp.

20. Latex cast, ventral external mould, GSC 96967, GSC loc. 113.

21. Latex cast, ventral external mould, GSC 96971, JBW loc. 135.

22. Latex cast, dorsal internal mould, GSC 96970, JBW loc. 63.

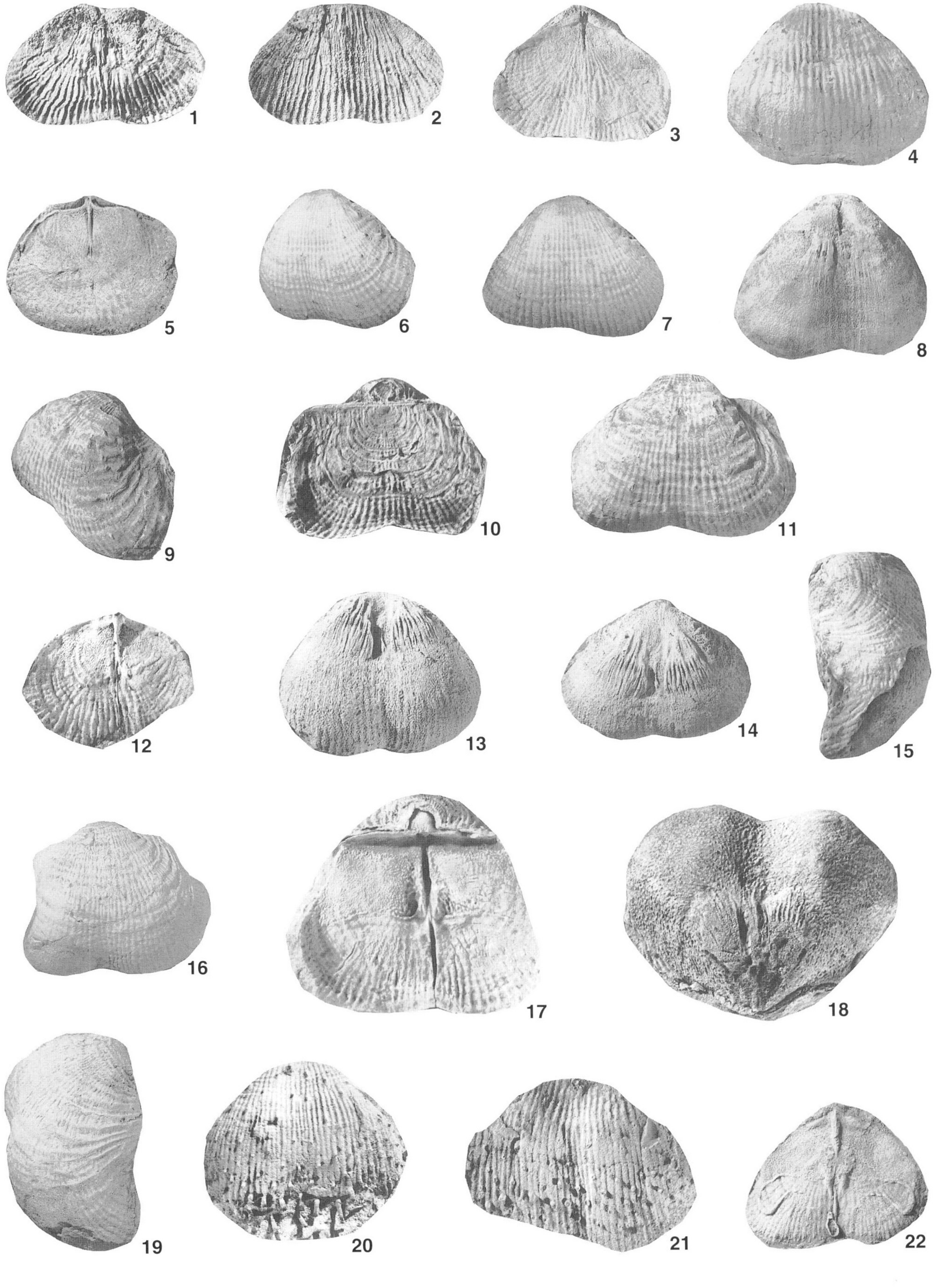
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PLATE 8

Figures 1–8. *Thamnosia spinosa* n. sp.

1, 2, 5. Ventral, dorsal, and lateral views, conjoined shell, GSC 96969, GSC loc. 57053.

3, 4, 7. Posterior, lateral, and anterior views, ventral valve, GSC 96972, JBW loc. 113.

6, 8. Lateral and anterior views, ventral valve, holotype, GSC 96968, GSC loc. 53712.

Figures 9–14. *Rugivestis arctica* n. sp.

9. Ventral view, ventral valve, GSC 96977, GSC loc. 53951; x2.
10. Dorsal external mould, GSC 96974, JBW loc. 113; x2.
11. Ventral internal mould, GSC 96975, JBW loc.109; x2.
12. Ventral view, ventral valve, holotype, GSC 96976, JBW loc. 109; x2.
13. Ventral view, ventral valve, GSC 96978, JBW loc. 113; x2.
14. Ventral view, ventral valve, GSC 96975, JBW loc. 109, x2.

Figures 15–26. *Calliprotonia inexpectum* (Cooper)

15–17, 23. Lateral, posterior, and anterior views, ventral internal mould, GSC 96983, JBW loc. 24; fig. 23 showing ornament (x5).

18. Latex cast, dorsal internal mould, GSC 96986, JBW loc. 24; x2.
19. Latex cast, dorsal external mould with ventral umbo, GSC 96990, JBW loc. 24.
20. Latex cast, ventral external mould, GSC 96985, JBW loc. 24.
21. Posterior view, ventral internal mould, GSC 96982, JBW loc. 24.
22. Latex cast, dorsal external mould with cardinal process, GSC 96984, GSC loc. 57053.
24. Dorsal view, conjoined internal mould, GSC 96987, JBW loc. 109.
25. Dorsal internal mould, GSC 96988, JBW loc. 109; x2.
26. Latex cast, dorsal internal mould, GSC 96989, JBW loc. 88; x2.

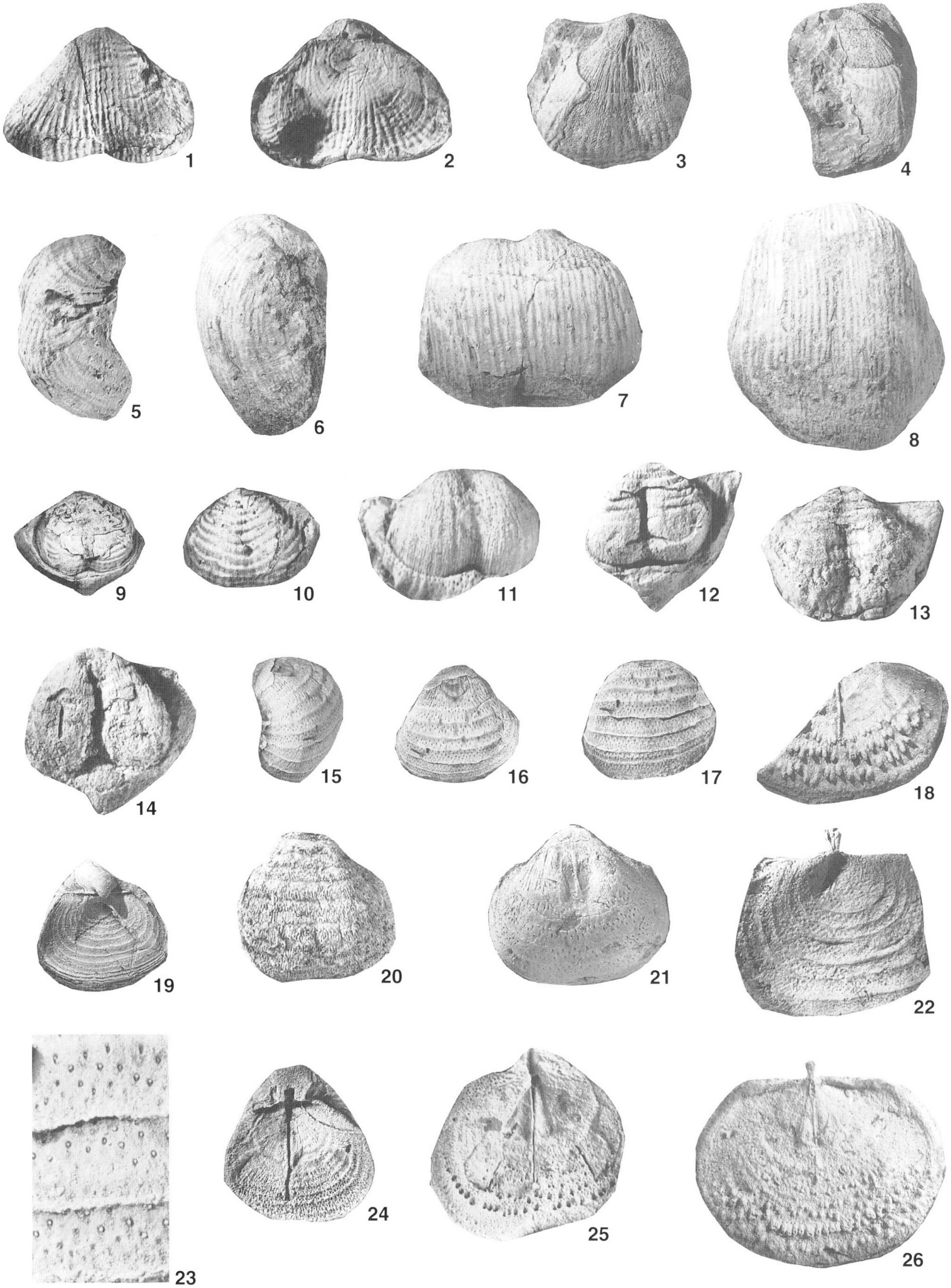
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PLATE 9

Figures 1–3. *Waagenoconcha parvispinosa* Cooper

1. Latex cast, dorsal internal mould, GSC 97001, JBW loc. 88.
2. Dorsal external mould, GSC 97000, GSC loc. 57053.
3. Dorsal external mould, GSC 97002, JBW loc. 88.

Figures 4–15. *Waagenoconcha permocarbonica* Ustritskiy

4. Ventral valve, GSC 96995, GSC loc. 53723.
5. Posterior view, ventral valve, GSC 96994, GSC loc. 53723.
6. Ventral valve, GSC 96992, GSC loc. 53723.
7. Dorsal internal mould, GSC 96996, JBW loc. 54.
8. Dorsal internal mould, GSC 96998, JBW loc. 109.

9, 15. Dorsal external mould, GSC 96997, JBW loc. 109; fig. 15 shows close-set ornament on marginal band (x2).

10, 13, 14. Lateral, ventral, and dorsal views, conjoined internal mould, GSC 96993, JBW loc. 109.

11. Dorsal view, conjoined shell, GSC 96991, JBW loc. 109.

12. Latex cast, dorsal internal mould, showing cardinal process, GSC 96999, JBW loc. 54; x5.

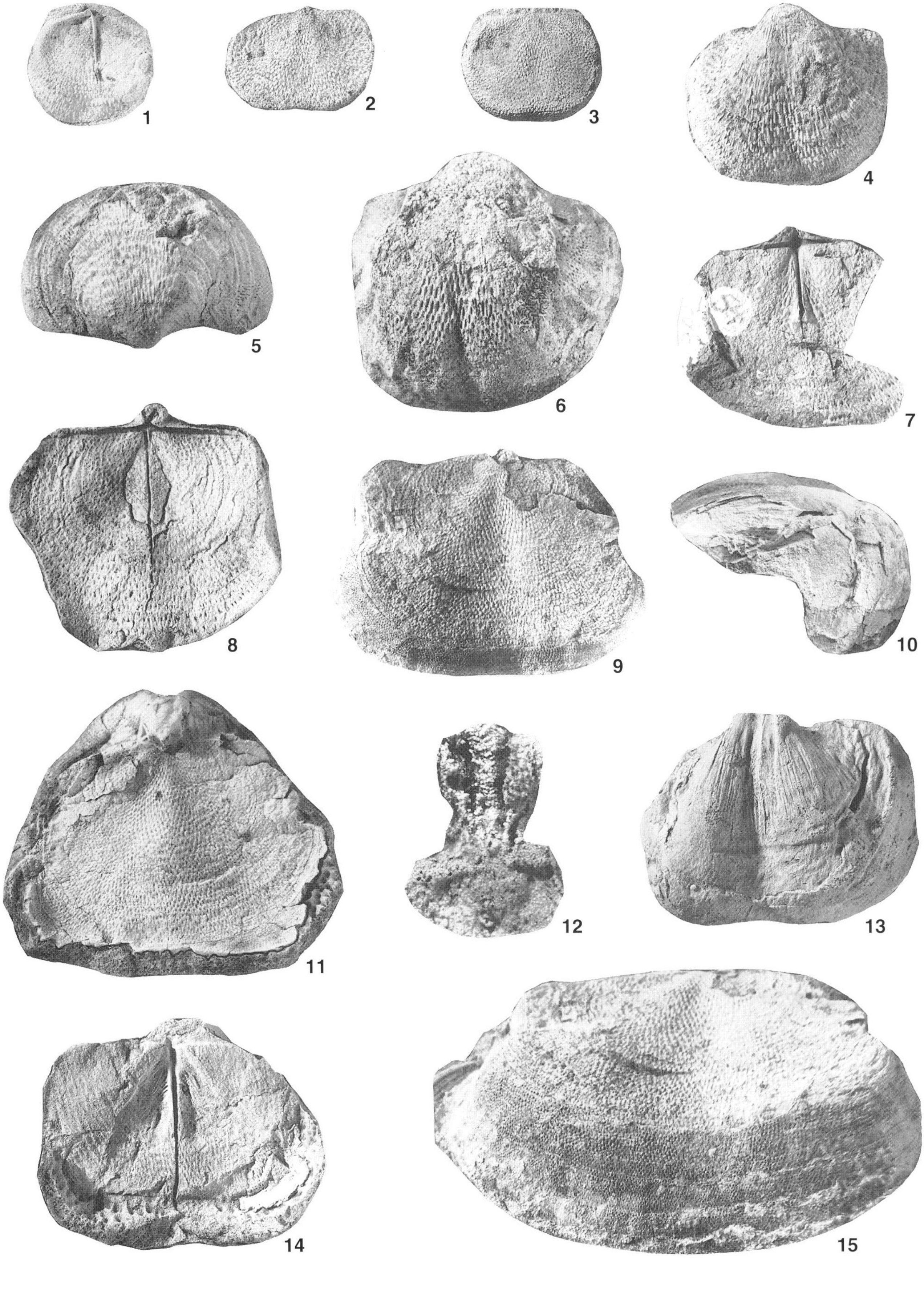
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PLATE 10

Figures 1–4. *Waagenoconcha permocarbonica* Ustritiskiy

1. Ventral view, ventral valve, GSC 96996, JBW loc. 54.
2. Lateral view, ventral valve, GSC 96994, GSC loc. 53723.
3. Anterior view, dorsal valve showing endospines, GSC 96991, JBW loc. 109; x2.
4. Dorsal view, conjoined shell, GSC 96992, GSC loc. 53723.

Figures 5–12. *Kochiproductus porrectus* (Kutorga)

5, 6. Dorsal and ventral views, cardinal process, latex cast of GSC 97004 (see fig. 10); x5, x3 respectively.

7, 10. Ventral and dorsal views, conjoined internal mould, GSC 97004, JBW loc. 109.

8. Dorsal internal mould, showing cardinal process and adductors, GSC 97103, JBW loc. 63.

9. Dorsal internal mould, GSC 97006, JBW loc. 24.

11. Latex cast, dorsal internal mould, GSC 97003, JBW loc. 559; x3.

12. Fragment of a dorsal external mould, GSC 97009, JBW loc. 109.

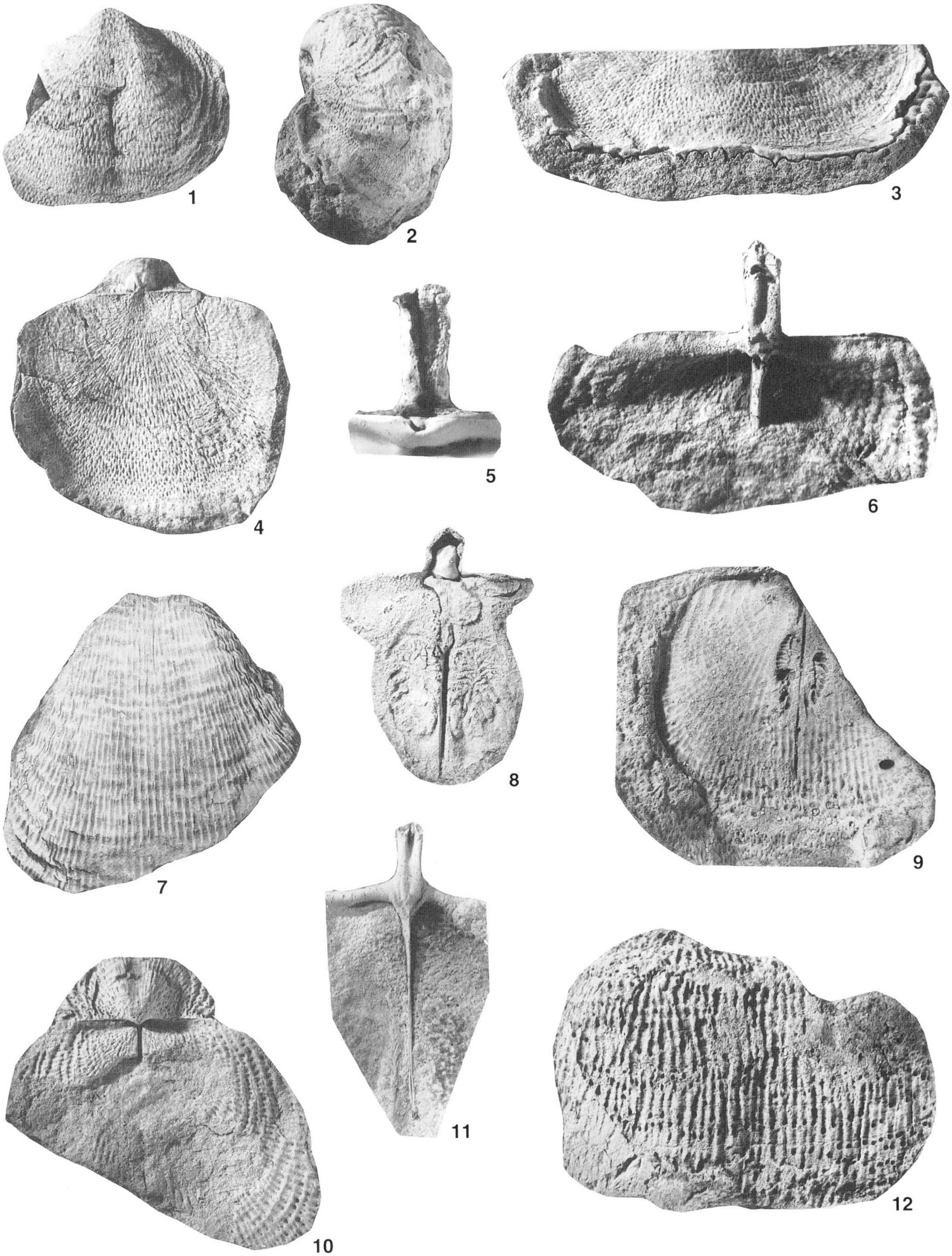
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PLATE 11

Figures 1–6. *Kochiproductus porrectus* (Kutorga)

1. Ventral external mould, showing ramps and spines, GSC 97005, JBW loc. 109.
2. Fragments of dorsal external and internal moulds (with dorsal internal mould of *Kutorginella yukonensis*), GSC 97104, JBW loc. 109.

3, 4. Dorsal internal mould with ventral umbo and dorsal external mould, GSC 97007, JBW loc. 541.

5. Ventral internal mould, GSC 97003, JBW loc. 559.
6. Dorsal external mould, GSC 97008, JBW loc. 541.

Figures 7–10, 12. *Kochiproductus saranaeanus* (Frederiks)

7. Dorsal external mould, GSC 97105, GSC loc. 53723.

8, 10, 12. Anterior, lateral, and posterior views, ventral valve, GSC 97010, GSC loc. 53723; fig. 9 shows ornament (x5).

Figure 11. *Reticulatia uralica* (Chernyshev)

Lateral view, ventral valve, showing hinge spines and a row of spines over ears on umbonal slopes, GSC 97106, GSC loc. 56917.

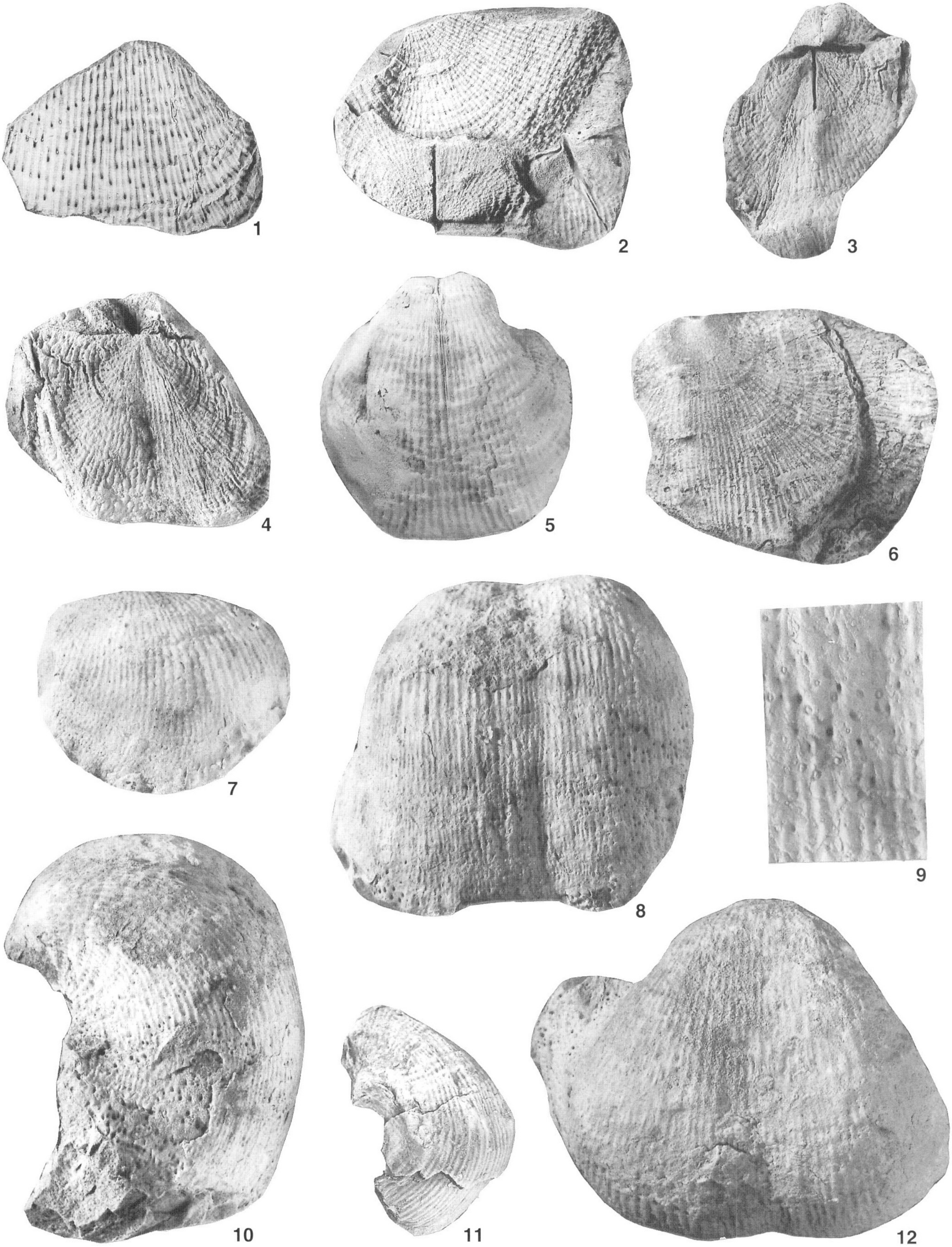
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PLATE 12

Figures 1–11. *Reticulatia uralica* (Chernyshev)

1, 11. Posterior and anterior views, dorsal external mould, GSC 97015, GSC loc. 53704.

2. Dorsal external mould, GSC 97018, JBW loc. 24.

3, 10. Lateral and posterior views, ventral valve, GSC 97016, GSC loc. 53704.

4. Lateral view, dorsal external mould, GSC 97015, GSC loc. 53704.

5. Dorsal view, conjoined shell, GSC 97107, GSC loc. 53704.

6. Dorsal view, conjoined shell, GSC 97108, GSC loc. 53704.

7. Dorsal view, conjoined shell, GSC 97017, GSC loc. 53704.

8. Dorsal interior, showing cardinal process and muscle field, GSC 97014, JBW loc. 57.

9. Posterior view, dorsal external mould with cardinal process, GSC 97022, JBW loc. 24.

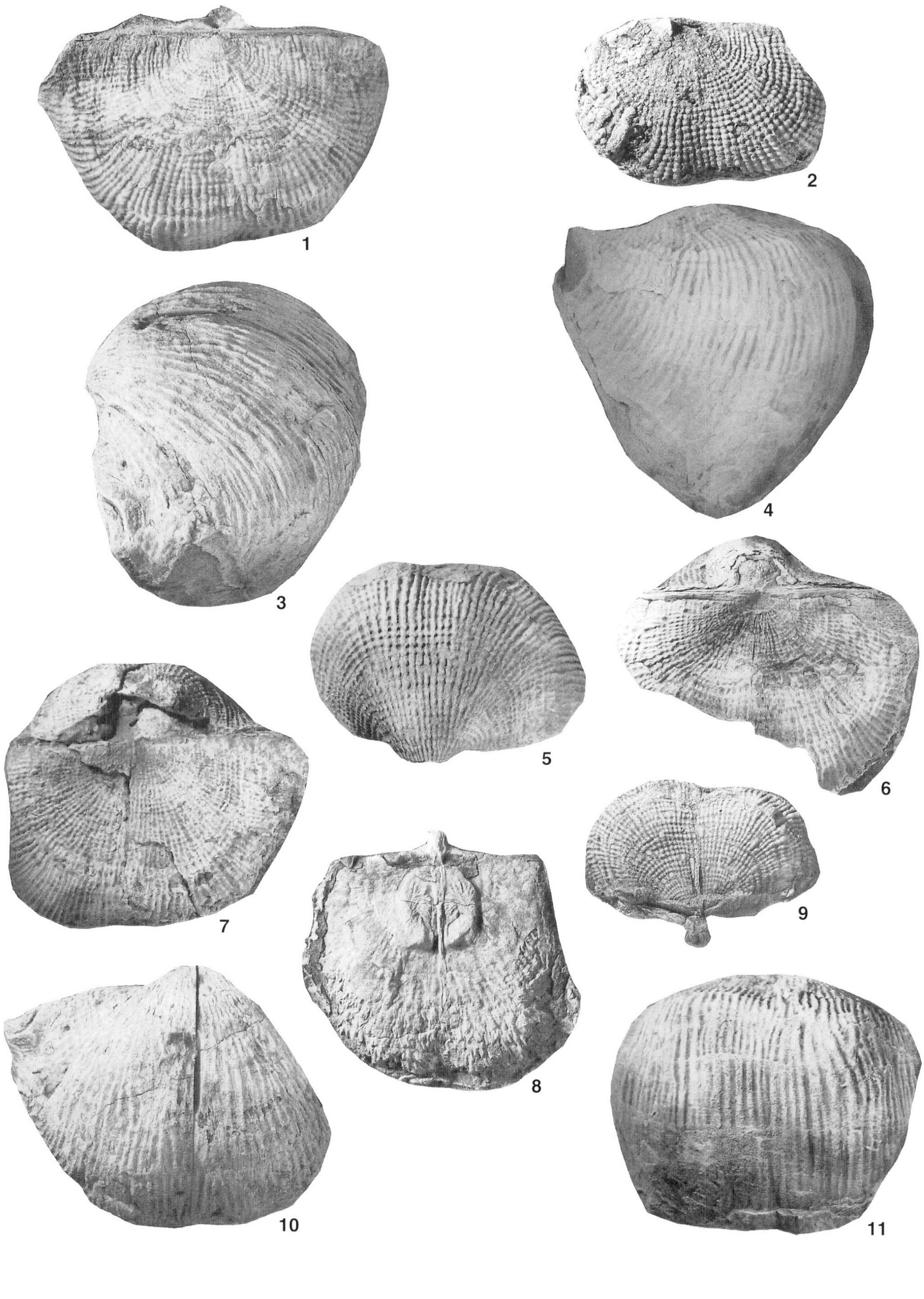
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PLATE 13

Figures 1, 2. *Reticulatia uralica* (Chernyshev)

Ventral and dorsal views, conjoined shell, GSC 97020, JBW loc. 57.

Figures 3–11. *Antiquatonia cooperi* Shi

3, 5, 6. Lateral, anterior, and posterior views, ventral valve, GSC 97019, JBW loc. 14.

4. Ventral view, ventral valve, GSC 97011, GSC loc. 53713.

7, 8. Posterior and lateral views, dorsal external mould, GSC 97013, JBW loc. 24.

9–11. Ventral, dorsal, and lateral views, conjoined shell, GSC 97012, JBW loc. 24.

Figures 12–17. *Chaoiella* sp.

12–15. Posterior, lateral, dorsal and ventral views, conjoined shell, GSC 97023, GSC loc. 53947.

16. Anterior view, dorsal external mould, GSC 97024, GSC loc. 53954.

17. Posterior view, dorsal external mould. GSC 97025, JBW loc. 9.

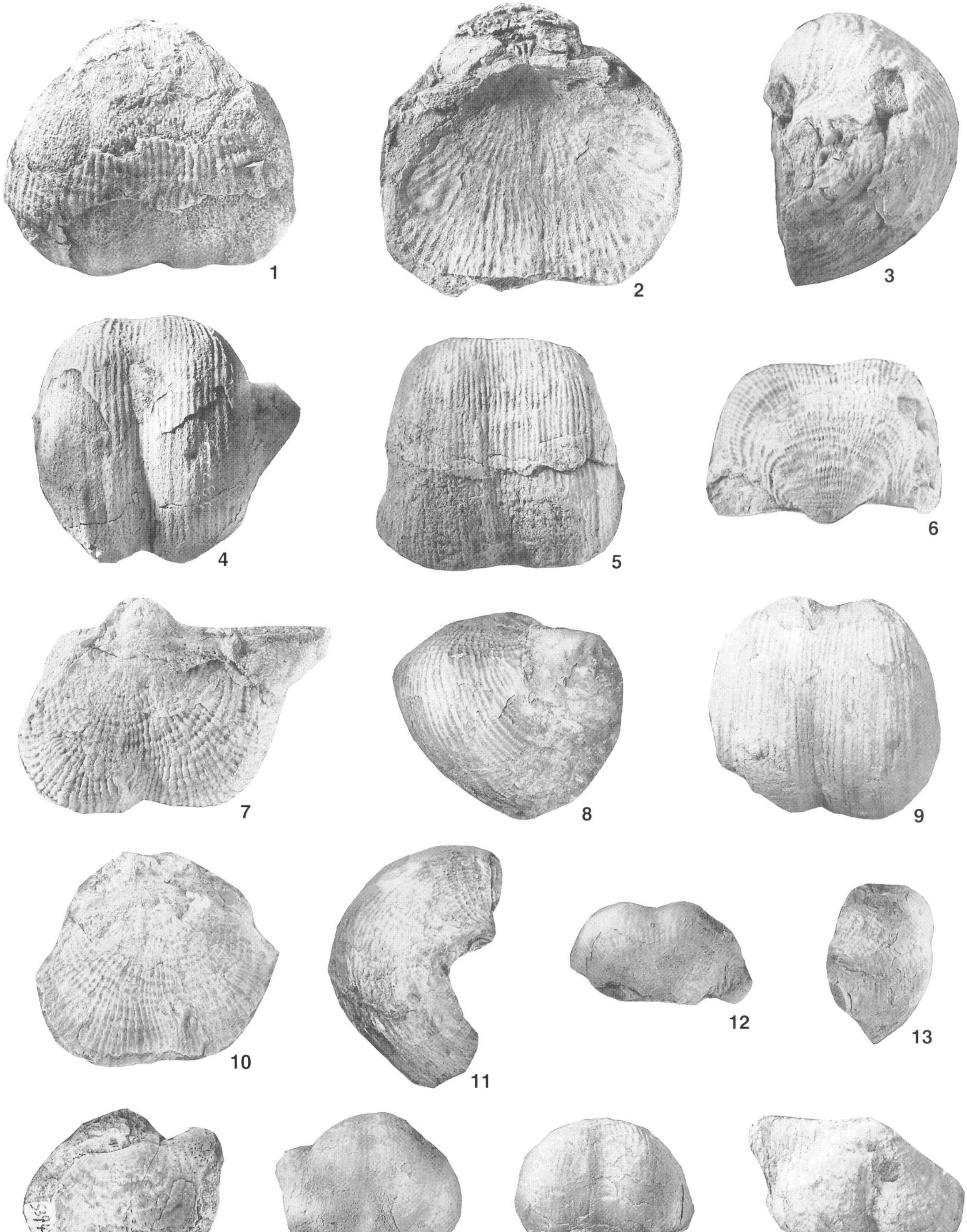
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PLATE 14

Figures 1–21. *Sowerbina bullocki* (Nelson and Johnson)

1. Dorsal view, dorsal valve with cardinal process, GSC 97033, GSC loc. 56937.
2. Lateral view, ventral valve, showing a large ear and striated diductors, GSC 97035, GSC loc. 56937.
3. Ventral internal mould, showing muscle field, GSC 97029, GSC loc. 56937.
4. Posterior view, ventral valve, showing a row of dimples near hinge margin, GSC 97030, GSC loc. 53856.
5. Ventral view, ventral valve, GSC 97034, GSC loc. 56937.
6. Dorsal view, dorsal valve, GSC 97110, GSC loc. 56937.

7, 15, 16. Posterior, anterior, and lateral views, ventral internal valve, GSC 97026, GSC loc. 53856.

8. Ventral view, ventral valve, GSC 97019, GSC loc. 53856.

9, 10. Lateral and ventral views, ventral internal mould, GSC 97034, GSC loc. 56937.

11. Dorsal external mould with cardinal process, GSC 97036, GSC loc. 56937.

12. Dorsal external mould, showing dorsal hinge spines, GSC 97028, GSC loc. 56937.

13, 14. Ventral and posterior views, ventral internal mould, GSC 97027, GSC loc. 56937.

17, 18. Ventral and dorsal views, cardinal process, GSC 97032, GSC loc. 53856; x4.

19. Lateral view, abraded ventral valve, showing microornament, GSC 97111, GSC loc. 53856.

21. Fragment of a dorsal valve, showing dorsal hinge spines, GSC 97112, GSC loc. 53856; x2.

Figures 22–26. *Tityrophoria nelsoni* Waterhouse

22, 23. Dorsal and ventral views, conjoined shell, GSC 97041, GSC loc. 57052.

24. Posterior view, ventral valve, GSC 97113, GSC loc. 56922.

25. Anterior view, ventral valve, GSC 97040, GSC loc. 56922.

26. Dorsal interior, showing cardinal and lateral ridges, GSC 97044, GSC loc. 56917.

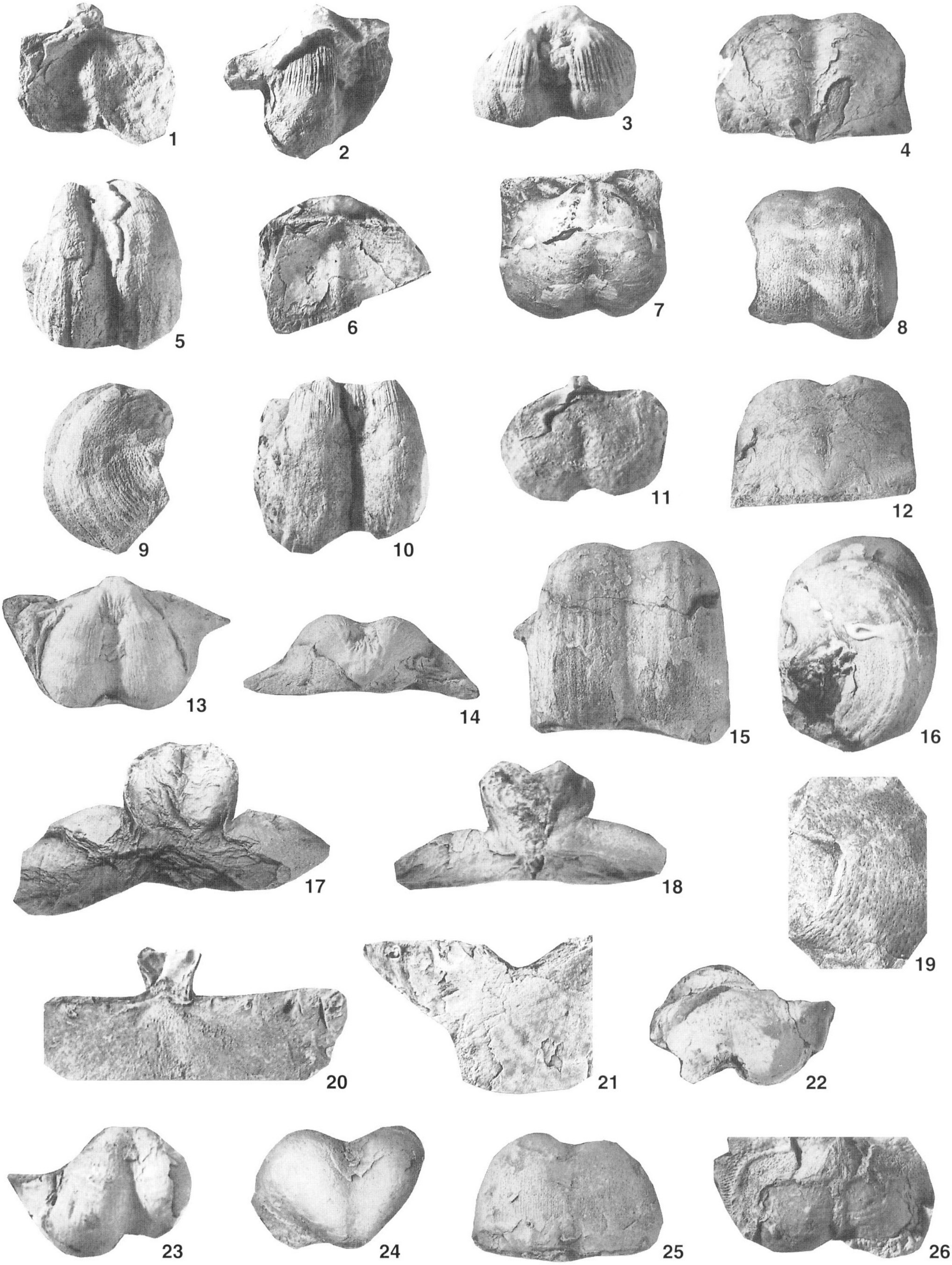
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PLATE 15

Figures 1–8. *Tityrophoria nelsoni* Waterhouse

1. Latex cast, ventral external mould, showing few coarse spines, GSC 97037, JBW loc. 56.
2. Ventral internal mould, showing adductor and diductors, GSC 97039, GSC loc. 57052.
3. Dorsal external mould, GSC 96880; GSC loc. 56922.
4. Ventral view of cardinal process, GSC 97346, GSC loc. 57052; x5.
5. Ventral internal mould, GSC 97114, GSC loc. 57052.
6. Posterior view, ventral valve, showing hinge spines, GSC 97043, GSC loc. 56922.
7. Ventral view, ventral valve, GSC 97038, GSC loc. 57052.
8. Dorsal interior, showing cardinal process, muscle field, and brachial ridges, GSC 97042, GSC loc. 56922.

Figures 9–24. *Globiella costellata* n. sp.

9–12, 15. Posterior, lateral, posterior–lateral, lateral,and dorsal views, conjoined shell, holotype, GSC 97060, GSC loc. 53720.

13. Ventral view, ventral valve, showing strut spines (see arrows), GSC 97115, GSC loc. 53774.

14. Posterior view, ventral valve, GSC 97062, GSC loc. 53705.

16, 21, 23. Posterior, anterior, and lateral views, dorsal external mould, GSC 97059, GSC loc. 53703.

17. Posterior view, ventral internal mould, showing the lobate, smooth ventral adductor, GSC 97061, GSC loc. 53951.

18. Dorsal external mould, GSC 97116, GSC loc.53703.

19. Ventral valve, GSC 97063, JBW loc. 113.

20. Ventral view, ventral valve, GSC 97062, GSC loc. 53705.

22. Posterior view, ventral valve, GSC 97117, GSC loc. 57266.

24. Ventral view, ventral valve, GSC 97064, GSC loc. 53705.

Figures 25–28. *Linoproductus dorotheevi* (Frederiks)

25. Fragment of a ventral valve, showing halteroid spines (see arrows), GSC 97068, JBW loc. 109.

26, 27. Ventral and dorsal views, conjoined shell, GSC 97069, JBW loc. 109.

28. Lateral view, ventral valve, GSC 97118, GSC loc. 56937.

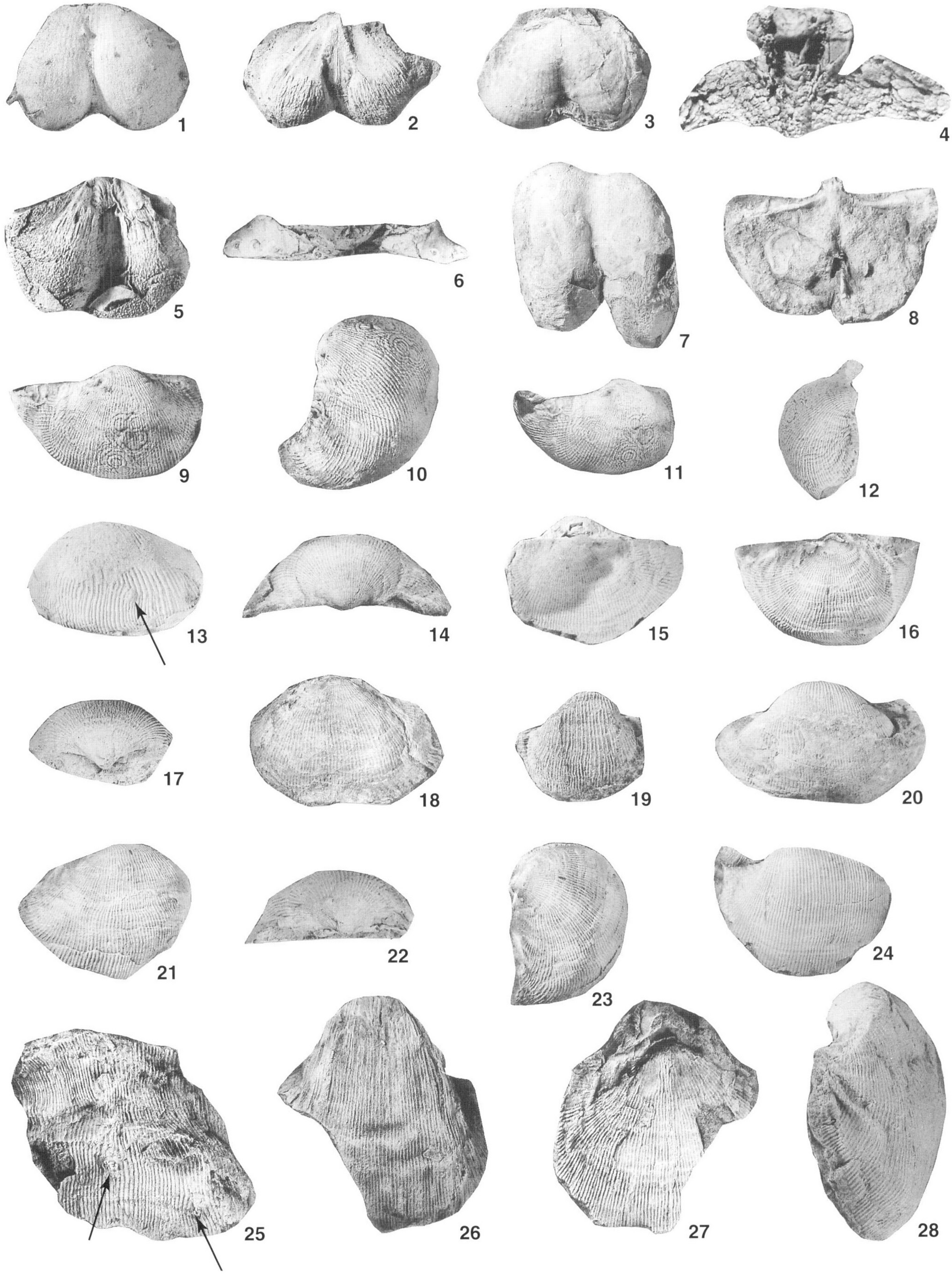
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PLATE 16

Figures 1–9, 11. *Linoproductus dorotheevi* (Fredericks)

1, 4. Ventral and dorsal views, conjoined shell, GSC 97066, JBW loc. 109.

2, 6. Ventral and posterior views, ventral internal mould, GSC 97067, GSC loc. 56937.

3. Abraded ventral valve, GSC 97118, GSC loc. 56937.

5, 7, 9. Posterior–lateral, ventral, and lateral views, ventral valve, GSC 97065, JBW loc. 109.

8. Ventral view, ventral valve, GSC 97070, JBW loc. 109.

11. Fragment of dorsal external mould, GSC 97074, JBW loc. 109.

Figures 10, 12. *Schrenkiella* sp.

10. Dorsal external mould, GSC 97072, JBW loc. 9.

12. Dorsal external mould, GSC 97073, JBW loc. 113.

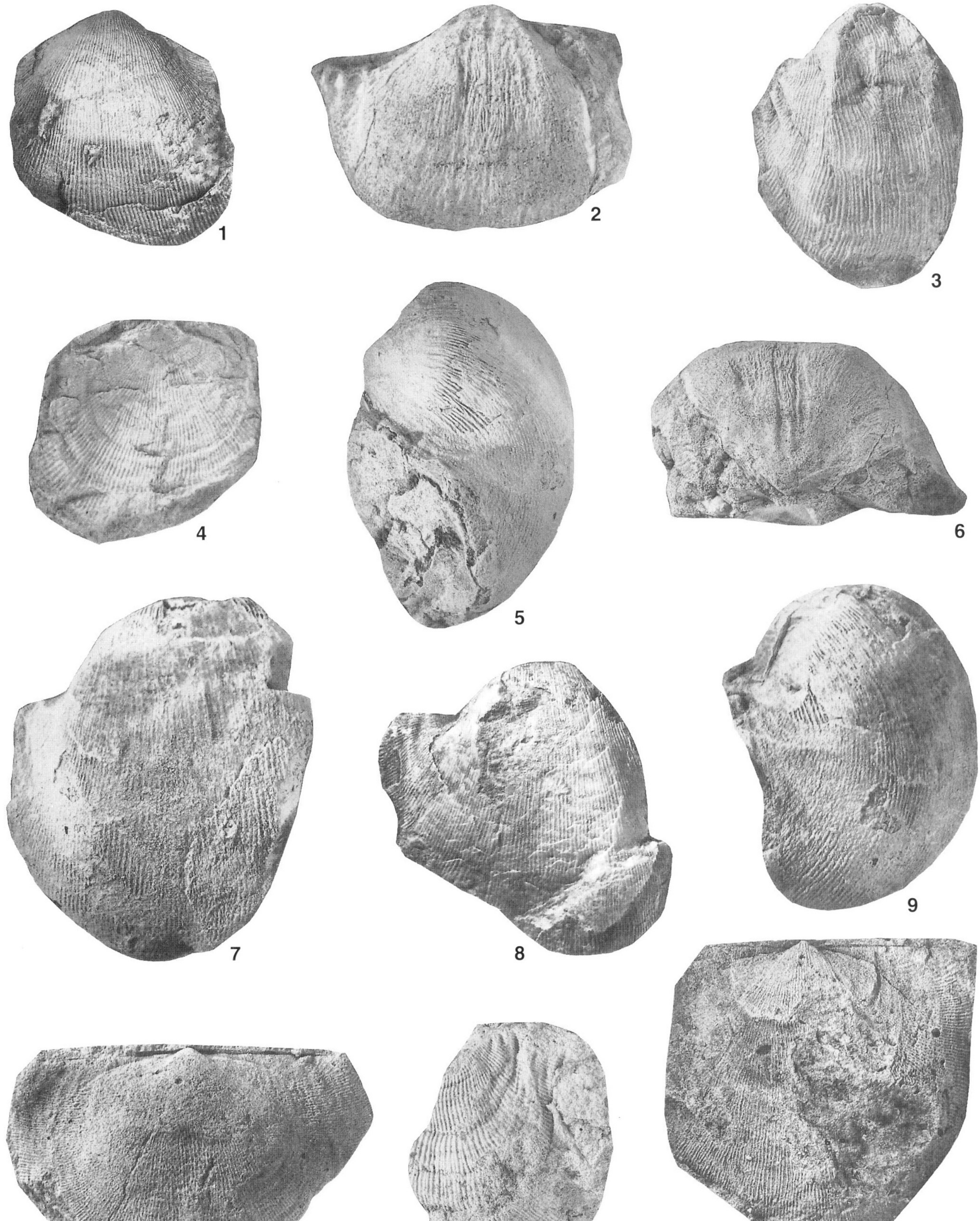
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PLATE 17

Figures 1–9. *Cancrinella cancriniformis* (Chernyshev)

1. Lateral view, ventral valve, GSC 97119, GSC loc. 53714.
2. Dorsal external mould, GSC 97075, GSC loc. 53714.

3, 6, 8. Anterior and posterior views, and enlargement (x2), dorsal external mould, GSC 97078, JBW loc. 508.

4, 5, 9. Posterior and anterior views, dorsal external mould with ventral trail, GSC 97076, GSC loc. 53714; fig. 9 showing ventral spines (x2).

7. Lateral view, ventral valve, GSC 97077, GSC loc. 53714.

Figures 10–20. *Cancrinella singletoni* Gobbett

10, 11. Posterior and lateral views, ventral valve, GSC 97120, JBW loc. 88; x2.

12, 14, 15, 18. Lateral, ventral, and dorsal views, conjoined shell, GSC 97080, JBW loc. 88; x2; fig. 18 enlarged to show spines (x5).

13. Anterior–lateral view, dorsal external mould, GSC 97121, JBW loc. 121; x2.

16, 17. Posterior and anterior views, ventral valve, GSC 97079, JBW loc. 89; x2.

19. External mould, ventral fragment, GSC 97081, JBW loc. 88; x2.5.

20. Latex cast, ventral external mould, GSC 97083, JBW loc. 89; x5.

Figures 21, 22, 24. *Terrakea*? sp.

21, 24. Latex cast and dorsal external mould, GSC 96848, JBW loc. 113.

22. Dorsal external mould with ventral fragment at front, GSC 97085, JBW loc. 537.

Figures 23, 25, 26. Linoproductid gen. sp. indet.

Latex cast, dorsal external mould, GSC 97084, JBW loc. 113, showing spine bases; x3; figs. 25, 26 latex cast and dorsal external mould.

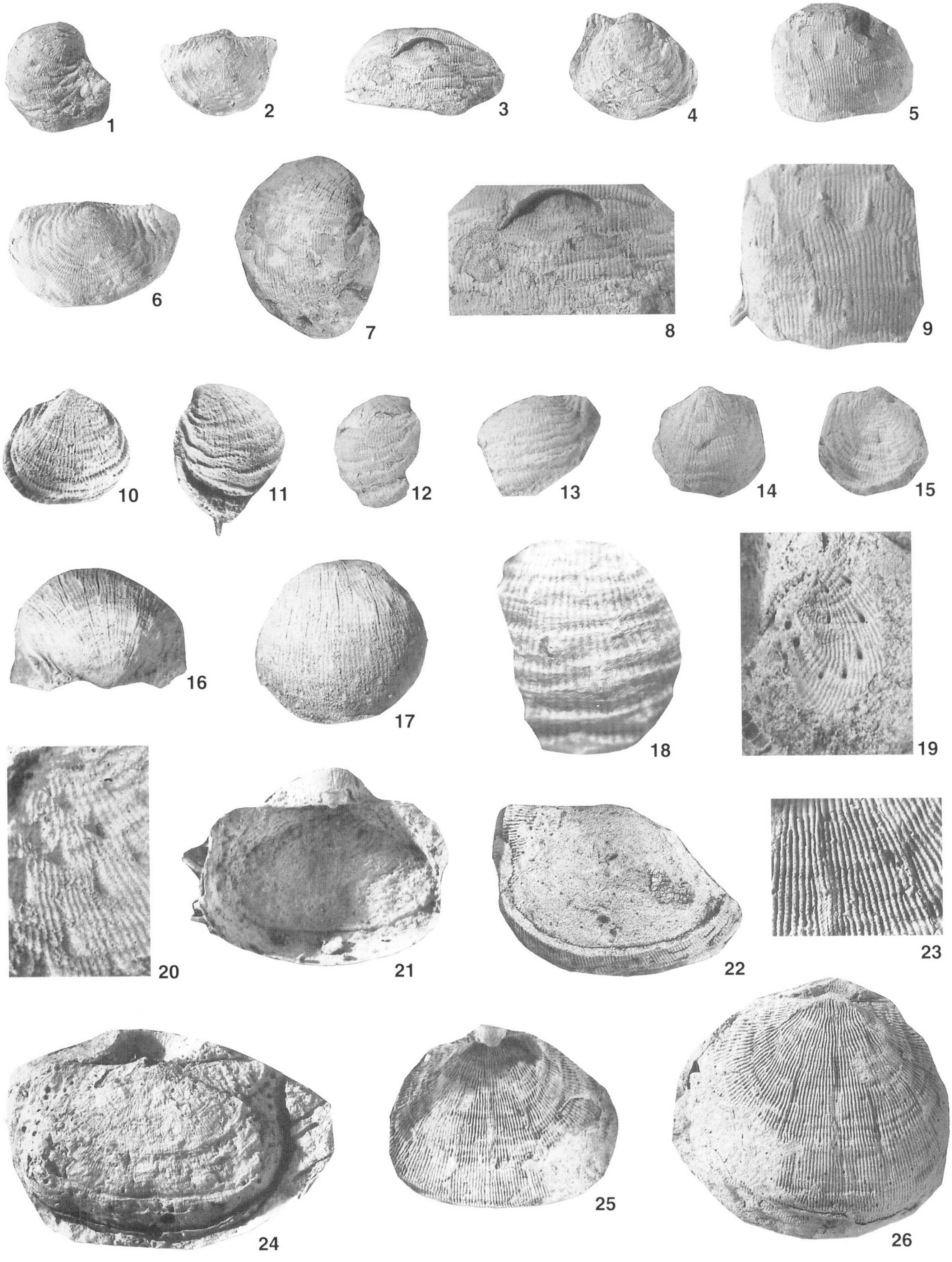
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PLATE 18

Figures 1–16. *Protoanidanthus umbonatus* n. sp.

1, 2. Posterior views, ventral internal mould, showing muscle field, GSC 97122, JBW loc. 89; x2.
3. Latex cast, dorsal internal mould, GSC 97124, JBW loc. 89; x2.
4. Dorsal external mould, GSC 97125, JBW loc. 88; x2.
5. Ventral internal mould, GSC 97127, BW loc. 89; x2.
6. Latex cast, ventral external mould, holotype, GSC 97128, JBW loc. 89; x2.
7. Dorsal external mould, GSC 97130, JBW loc. 89; x2.
8. Ventral internal mould, GSC 97126, JBW loc. 89; x2.
9. Ventral internal mould, GSC 97129, JBW loc. 64; x2.
10. Latex cast, ventral external mould, GSC 97131, JBW loc. 57; x2.
11. Latex cast, ventral external mould, GSC 97132, JBW loc. 89; x2.
12. Complete dorsal external mould, showing small dorsal ears, GSC 97123, JBW loc. 89; x2.
13. Latex cast, ventral internal mould with dorsal valve, GSC 97133, JBW loc. 89; x2.
14. Latex cast, ventral external moulds, GSC 97134, JBW loc. 89; x2.
15. Dorsal internal mould, GSC 97123, JBW loc. 89; x2.
16. Latex cast, dorsal internal mould, GSC 97136, JBW loc. 89; x2.

Figures 17–24. *Anidanthus* cf. *A. boikowi* Abramov and Grigor'yeva

17. Posterior view, ventral valve, GSC 97140, JBW loc. 2; x2.
18. Posterior view, ventral internal mould, GSC 97137, JBW loc. 14.
19. Ventral view, ventral valve, GSC 97139, JBW loc. 2; x2.
20. Posterior view, dorsal external mould, GSC 97138, JBW loc. 2; x2.
21. Ventral view, ventral valve, GSC 97142, JBW loc. 2; x2.
22. Ventral view, ventral valve, showing a weak sulcus, GSC 97140, JBW loc. 2; x2.
23. Posterior view, ventral valve, GSC 97141, JBW loc. 2; x2.
24. Dorsal interior, showing cardinal process and large alate dorsal ear, GSC 97143, JBW loc. 526; x2.

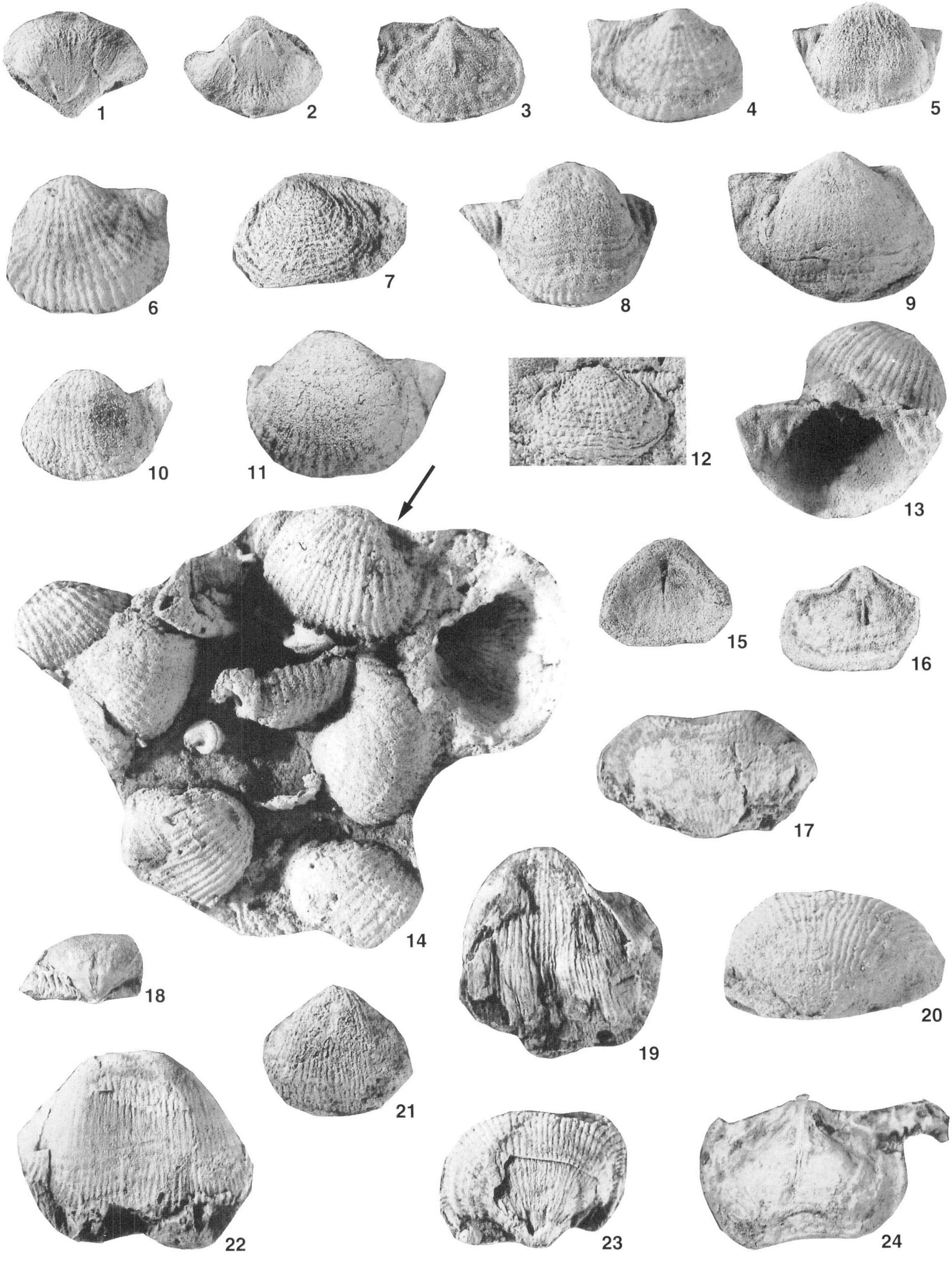
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PLATE 19

Figures 1–32. *Yakovlevia transversa* (Cooper)

1, 3. Anterior and posterior views, ventral valve, GSC 97146, GSC loc. 53999.
2. Posterior view, ventral valve, GSC 97058, JBW loc. 24.
4. Latex cast, dorsal internal mould, GSC 97055, JBW loc. 88.
5, 19. Lateral and anterior views, ventral valve, GSC 97049, GSC loc. 53721.
6. Posterior view, ventral valve, GSC 97153, GSC loc. 53946.
7, 8. Ventral and posterior views, ventral internal mould, GSC 97144, GSC loc. 53999.
9, 16. Posterior and anterior views, ventral valve, GSC 97045, GSC loc. 53721.
10. Posterior view, dorsal external mould, GSC 97148, GSC loc. 53703.
11. Ventral internal mould, showing muscle scars, GSC 97152, JBW loc. 88.
12, 26. Latex cast and ventral internal mould, showing muscle scars, GSC 97051, JBW loc. 88.
13. Posterior view, ventral valve, GSC 97047, GSC loc. 53721.
14. Latex cast, dorsal internal mould, GSC 97052, GSC loc. 88.
15, 29. Anterior and posterior views, ventral valve, GSC 97154, GSC loc. 53862.
17. Anterior view, ventral valve, GSC 97149, GSC loc. 56972.
18. Lateral view, ventral valve, GSC 97147, GSC loc. 53703.
20, 27. Anterior and posterior views, ventral valve, GSC 97054, GSC loc. 56972.
21. Posterior view, ventral valve, GSC 97658, GSC loc. 57141.
22. Posterior view, conjoined shell, showing ginglymus, GSC 97056, GSC loc. 53703; x2.
23. Dorsal external mould, GSC 97155, GSC loc. 53860.
24. Posterior view, ventral valve, GSC 97046, GSC loc. 56972.
25. Lateral view, ventral internal mould, showing lateral ridge, GSC 97053, GSC loc. 53860.
28. Posterior view, ventral internal mould, GSC 97057, JBW loc. 113.
30. Dorsal external mould, GSC 97156, GSC loc. 53860.
31. Dorsal view, conjoined shell, GSC 97145, GSC loc. 53721.
32. Posterior view, ventral valve, GSC 97050, GSC loc. 53703.

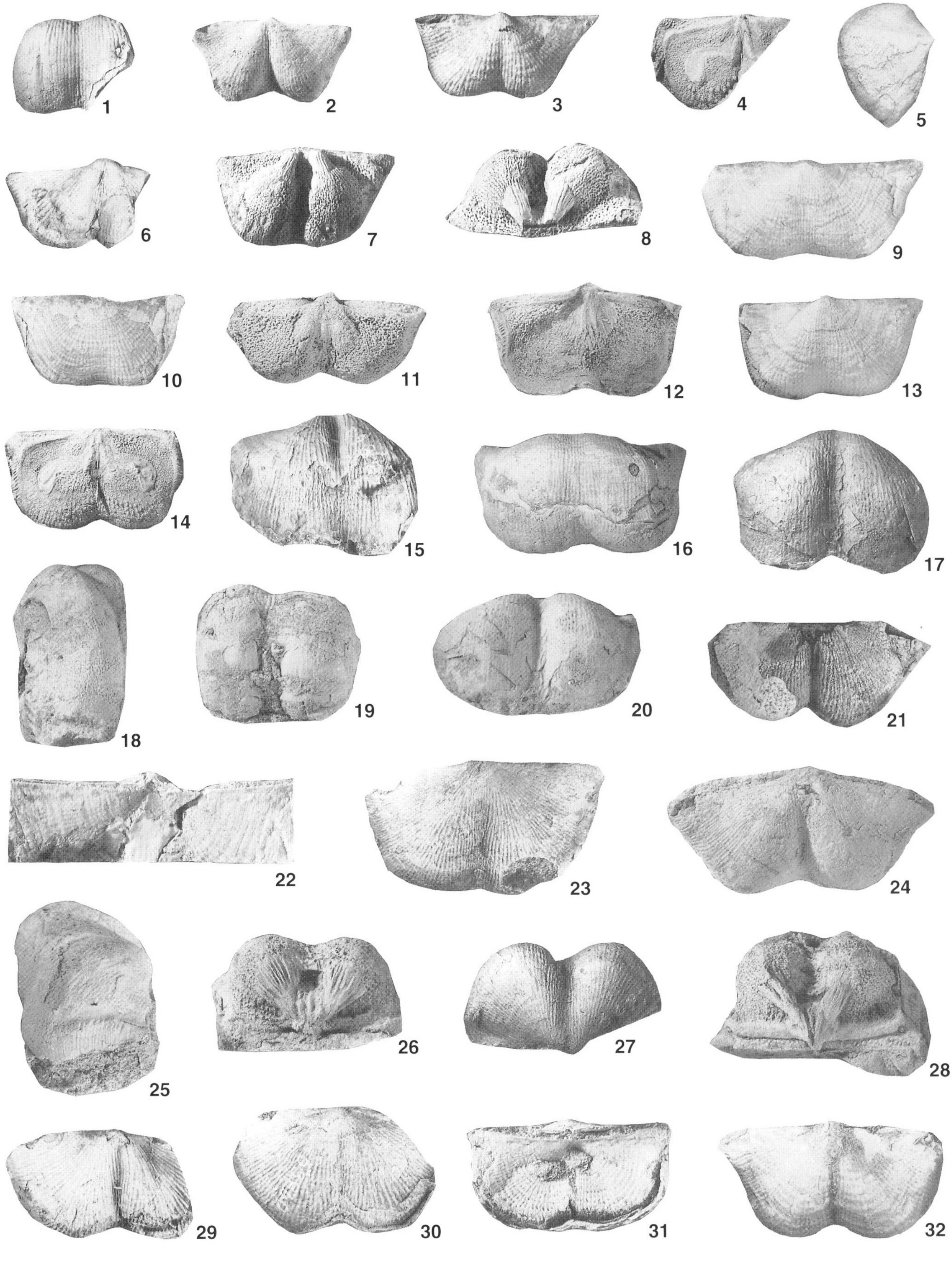
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PLATE 20

Figures 1–13. *Rhynoleichus dorsoconvexa* n. sp.

1, 3, 4. Posterior, dorsal, and ventral views, conjoined internal mould, showing ventral and dorsal internal plates, GSC 97159, JBW loc. 24.

2, 7. Anterior and dorsal views, conjoined internal mould, GSC 97162, GSC loc. 53952.

5. Ventral internal mould, GSC 97158, GSC loc. 53812.

6. Ventral internal mould, GSC 97160, JBW loc. 2.

8–12. Ventral posterior, lateral, ventral-anterior, anterior, posterior views, conjoined shell, holotype, GSC 97157, JBW loc. 15.

13. Dorsal internal mould, GSC 97161, GSC loc. 53812; x2.

Figures 14–27. *Septacamera triangulata* n. sp.

14. Dorsal valve, GSC 97165, GSC loc. 56917.

15, 16. Latex cast and dorsal internal mould, GSC 97166, GSC loc. 57052.

17, 22. Ventral internal mould and latex cast, showing spondylium and pallial markings, GSC 97164, GSC loc. 57275.

18. Ventral internal mould with partly preserved exterior, GSC 97171, GSC loc. 56922.

19, 20. Latex cast and dorsal internal mould, GSC 97168, GSC loc. 56922.

21. Lateral view, dorsal valve, GSC 97169, GSC loc. 56922.

23. Ventral valve, GSC 97167, GSC loc. 57052.

24. Ventral valve, GSC 97172, GSC loc. 57052; x2.

25. Dorsal internal mould, GSC 97168, GSC loc. 56922.

26. Ventral interior, GSC 97170, GSC loc. 56922; x2.

27. Ventral valve, holotype, GSC 97163, GSC loc. 57275.

Figures 28–34. *Rhynchopora magna* Cooper

28, 29. Ventral and dorsal views, conjoined internal mould, GSC 97175, JBW loc. 2.

30, 31. Ventral and lateral views, conjoined shell, GSC 97176, GSC loc. 53714.

32, 33. Ventral and lateral views, conjoined shell, GSC 97177, GSC loc. 53714.

34. Anterior view, conjoined shell, GSC 97174, JBW loc. 88.

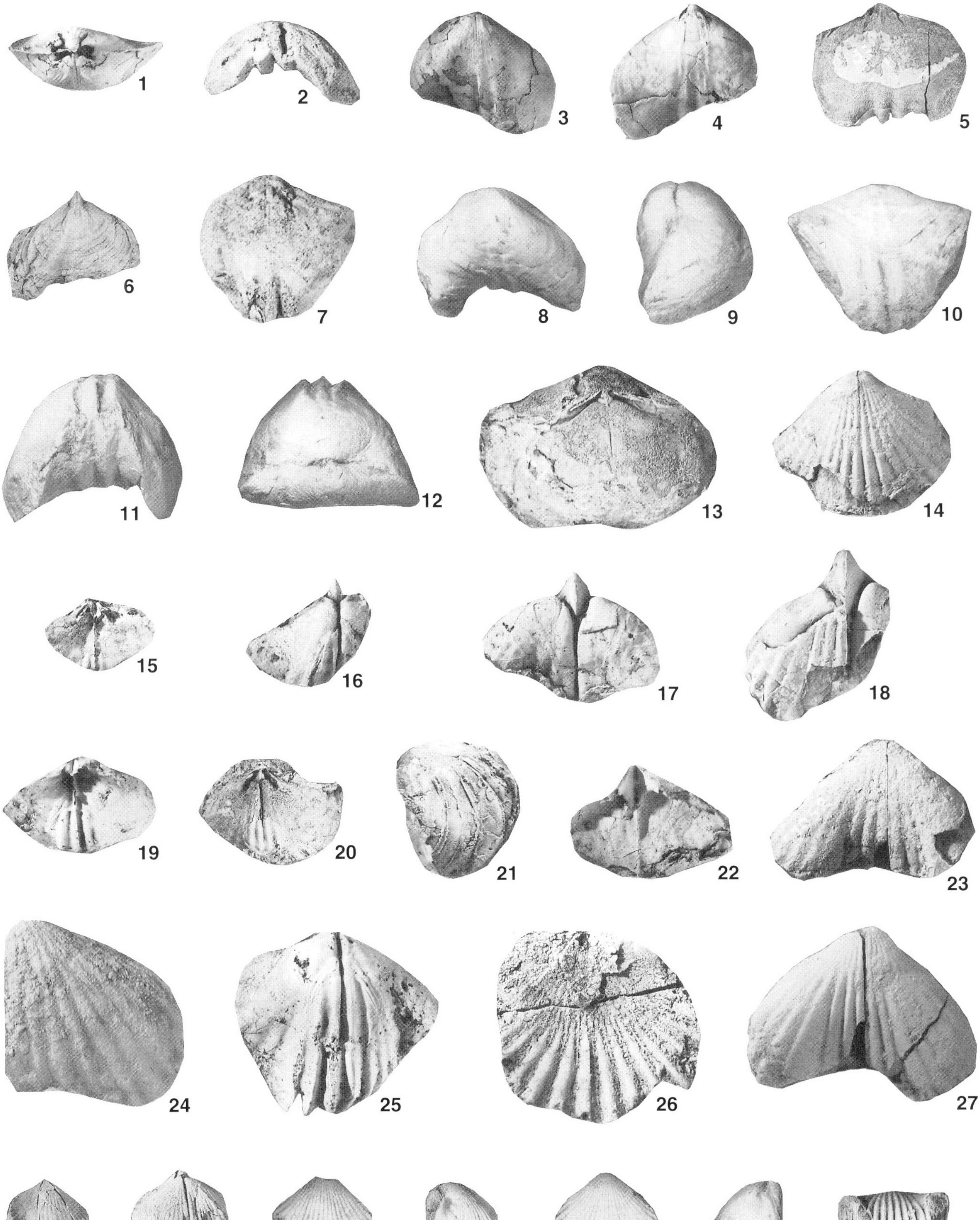
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PLATE 21

Figure 1–3. *Rhynchopora magna* Cooper
1. Dorsal view, conjoined shell, GSC 97178, GSC loc. 53714.
2. Dorsal view, conjoined internal mould, GSC 97173, JBW loc. 113.
3. Posterior view, conjoined shell, GSC 97177, GSC loc. 53714.

Figures 4–14. *Stenoscisma mutabilis* (Chernyshev)
4. Ventral valve, GSC 97174, GSC loc. 53722.
5. Posterior view, conjoined internal mould, GSC 97185, GSC loc. 53999.
6. Ventral valve, GSC 97183, JBW loc. 57.
7. Ventral valve, GSC 97182, JBW loc. 508.
8. Ventral internal mould, GSC 97181, GSC loc. 57141.

9–13. Anterior, ventral, dorsal, lateral, and dorsal views, conjoined shell, GSC 97180, JBW loc. 57.

14. Ventral valve, GSC 97659, JBW loc. 57.

Figures 15–22. *Camerisma* (*Callaiapsida*) *pentameroides* (Chernyshev)

15. Lateral view, conjoined internal mould, GSC 97186, GSC loc. 57053.

16, 17. Ventral and posterior views, conjoined internal mould, GSC 97189, GSC loc. 57053.

18, 19. Ventral and anterior views, ventral internal mould, GSC 97188, JBW loc. 88.

20. Posterior view, conjoined shell, GSC 97190, JBW loc. 113.
21. Lateral view, conjoined shell, GSC 97187, GSC loc. 57053.
22. Latex cast, ventral internal mould, GSC 97191, JBW loc. 109.

Figure 23. *Hustedia* cf. *H. remota* (Eichwald)

Ventral valve, GSC 97192, JBW loc. 109; x2.

Figures 24–29. *Composita bamberi* n. sp.

24, 25. Posterior and lateral views, conjoined internal mould, GSC 97194, GSC loc. 53703.

26–29. Anterior, ventral, dorsal, and lateral views, conjoined shell, holotype, GSC 97195, GSC loc. 53703.

Figures 30, 31. *Composita* sp.

Dorsal and ventral views, immature shell, GSC 97194, GSC loc. 53703; x2.

Figures 32–44. *Ogilviecoelia inflata* n. gen. et sp.

32. Ventral view, ventral valve, GSC 97198, GSC loc. 53716; x2.
33. Ventral internal mould, showing muscle impressions, GSC 97205, GSC loc. 53999; x2.

34, 42. Anterior lateral and lateral views, ventral valve, GSC 97196, GSC loc. 53715; x2.

35, 37, 40. Lateral, dorsal, and ventral views, conjoined shell, holotype, GSC 97201, GSC loc. 53715; x2.

36. Ventral view, ventral valve, GSC 97199, GSC loc. 53715; x2.
38. Dorsal view, conjoined internal mould, GSC 97197, GSC loc. 53716; x3.
39. Latex cast, ventral internal mould, GSC 97203, GSC loc. 53999; x3.
41. Dorsal view, conjoined shell, GSC 97200, GSC loc. 53716; x2.
43. Latex cast, ventral internal mould, showing interarea and median septum, GSC 97204, GSC loc. 53999; x2.
44. Dorsal internal mould, showing large, depressed ventral muscle field, GSC 97202, JBW loc. 57; x6.

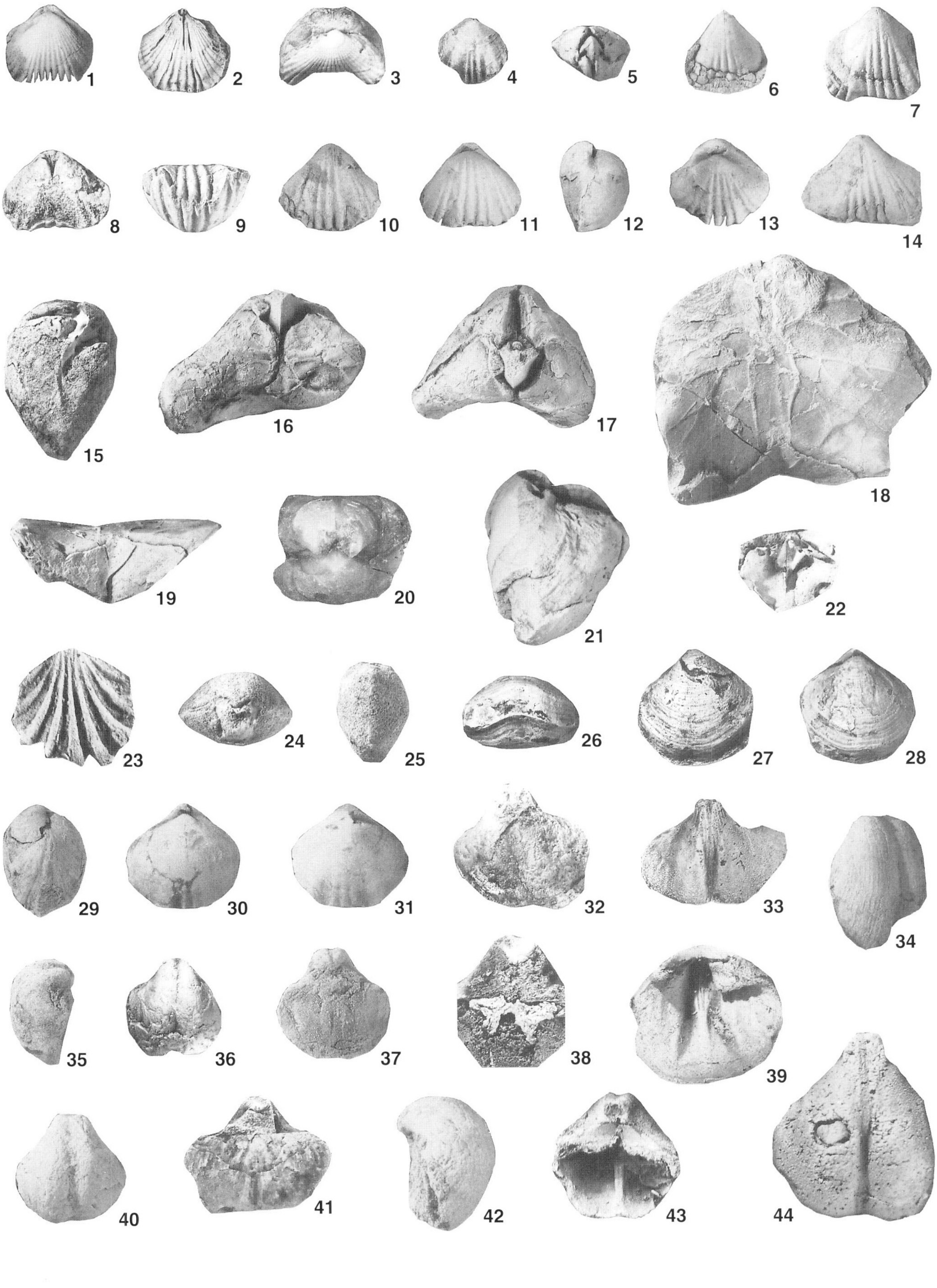
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PLATE 22

Figures 1–20. *Tumarinia yukonica* n. sp.

1, 4, 7, 8. Dorsal-posterior, dorsal, anterior, and ventral views, conjoined shell, GSC 97207, GSC loc. 53714.

2, 3, 6. Dorsal, ventral, and oblique anterior views, conjoined shell, GSC 97208, GSC loc. 53714.

5. Latex cast, dorsal external mould, GSC 97210, JBW loc. 113.

9–11. Ventral, dorsal, and posterior views, conjoined shell, holotype, GSC 97206, GSC loc. 53714.

12. Immature dorsal valve, GSC 97209, GSC loc. 53713.

13. Posterior view, latex cast, ventral internal mould (see fig. 18), GSC 97212, JBW loc. 113.

14. Latex cast, dorsal interior, GSC 97214, JBW loc. 88.

15. Ventral valve, GSC 97212, JBW loc. 113.

16. Dorsal view, conjoined shell, GSC 97213, GSC loc. 53714.

17, 18, 20. Posterior view, latex cast, and anterior view, ventral internal mould, GSC 97212, JBW loc. 113 (see fig. 15).

19. Latex cast, dorsal external mould, showing micro-ornament, GSC 97210 (also see fig. 5); x8.5.

Figures 21–25. *Yukonella plana* n. gen. et sp.

21. Latex cast, dorsal external mould, GSC 97222, GSC loc. 53774.

22. Latex cast, dorsal internal mould, GSC 97220, GSC loc. 53774.

23, 25. Latex cast, ventral external mould and the same specimen enlarged to show micro-ornament, GSC 97216, GSC loc. 53774; fig. 25 x9.

24. Latex cast, ventral internal mould, GSC 97215, GSC loc. 53774.

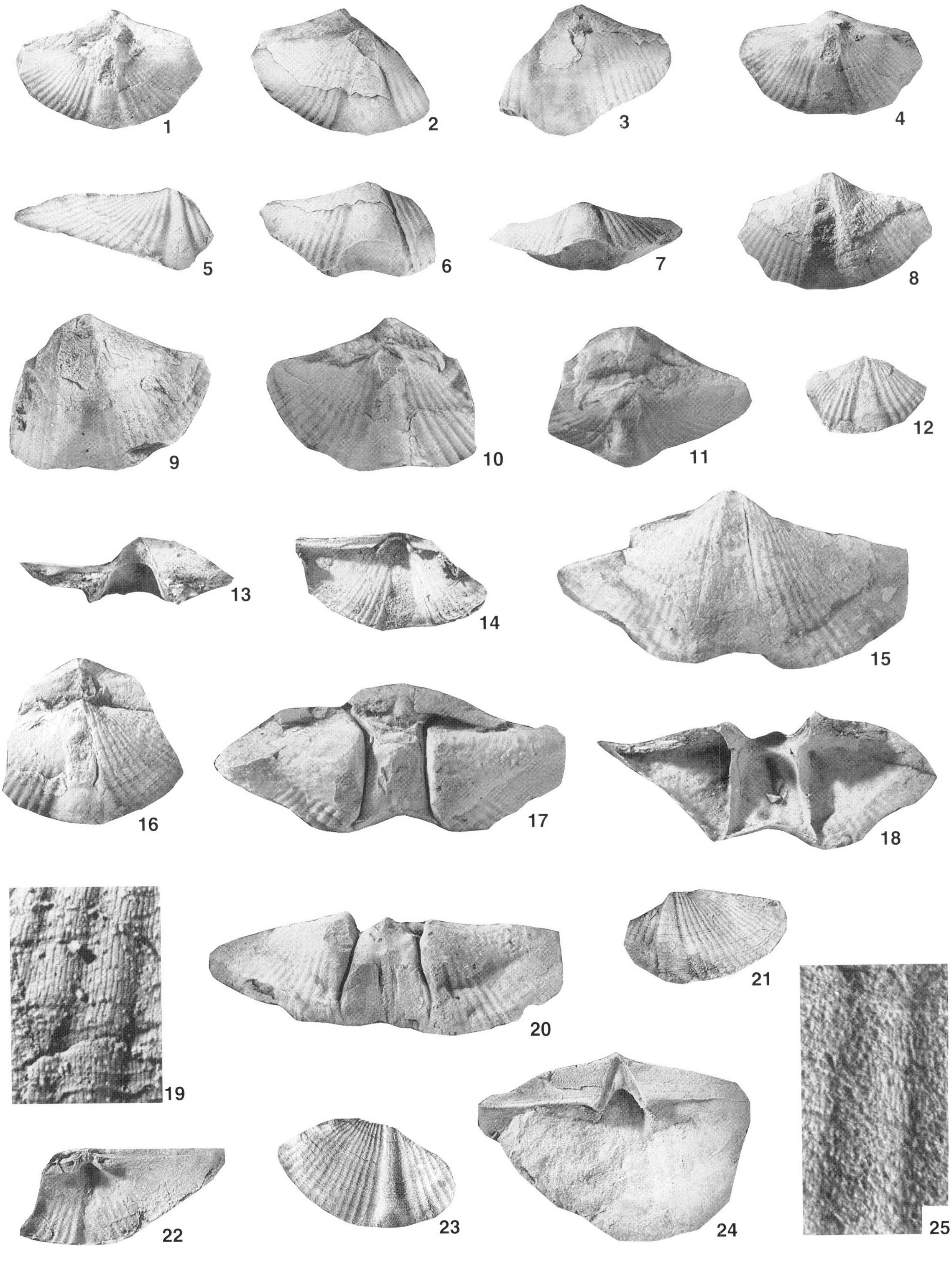
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PLATE 23

Figures 1–7. *Yukonella plana* n. gen. et sp.

1. Dorsal view, ventral valve, showing delthyrial plate, GSC 97219, GSC loc. 53774.
2. Ventral valve, holotype, GSC 97217, GSC loc. 53774.
3. Ventral internal mould, GSC 97218, GSC loc. 53774.
4. Latex cast, ventral internal mould, GSC 97227, GSC loc. 53774.
5. Ventral (incomplete) and dorsal valves, GSC 97223, GSC loc. 53774.
6. Latex cast, ventral internal mould, GSC 97221, GSC loc. 53774.
7. Dorsal valve, GSC 97224, GSC loc. 53774.

Figures 8, 9, 11–16. *Yukonospirifer yukonensis* n. gen. et sp.

8, 9, 11–13. Lateral, anterior, ventral, dorsal, and posterior views, conjoined shell, holotype, GSC 97225, GSC loc. 53713.

14. Latex cast, ventral external mould, GSC 97226, JBW loc. 113 (see figs. 15, 16).

15, 16. Ventral and posterior views, ventral valve, GSC 97226, JBW loc. 113.

Figure 10. Brachythridid or syringothyridid gen. et sp. indet.

Dorsal internal mould, GSC 97614, JBW 113.

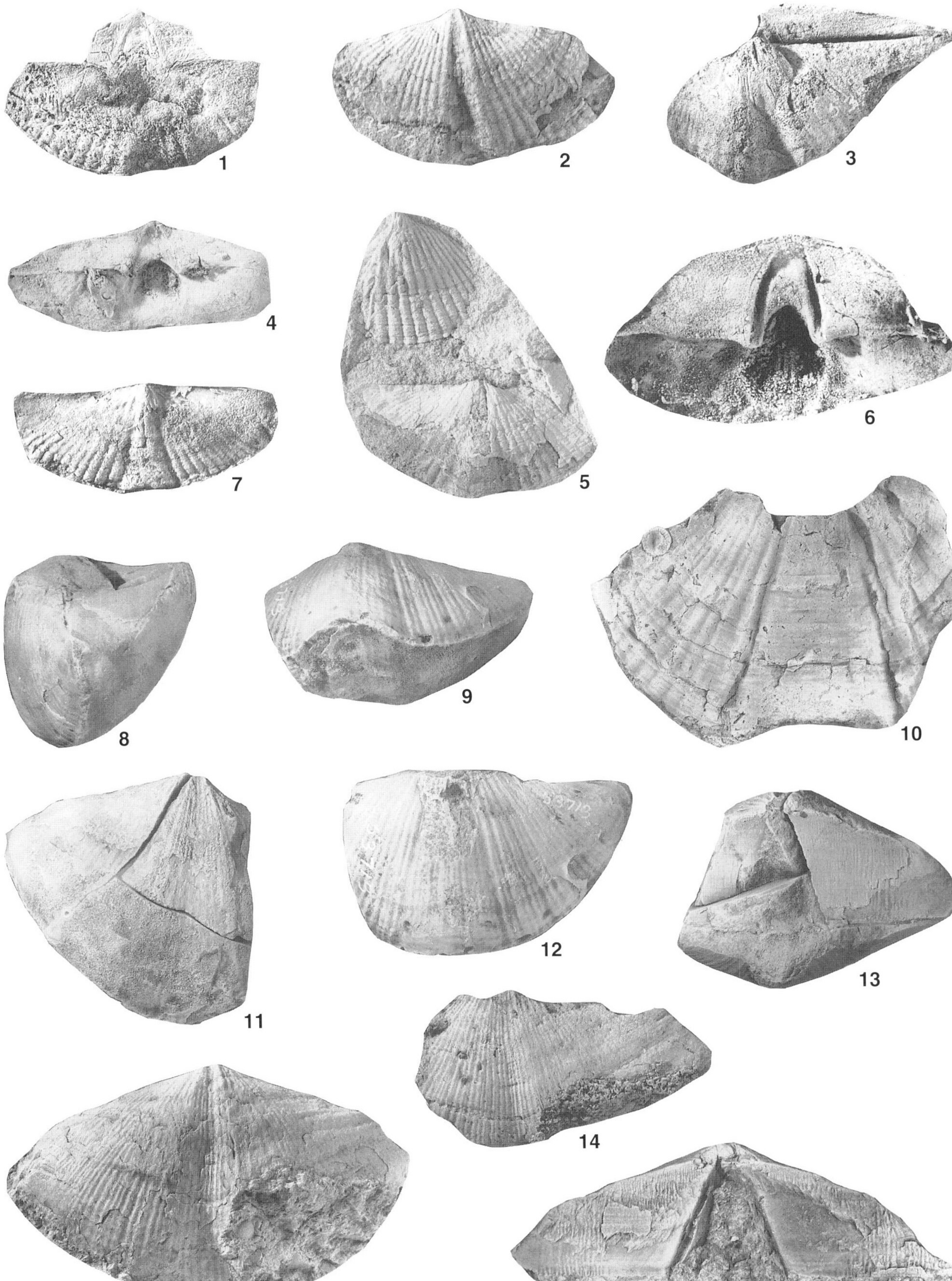
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PLATE 24

Figures 1–20. *Spiriferella pseudodraschei* Einor

1. Latex cast, ventral external mould, GSC 97233, JBW loc. 88.
2. Posterior view, ventral valve, GSC 97660, JBW loc. 88.

3, 4. Posterior and lateral views, ventral valve, GSC 97239, JBW loc. 54.

5. Latex cast, dorsal external mould, GSC 97231, JBW loc. 88.
6. Latex cast, ventral internal mould, GSC 97230, JBW loc. 89.
7. Latex cast, dorsal internal mould, GSC 97229, JBW loc. 110.
8. Latex cast, dorsal external mould, GSC 97232, JBW loc. 109.
9. Posterior view, conjoined shell, GSC 97238, JBW loc. 88.
10. Posterior view, ventral valve, GSC 96927, JBW loc. 88.
11. Dorsal valve, GSC 97234, JBW loc. 109.
12. Dorsal view, conjoined internal mould, GSC 97235, JBW loc. 110.
13. Ventral valve, GSC 97236, JBW loc. 109.
14. Ventral internal mould, GSC 97237, JBW loc. 88; x2.
15. Latex cast, dorsal external moud, showing median groove on dorsal fold, GSC 97549, JBW loc. 24; x2.
16. Latex cast, ventral external mould, GSC 97552, JBW loc. 89; x2.
17. Latex cast, ventral internal mould, GSC 97551, JBW loc. 24.
18. Latex cast, ventral internal mould, GSC 97550, JBW loc. 88; x2.
19. Ventral valve, GSC 97661, JBW loc. 88.
20. Dorsal valve, GSC 97237, JBW loc. 88; x2.

Figures 21–32. *Spiriferella saranae* (Verneuil)

21. Latex cast, ventral internal mould, GSC 97561, JBW loc. 113; x2.

22, 23. Lateral and ventral views, ventral valve, GSC 97553, JBW loc. 558.

24, 30. Posterior and internal views, ventral valve, GSC 97560, JBW loc. 113; fig. 30 x2.

25, 28, 29. Posterior, ventral, and lateral views, ventral valve, GSC 97555, JBW loc. 558.

26, 32. Latex cast, ventral valve and enlargement showing micro-ornament, GSC 97559, JBW loc. 558; fig. 32 x3.

27. Posterior view, ventral valve, GSC 97557, JBW loc. 558.

31. Dorsal view, conjoined shell, GSC97558, JBW loc. 558.

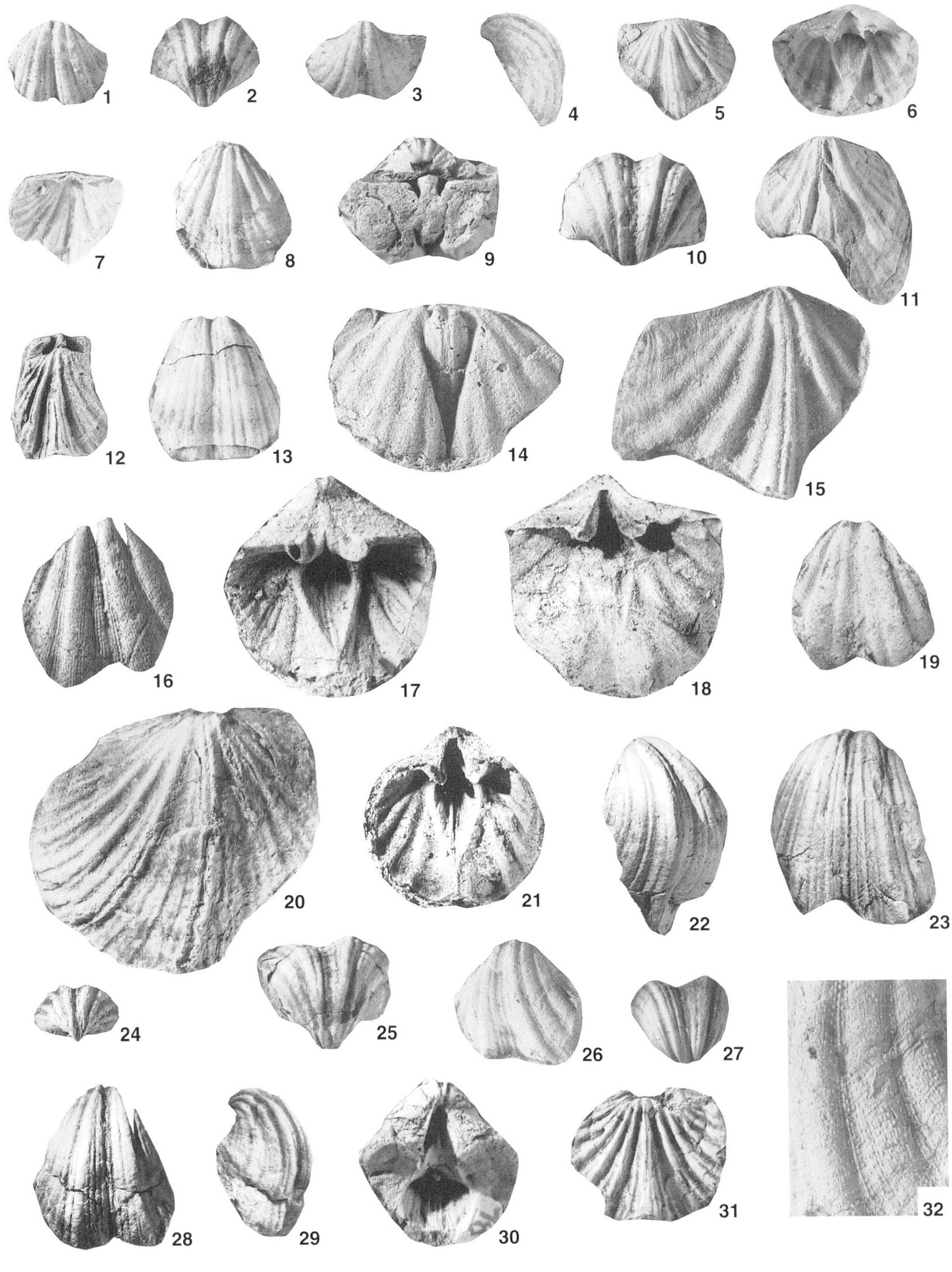
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PLATE 25

Figures 1–5. *Siriferella saranae* (Verneuil)

1. Latex cast, dorsal internal mould, GSC 97565, JBW loc. 113.

2, 4. Ventral and posterior views, ventral internal mould, GSC 97556, JBW loc. 558; fig. 4 x2.

3. Ventral view, conjoined internal mould, GSC 97558, JBW loc. 558.

5. Latex cast, ventral internal mould, GSC 97562, JBW loc. 113; x2.

Figures 6–10. *Spiriferella* sp.

6. Ventral valve, GSC 97564, JBW loc. 57; x2.

7–10. Ventral, dorsal, posterior, and lateral views, ventral valve, GSC 97563, JBW loc. 57.

Figures 11–15. *Alispiriferella ordinaria* (Einor)

Anterior, lateral, posterior, ventral, and dorsal views, conjoined shell, GSC 97566, GSC loc. 53714.

Figures 16–28. *Timaniella convexa* n. sp.

16. Latex cast, ventral internal mould, GSC 97570, JBW loc. 526.

17. Ventral valve, GSC 97575, JBW loc. 526.

18, 21. Ventral and posterior views, ventral valve, holotype, GSC 97568, JBW loc. 526.

19. Latex cast, ventral external mould, GSC 97573, JBW loc. 526.

20. Latex cast, ventral internal mould, GSC 97572, JBW loc. 526; x2 (see also fig. 26).

22. Latex cast, ventral valve, GSC 97567, JBW loc. 526; x2 (see also fig. 26).

23. Latex cast, ventral external mould, GSC 97655, JBW loc. 526; x2 (see also fig. 27).

24. Latex cast, dorsal internal mould, GSC 97574, JBW loc. 526.

25. Latex cast, ventral internal mould, GSC 97571, JBW loc. 526.

26. Latex cast, ventral valves, GSC 97567 (upper right) and GSC 97572 (lower left), JBW loc. 526 (see also figs. 20, 22).

27. Latex cast, ventral external mould (left, GSC 97655, see fig. 23) and dorsal internal mould (right), GSC 97569, JBW loc. 526.

28. Latex cast, dorsal external mould, GSC 97576, JBW loc. 526; x2.

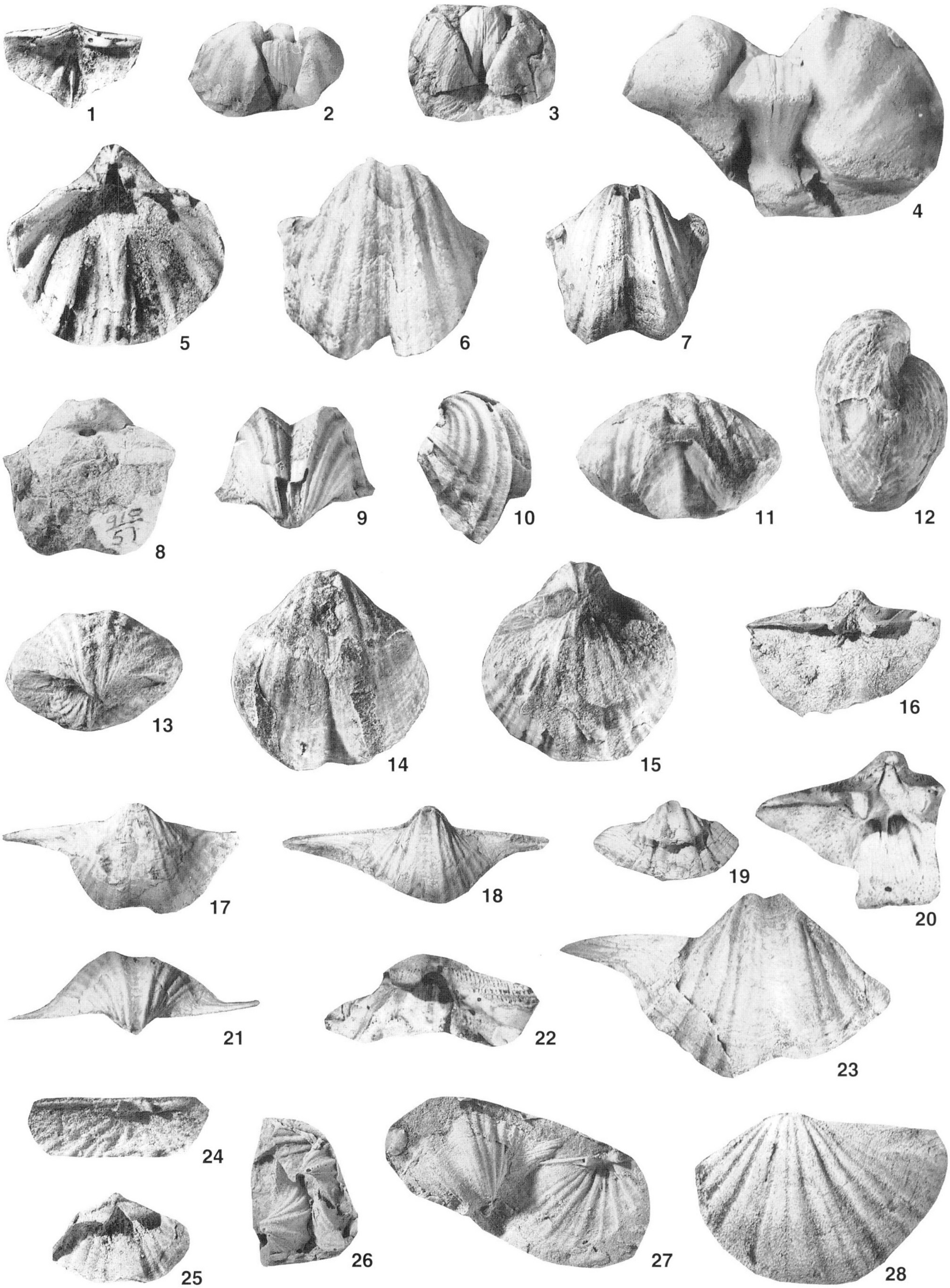
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PLATE 26

Figures 1, 2. Spiriferacea gen. et sp. indet.

Lateral and ventral views, ventral valve, GSC 97577, GSC loc. 53954.

Figures 3–9. *Neospirifer* sp.

3, 8. Posterior and ventral views, ventral valve, GSC 97582, JBW loc. 113.

4. Latex cast, ventral external mould, GSC 97581, JBW loc. 113.

5. Dorsal valve, GSC 97578, JBW loc. 109.

6, 7. Posterior and ventral views, conjoined shell, GSC 97580, JBW loc. 54; x2.

9. Fragment of ventral internal mould, GSC 97579, JBW loc. 109.

Figures 10, 11. *Lepidospirifer*? sp.

10. Latex cast, dorsal external mould, GSC 97584, JBW loc. 24; x2.

11. Latex cast, dorsal external mould, GSC 97583, JBW loc. 24; x2.

Figures 12–14. *Purdonella nikitini* (Chernyshev)

12. Ventral view, ventral fragment, GSC 97586, GSC loc. 53705.

13, 14. Posterior and ventral views, conjoined shell, GSC 97585, GSC loc. 53720.

Figures 15–20. *Larispirifer ettrainensis* n. sp.

15, 16. Dorsal and ventral views, crushed conjoined shell, GSC 97601, GSC loc. 53954.

17, 18. Posterior views, ventral valve, holotype, GSC 97596, GSC loc. 53712.

19. Ventral valve, GSC 97600, JBW loc. 11.

20. Lateral view, ventral valve, GSC 97597, JBW loc. 113.

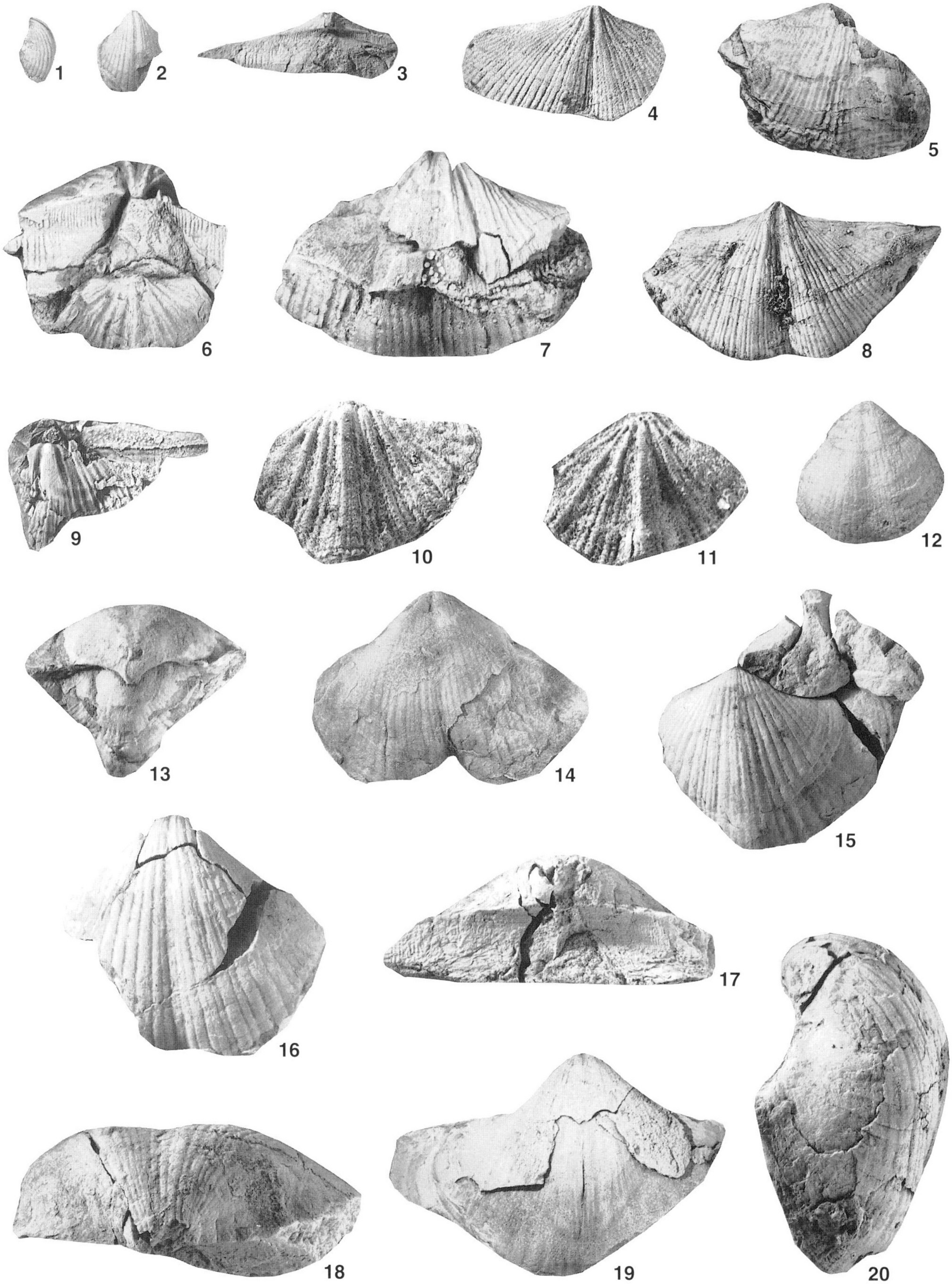
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PLATE 27

Figures 1–7. *Larispirifer ettrainensis* n. sp.

1. Ventral valve, GSC 97597, JBW loc. 113.
2. Ventral valve, GSC 97602, GSC loc. 57053.
3. Ventral internal mould with apical part of a ventral valve, showing subparallel and fused adminicula, GSC 97595, JBW loc. 88.

4, 6. Ventral interior and internal moulds, GSC 97599, JBW loc. 57.

5. Ventral valve, holotype, GSC 97596, GSC loc. 53712 (see Pl. 26, figs. 17, 18).

7. Dorsal view, conjoined shell, GSC 97598, GSC loc. 57266.

Figures 8–12. *Domokhotia junglensis* n. sp.

8. Latex cast, ventral internal mould, showing thin adminicula, GSC 97588, JBW loc. 109; x2 (see also Pl. 28, fig. 4).
9. Dorsal internal mould, GSC 97591, JBW loc. 88.
10. Crushed dorsal internal mould, GSC 97590, JBW loc. 11.

11, 12. Ventral and dorsal views, conjoined shell, holotype, GSC 97589, JBW loc. 109.

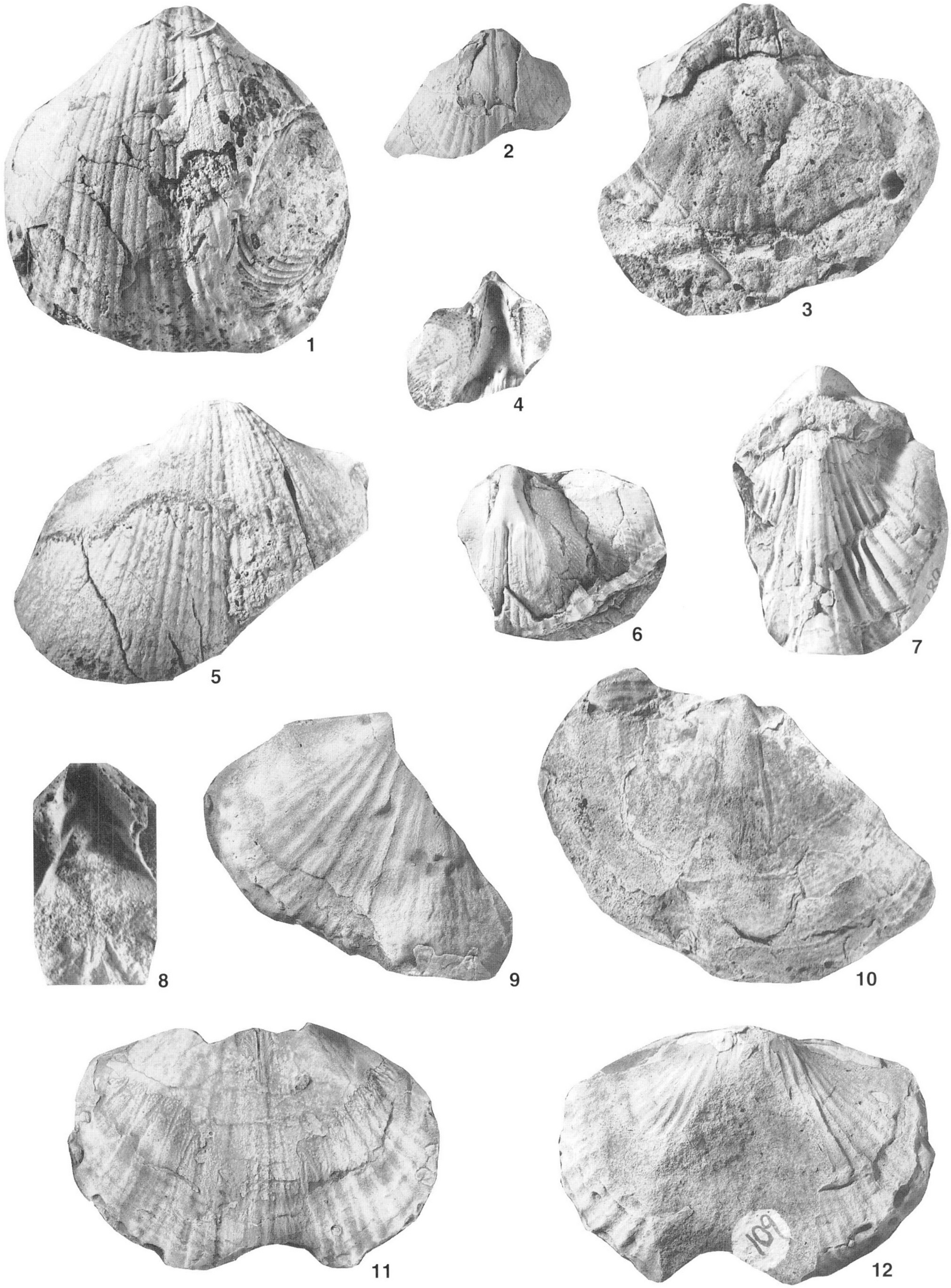
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PLATE 28

Figures 1–5. *Domokhotia junglensis* n. sp.

1. Latex cast, ventral external mould, GSC 97593, JBW loc. 88.

2, 3. Latex cast and dorsal external mould, GSC 97594, JBW loc. 109.

4. Latex cast, ventral internal mould, GSC 97588, JBW loc. 109.

5. Latex cast, ventral external mould, GSC 97592, JBW loc. 88.

Figures 6–8. *Tomiopsis ovulum* Waterhouse

6. Ventral external mould with fragmentary shell attached, GSC 97604, GSC loc. 53818.

7, 8. Ventral and posterior views, conjoined shell, GSC 97603, GSC loc. 53703.

Figures 9–12. *Spirelytha* sp.

9–11. Latex cast, posterior and ventral views, conjoined internal mould (figs. 9, 10 taken after the specimen was dissolved), GSC 97612, JBW loc. 505.

12. Ventral view, conjoined internal mould, GSC 97613, JBW loc. 545.

Figures 13–21. *Spirelytha fredericksi* Archbold and Thomas

13. Ventral internal mould, GSC 97610, JBW loc. 89.

14. Dorsal view, conjoined shell, GSC 97609, GSC loc. 53720.

15, 16. Ventral and dorsal views, conjoined internal mould, GSC 97605, JBW loc. 558.

17. Latex cast, ventral external mould of GSC 97605 (see figs. 15, 16), GSC 97605a, JBW loc. 558.

18. Fragment of a ventral internal mould, GSC 97611, JBW 24.

19, 21. Ventral external mould and enlargement showing biramous spines, GSC 97607, JBW loc. 24; fig. 21 x6.

20. Crushed dorsal valve, GSC 97608, JBW loc. 24.

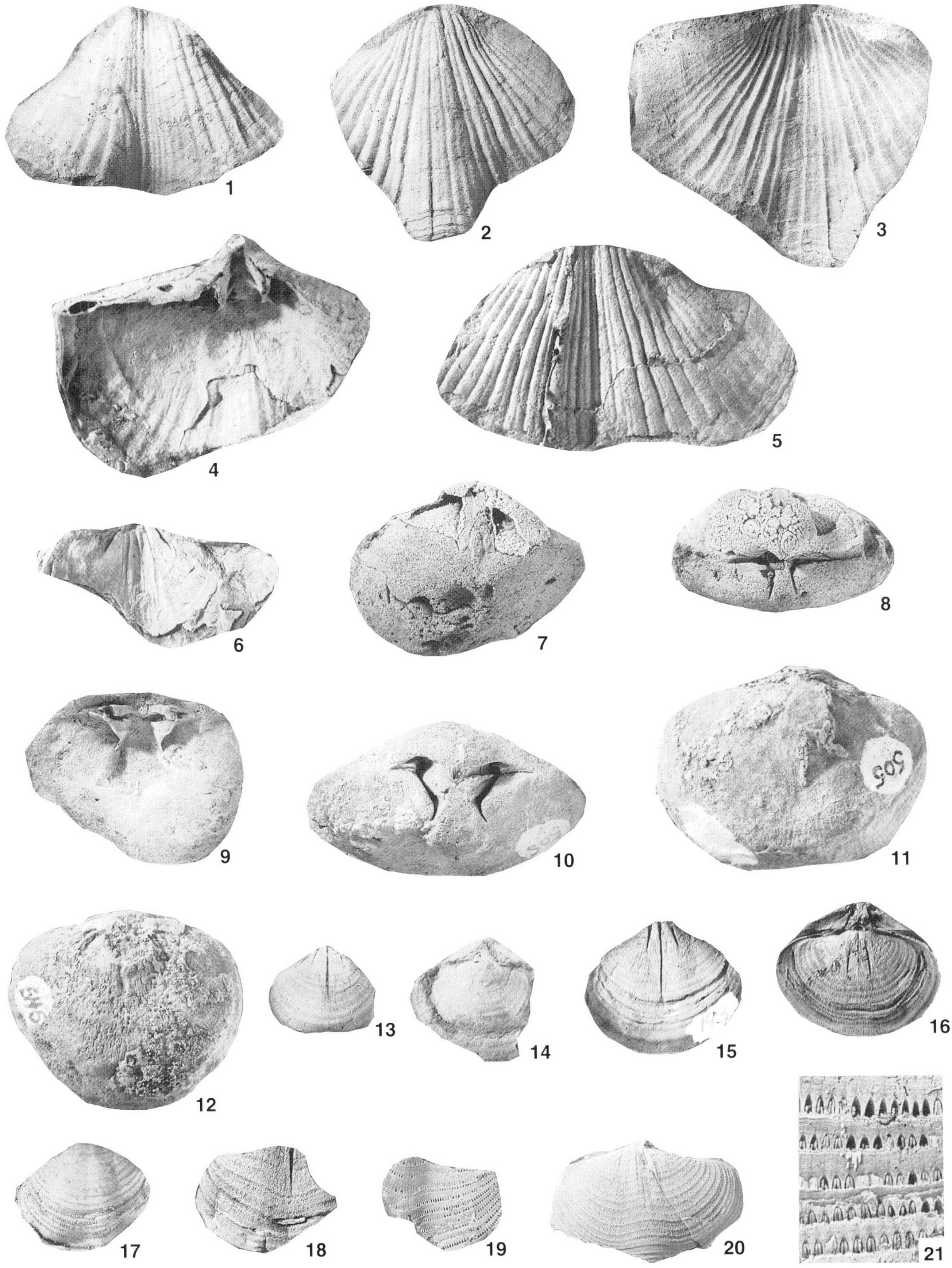
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PLATE 29

Figures 1–4. *Brachythyris* sp.

1–3. Lateral, posterior, and ventral views, ventral valve, GSC 97616, JBW loc. 113.

4. Ventral valve, GSC 97615, GSC loc. 57052.

Figures 5–19. *Tiramnia canadica* n. sp.

5. Ventral internal mould, holotype, GSC 97619, JBW loc. 109.

6. Ventral internal mould, GSC 97625, JBW 113.

7. Ventral internal mould, GSC 97626, JBW 113.

8. Latex cast, ventral internal mould, GSC 97627, GSC loc. 53947.

9. Ventral internal mould, GSC 97620, JBW loc. 113.

10. Ventral internal mould, GSC 97624, GSC loc. 57266.

11. Ventral valve, GSC 97623, JBW loc. 113.

12, 13. Anterior and ventral views, ventral internal mould, GSC 97617, JBW loc. 24.

14, 15. Ventral and lateral views, ventral internal mould, showing ventral muscle field and pallial markings, GSC 97628, GSC loc. 53947.

16. Ventral valve, GSC 97622, GSC loc. 53947.

17. Ventral valve, GSC 97621, GSC loc. 53947.

18, 19. Lateral and dorsal views, crushed shell, GSC 97618, GSC loc. 53947.

Figures 20–23. *Spiriferellina*? sp.

20. Latex cast, ventral external mould, GSC 97631, JBW loc. 89; x3.

21, 23. Latex cast, ventral external mould, GSC 97630, JBW loc. 559; x2, x4, respectively.

22. Latex cast, dorsal internal mould, GSC 97629, JBW loc. 559; x2.

Figures 24–30. *Dielasma rectimarginatum* Cooper

24. Ventral valve (right) and dorsal internal mould (left), GSC 97633, GSC loc. 53999.

25, 26, 30. Dorsal and ventral–posterior views, conjoined internal mould, GSC 97634, GSC loc. 53999; enlargement of ventral aspect, showing punctae; x6.

27. Ventral internal mould, GSC 97635, GSC loc. 53999.

28, 29. Posterior and dorsal views, dorsal internal mould, GSC 97632, GSC loc. 53999; x2.

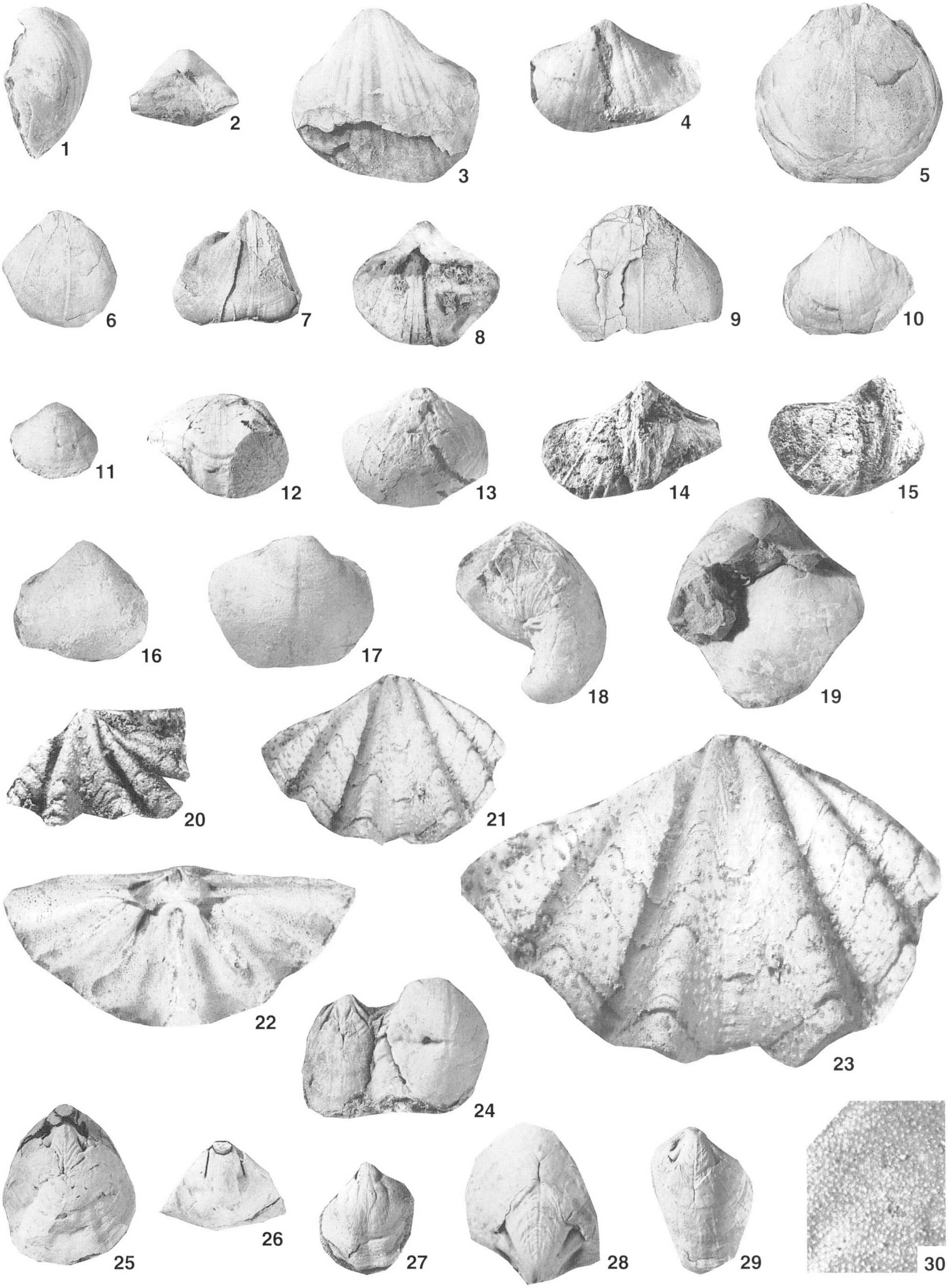
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PLATE 30

Figures 1–12. *Dielasma brevicostatum* Cooper

1, 2. Dorsal and ventral views, conjoined shell, GSC 97639, GSC loc. 53714.
3. Dorsal valve, GSC 97636, GSC loc. 53714.
4. Ventral valve, GSC 97641, GSC loc. 53704.
5, 6. Anterior and oblique anterior views, ventral valve, GSC 97638, GSC loc. 53714.
7–9. Lateral, ventral, and dorsal views, conjoined immature shell, GSC 97640, GSC loc. 57053; x2.
10–12. Ventral, lateral, and dorsal views, conjoined shell, GSC 97637, GSC loc. 53714.

Figure 13. *Deltopecten*? sp.

Internal mould, right valve, GSC 96843, JBW loc. 537.

Figures 14–16. *Acanthopecten licharewi* (Frederiks)

14. External mould of right valve (?), GSC 96846, GSC loc. 56923.
15. Latex cast, left valve internal mould, GSC 96844, JBW loc. 113.
16. Left valve, GSC 96845, JBW loc. 109.

Figures 17, 18. *Etheripecten* sp. A

External mould and latex cast, left valve, GSC 96842, JBW loc. 2.

Figures 19, 20. *Etheripecten* sp. B.

19. Latex cast, left valve internal mould, GSC 96841, GSC loc. 57053; x2.
20. Latex cast, left valve external mould, GSC 96840, JBW loc. 113.

Figures 21, 22. *Streblochondria* sp.

Left valve and external mould, GSC 96847, JBW loc. 24.

Figures 23–27. *Exochorhynchus similis* (Lyutkevich and Lobanova)

23, 27. Anterior and left views, conjoined shell, GSC 97649, JBW 109.
24. Left view, conjoined shell, GSC 97651, JBW loc. 109.
25. Anterior view, conjoined shell, GSC 97650, JBW loc. 580.
26. Left valve external mould showing micro-ornament, GSC 97643, JBW loc. 109, x6.

Figure 28. *Tabantalites bifurcatus* Ruzhencev

Internal mould, GSC 97642, GSC loc. 57053; x2.

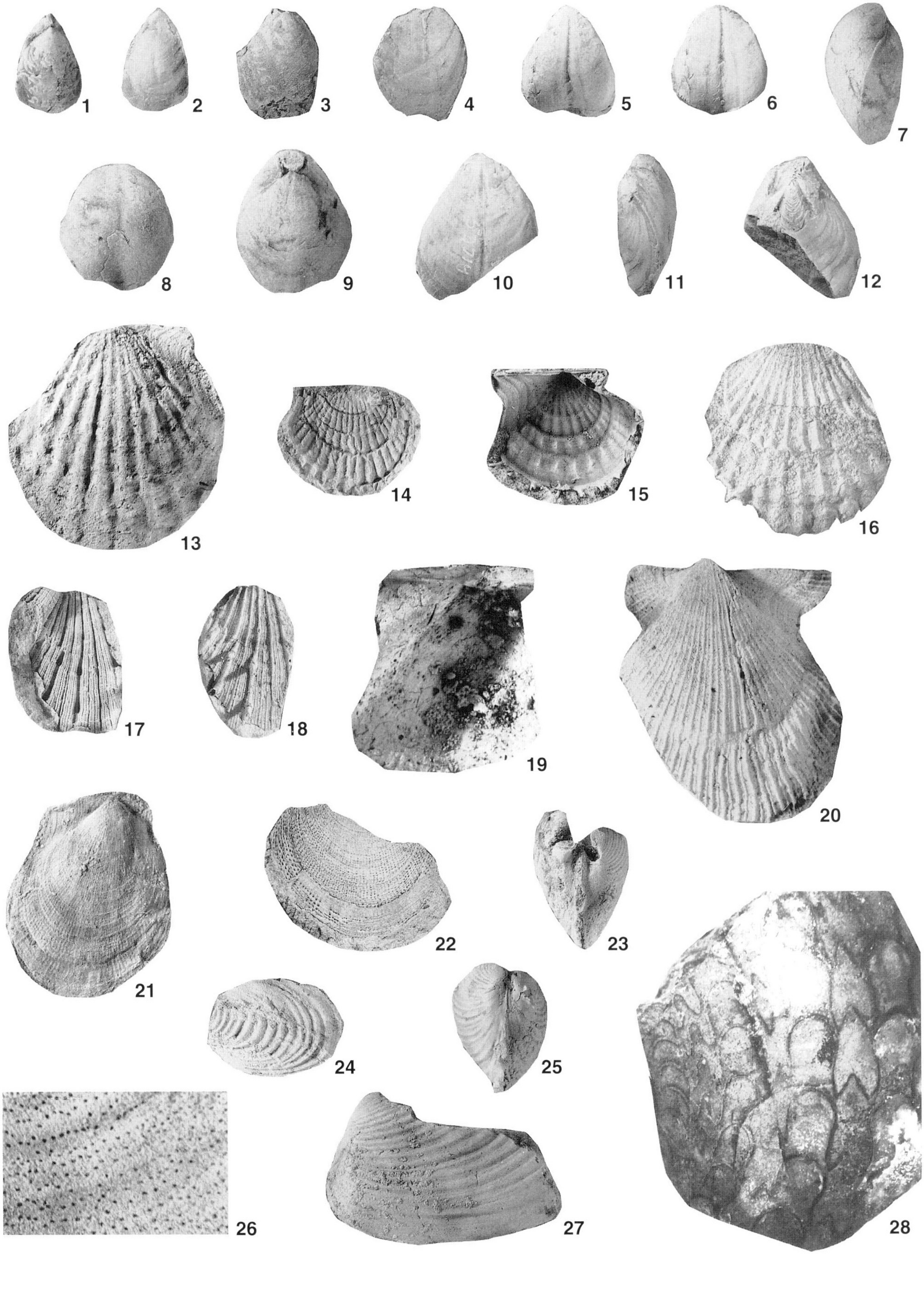
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PLATE 31

Figures 1–14. *Exochorhynchus similis* (Lyutkevich and Lobanova)

1, 2, 12. Left, right, and anterior views, conjoined shell, GSC 97644, JBW loc. 113.

3, 7, 9. Dorsal, left, and right views, conjoined internal mould, GSC 97646, JBW loc. 109.

4, 10. Right and left views, conjoined shell, GSC 7648, JBW loc. 109.

5, 6. Left and right views, conjoined shell, GSC 97645, JBW loc. 537.

8, 14. Ventral and dorsal views, conjoined internal mould, GSC 97647, JBW loc. 537.

11, 13. Left and dorsal views, conjoined internal mould, GSC 97650, JBW loc. 580.

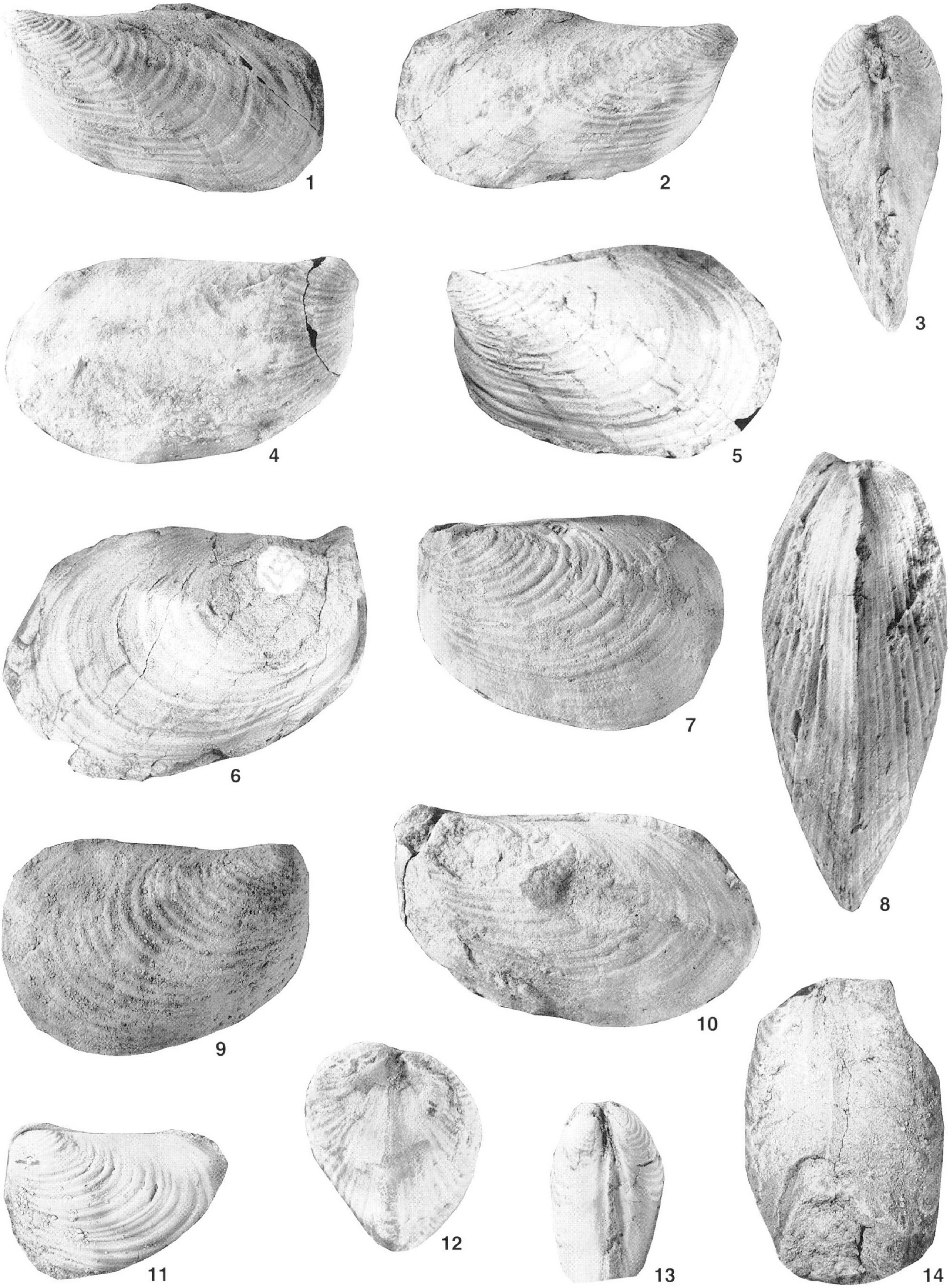
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PLATE 32

Figure 1. *Reticulatia uralica* (Chernyshev)

Longitudinal section, dorsal valve, showing cardinal process and median septum, GSC 97016, GSC loc. 53704; x6.

Figures 2–4. *Camerisma* (*Callaiapsida*) *pentameroides* (Chernyshev)

2. Transverse section, dorsal valve at about 6 mm from umbo, showing intercamarophorial plate and hinge plate, GSC 97666, JBW loc. 113; x7.
3. Transverse section, ventral valve of same specimen, showing spondylium, GSC 97666, JBW loc. 113; x7.
4. Transverse section, dorsal valve at about 4 mm from umbo, showing initial camarophorium surrounded by umbonal thickening, GSC 97667, JBW loc. 113; x6.5.

Figures 5, 6. *Tumarinia yukonica* n. sp.

Transverse serial sections, conjoined shell at 10 to 15 mm from ventral umbo, showing internal plates and spiralia, GSC 97668, GSC loc. 53714.

Figure 7. *Yukonospirifer yukonensis* n. gen. et sp.

Transverse section, ventral valve at about 14 mm from umbo, showing adminicula and delthyrial plate, GSC 97226, GSC loc. 113.

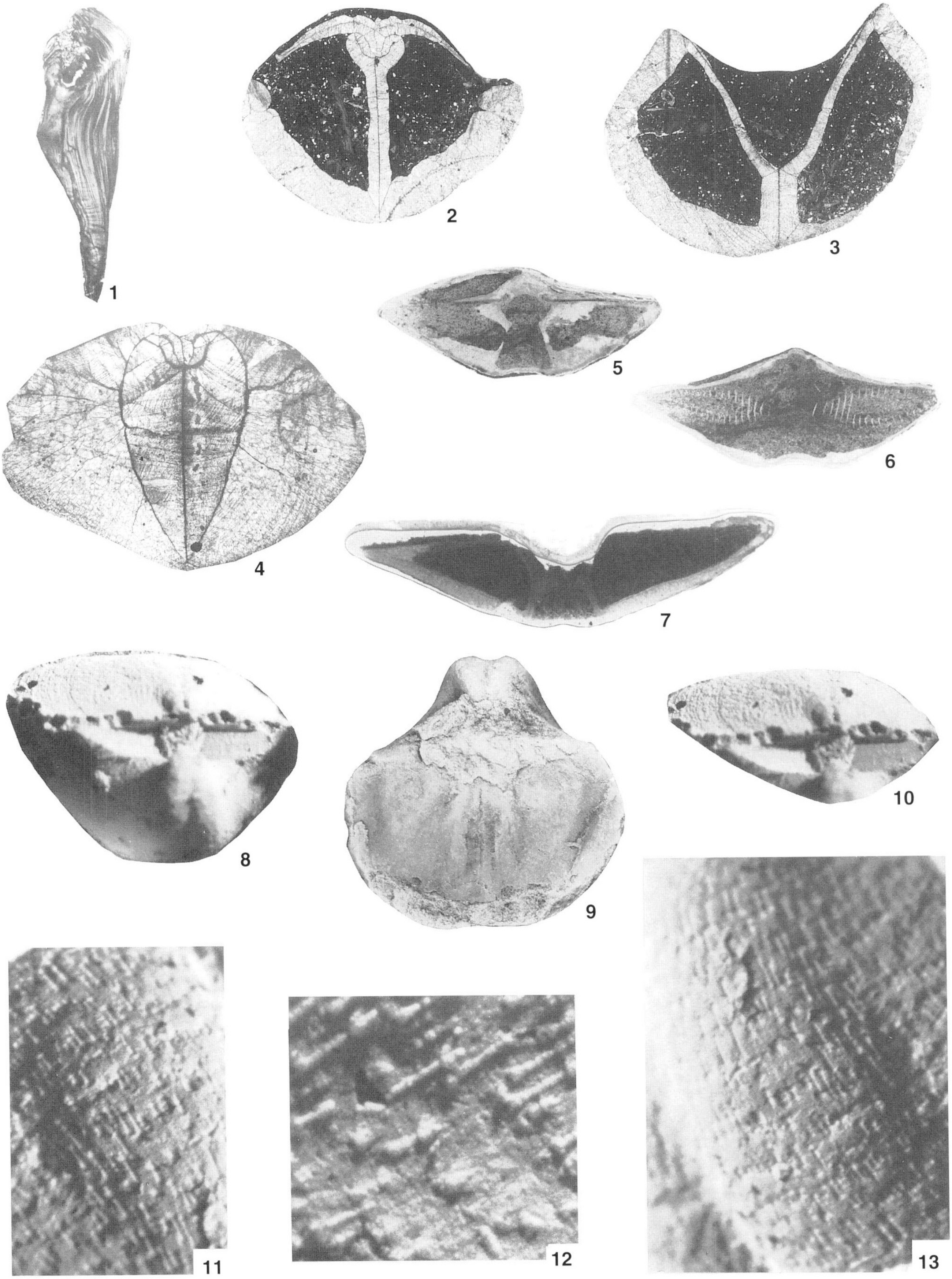
Figures 8–13. *Ogilviecoelia inflata* n. gen. et sp.

8, 10. Posterior views, latex cast, external mould, showing short umbonal slopes, GSC 97669, JBW loc. 57; x4.

9. Dorsal view, conjoined shell, showing dorsal muscle impressions and crural plates, holotype, GSC 97201 (also see Pl. 21, fig. 37), JBW loc. 53705; x5.

11, 12. Aspects of a ventral external mould, showing fine, short, and elongate ridges (see fig. 13 for grooves on original shell), GSC 97670, JBW loc. 57; x10, x15 respectively.

13. Latex cast, ventral external mould showing micro-ornament of fine elongate grooves, GSC 97670, JBW loc. 57; x10.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